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The effects of winter waterlogging on the growth, development and yield of UK varieties of winter wheat

Dickin, Edward

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THE EFFECTS OF WINTER WATERLOGGING ON THE GROWTH, DEVELOPMENT AND YIELD OF UK VARIETIES OF WINTER WHEAT

By Edward Dickin

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University of Wales, Bangor
School of Agricultural and Forest Sciences
Henfaes Research Centre
Abergwyngregyn
Llanfairfechan
Gwynedd
LL33 0LB

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ABSTRACT

Climate change models predict an increase in the amount and intensity of winter rainfall in the UK. A series of experiments using both container grown plants and field trials was undertaken, to investigate the effect of winter waterlogging on the growth, development and yield of current varieties of winter wheat. The interaction of waterlogging with other factors such as summer drought, seed rate, and sowing date was also investigated. In the field, waterlogging decreased plant population, and uptake of nitrogen over winter from 50 kg/ha to 25 kg/ha. Plants formed new porous nodal roots, which were able to penetrate below the water level. All the varieties tested had a good ability to recover from damage by waterlogging. Plant dry weights per area of waterlogged plots were 50% of controls at the end of treatment in March, 75% at anthesis and 85-90% at harvest. In all varieties except Xi-19, recovery was due to increased number of tillers per plant, a higher proportion of which survived to form an ear. Xi-19 increased the number of grains per ear and the weight of individual grains. Waterlogging early in the season (autumn and early winter) killed more plants, but allowed longer for surviving plants to recover and compensate. Spring waterlogging caused the greatest decrease in grain yield. Sowing in September allowed autumn and spring tillering, thus two chances for compensatory growth. November sown plants did not tiller until spring, and if waterlogging occurred at this time yields were especially poor. Waterlogging did not make crops more vulnerable to subsequent drought or lodging, but the incidence of take-all and stem-base disease did appear to increase. Despite the lack of disparity in tolerance, varieties did appear to have different responses to waterlogging. Varieties with a higher growth rate and demand on resources due to weaker winter dormancy (Xi-19) appeared to suffer more leaf chlorosis than those with a stronger dormancy (Claire). Deben had good ability to recover due to its high tillering rate in spring, and had the largest yield. Hereward showed the smallest decrease in yield, but had the lowest yield under control and waterlogged conditions. It was hoped that it would be possible to find a simple screening method to identify tolerant varieties at an early stage. Unfortunately plant appearance during waterlogging was not predictive of final yield. Research into stress tolerance has tended to concentrate on identifying 'stress genes' but in this case it appears that multi-gene traits are more important in determining crop yield.

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List of Abbreviations Used

ABA	abscisic acid
ACC	1- aminocyclopropane-carboxylic acid
ANP	anaerobic polypeptide – synthesised in response to waterlogging
BBSRC	Biotechnology and Biological Sciences Research Council
DW	Dry Weight
Eh	soil redox potential
GAI	Green Area Index
HGCA	Home Grown Cereals Authority
PGR	Plant Growth Regulator
NABIM	National Association of British and Irish Millers
NIAB	National Institute of Agricultural Botany
Rubisco	ribulose bisphosphate oxidase-carboxylase
TGW	Thousand Grain Weight

Chapter 1: INTRODUCTION and LITERATURE REVIEW

1.1. INTRODUCTION

Although all plants need water, excess moisture in the soil can be as much a limiting factor to crop growth as drought. For example, work in India by Chaudhary *et al.* (1975) found that whilst a higher soil water table increased maize yields in dry years it could reduce yield in wet years. In the same way, increased rainfall usually had a positive effect on grain yields in the semi arid wheat belt of Australia, except in the south west of Western Australia, where rainfall after sowing could waterlog the vulnerable duplex soil in that region and reduce yield (Stephens and Lyons, 1998). As anecdotal evidence of the effect of waterlogging on UK crops, average winter wheat yields for harvest 2001 on my family's farm in Lincolnshire, following the wet autumn of and winter 2000-2001 were around 7.5 t/ha (3 t/acre), in contrast to an average of nearly 10 t/ha (4 t/acre) for harvest 2002. This was growing the same varieties with a similar crop management regime, in terms of rotation, agrochemical inputs and fertilizers. In this case the physiological effects of waterlogging had interacted with other factors related to the wet autumn, including poor seedbed conditions and delayed sowing. Therefore waterlogging may be considered as a form of plant stress, with a deleterious effect on crop yields.

The cause of the limitation to plant growth is the replacement of the soil atmosphere with water as the soil pores are saturated. Plant root systems produce the energy needed for growth and active uptake of nutrients by aerobic respiration of photosynthates, transported from the shoot via the phloem. In fact up to half of all carbon captured during vegetative growth is partitioned to the root system (Gregory, 1994). Oxygen for this process is taken up from the soil atmosphere, which is of the same composition, under normal circumstances as the free atmosphere. Movement of gas into and out of the soil achieves equilibrium between the soil atmosphere and the atmosphere above ground, and is achieved either by diffusion, mass flow (bulk movement of gas, caused by expansion or contraction of the soil), or movement of water carrying dissolved gasses. By these processes, CO_2 produced by the respiration of plant roots and soil organisms moves out and O_2 moves into the soil (Rowell, 1994). Diffusion is the most important of these mechanisms and occurs through gas filled pores in the soil. Saturation of the soil pores interrupts this process, as the diffusion of oxygen through water is ten thousand times slower than in air (Grable, 1966). Oxygen is used up by the respiration of the soil fauna and flora more rapidly than it can be replaced, leading to hypoxia and eventually anoxia, sometimes within hours. In addition levels of CO_2 and ethylene produced by roots and soil fauna increase, due to the slower rates of gas diffusion out of the soil. During the first few days of waterlogging the soil pH decreases, due to increased CO_2, but then increases and stabilises as a result of reduction processes, especially that of iron (Ponnamperuma, 1972). Marsh soils with high organic matter content have a lower pH limit, possibly due to humic acids (Ruttner, 1963). Such humic acids are intermediates in the eventual formation of methane from anaerobic digestion of organic matter, and whilst they are phyto-toxic, are transitory and only become a serious problem in soils with very high organic matter content (Ponnamperuma, 1972). For comprehensive reviews of soil chemistry during waterlogging, see those by Ponnamperuma (1972 and 1984).

1.2. DEFINITION OF WATERLOGGING

In this study waterlogging will be defined as having occurred when the soil's pore spaces are filled with water so that oxygen becomes limiting to root growth. Grable (1966) states that this state is reached when air filled porosity of the soil falls below 10%. When the soil is waterlogged or hypoxic the shoot is still in an aerobic environment and able to supply the roots with some oxygen, flooding suggests that some, or all, of the shoot is submerged. Species tolerant to waterlogging, such as rice (*Oryza sativa*), may be killed by inundation, so flooding will not be considered in this study. The type of waterlogging differs with soil type. Heavy clay and sodic soils waterlog because of their impermeability and so the surface layers become saturated and water may be seen ponded on the surface. Duplex soils (discussed below) and those where a pan has formed waterlog upwards from the subsoil.

1.3. MEASURING AND QUANTIFYING WATERLOGGING

The differences between soils and the type of waterlogging that they are likely to experience means that waterlogging is difficult to measure and quantify in the field.

On clays, and other soils where waterlogging occurs from the top downwards due to poor infiltration of water, the percentage of surface area covered by ponding and the duration can sometimes be related to yield losses (Melhuish *et al.*, 1991). When waterlogging occurs from the bottom upward it can be measured using small plastic dip wells known as piezometer tubes (Setter and Waters, 2003). However this method is unreliable in the case of heavy clays where the tubes fill from the saturated surface soil layer. The depth of the water table and the duration of the waterlogging period may be combined using the sum of excess water for the top 30cm of soil (SEW_{30}) (Setter and Waters, 2003). For example 10 days waterlogging to the soil surface is equal to 30 days waterlogging to 20cm below the surface (a layer of 10cm depth from 30cm to 20cm below the soil) for 30 days as both treatments have a SEW_{30} of 300. The criticism of this method is that the depth of the water table determines the depth of root penetration possible. A pot experiment found that adventitious roots of wheat were restricted to a maximum of 85-116mm below the level of the water table (Malik *et al.*, 2001). Growth of plants waterlogged with the water table 200mm below the soil surface recovered to the same level as continuously drained controls within 14 days after draining, but those plants waterlogged to the soil surface or 100mm below only partially recovered. Soil air filled porosity can be measured by calculating the difference between the soil bulk density and the soil particle density, which is the total porosity. Then the volume occupied by water is subtracted from the total pore volume, the difference being the air filled porosity (Rowell, 1994). McDonald and Gardner (1987) found a 0.29 t ha^{-1} decrease in wheat yield for every 1% decrease in soil air filled porosity during the thirty days before anthesis. The soil redox potential (Eh) may be used as a measurement of the available oxygen in the soil, as molecular oxygen is considered absent at Eh values of 350 mV or less (Setter and Waters, 2003). Drained soils typically have a value of around 600 mV. Thompson *et al.* (1992) found that 21 days of waterlogging reduced soil redox potential from + 600mV to -100 mV in an experiment, using sandy duplex soil filled pots. Seven days of subsequent drainage allowed the Eh to increase to +400 mV. Quantification of aeration in waterlogged soils by measurement of redox potential and oxygen flux using a platinum electrode or sampling for dissolved and gaseous oxygen is not simple, especially if comparisons are attempted between methods (Blackwell, 1983). These methods only sample from a small volume, for example the soil immediately around an electrode, and as most field soils have a heterogeneous structure obtaining representative results is difficult. The problem is exacerbated in blocky clay soils, where sampling within or between blocks may give different results.

As waterlogging may also be defined as soil hypoxia, its effects on plants can be studied using methods to replicate hypoxic growing conditions in the rooting medium without applying water to excess. Many studies into waterlogging using hydroponics systems use flushing with N_2 gas to remove O_2 and simulate hypoxia. However this also flushes out CO_2 and ethylene, which accumulate in waterlogged soil and affect plant growth. A better simulation of waterlogged soil conditions can be achieved by adding 1% agar to the growth media to slow convection and replicate the slow movement of gasses in waterlogged soil (Wiengweera *et al.,* 1997).

1.4. THE EXTENT OF THE PROBLEM

1.4.1. Globally

Approximately 70 million hectares of wheat are sown in the world, and of this area, an estimated 15-20% is affected by waterlogging each year (Setter and Waters, 2003). Problems may be due to high total rainfall, distribution of rainfall, poor soil structures or a combination of these factors. Perversely, waterlogging is often a problem in arid areas. This occurs as a consequence of the use of irrigation in semi arid regions such as parts of northern India and Pakistan, and the Middle East (Setter and Waters, 2003). Flood irrigation can cause transient hypoxia and high levels of sodium carbonate and bicarbonate in irrigation water leads to soil sodicity (Sharma and Swarup, 1988). Surface water has difficulty in infiltrating sodic soils, causing waterlogging at the soil surface. Salinity is also often a problem on irrigated land and interacts with waterlogging, with a severe effect on plant growth. Unfortunately these problems with irrigated land are likely to worsen in the future, as an increase in global food production of 3% per annum is required over the next 20 years, and one third of the World's land surface is arid or semi arid (Flowers and Yeo, 1995). The interaction between waterlogging and salinity is very important globally and especially in the developing world, but not applicable to UK cereal growing, as irrigation is not normally used on cereal crops. For an in depth review of this subject see that by Barrett-Lennard (2003). In Western Australia, duplex soils suffer from waterlogging problems, especially when heavy rain occurs during crop establishment (Stephens and Lyons, 1998). Duplex soils consist of a sandy topsoil, which is rapidly penetrated by rain water, overlaying an impermeable clay subsoil (Tennant *et al.*, 1992). Heavy rainfall can create a perched water table, and hypoxic topsoil conditions, several metres above the true water table. Wheat suffers yield loss when grown in the rice –wheat systems in Asia, where soil structure is deliberately damaged to aid flooding in the paddy fields. The water used to irrigate the rice paddies may also cause sodicity and this combines with the problems of compacted subsoils to cause waterlogging of wheat crops following rice (Setter and Waters, 2003). In USA it is estimated that only 12.1% of soils are free of some kind of physiochemical problem; 44.9% being too dry, 16.5% too wet and 15.7% too cold (Boyer, 1982). These figures show that waterlogging is an important type of plant stress and these stresses explain the disparity between record and average crop yields. For example, average maize yields in USA were 4.6 tha^{-1} compared with the record yield of 19.3 tha^{-1} (Boyer, 1982). The lower Mississippi Valley of Louisiana suffers from waterlogging problems due to the silt-clay soils and level topography, causing wheat yields in the area to be much lower than the average for the rest of the USA (Musgrave, 1998). This waterlogging vulnerable soil, with low porosity and poor drainage, interacts with high rainfall during establishment and tillering. In the north east of North America a combination of low temperatures and flooding caused by snow melt can lead to plants and soils being encased in ice, inhibiting the movement of oxygen (McKersie and Hunt, 1987). Here hypoxia interacts with freezing and desiccation by cold dry winds to present serious challenges to the survival of winter cereals.

1.4.2. In the UK

As illustrated by the examples in the previous section, waterlogging is a problem for cereal growers in temperate and tropical climates and on a range of soil types throughout the world, and the UK is no exception. In the UK 40% of land in cereal production is heavy clay, likely to experience waterlogging problems (Cannell *et al.*, 1980). In fact clay soils are traditionally referred to as 'heavy', because their high water holding capacity means they are hard work to turn over, when cultivating. This explains why such soils, despite their fertility, were virtually ignored until the late seventh century, when Saxon settlers began using the heavy ox-ploughs needed to work them (Stenton, 1971). Throughout the Middle Ages, until the Enclosure Acts, which peaked in the late 18th century, peasants were allocated strips of the large commonly held fields each year, so there was no incentive to improve the land. Following Enclosure the new generation of 'improving farmers' set about draining their newly enclosed fields so that they could take advantage of the new advances in crops and machinery, and one of the leading engineers employed in this work was William Smith, surveyor and drainer, but more famous as the creator of the world's first geological map. Smith described a spring journey through the countryside of the Vale of Evesham, writing in his diary that '...the weather changed to wet and cold, ... and the barley and other corn on the stiff lands I had to survey turned to yellow in the furrows and in all moist places (Winchester, 2001). Undoubtedly he was describing leaf chlorosis caused by waterlogging, and incidentally, the Letcombe experiments used clay of the Evesham series, described as a typical soil with surface water problems, and barley, singled out by Smith, was found to more intolerant of waterlogging than wheat and oats (Cannell *et al.,* 1984; Cannell *et al.,* 1985). Although many agricultural soils prone to waterlogging have been drained over the centuries, which theoretically limits the water content to field capacity, future patterns of rainfall may well interact with clay soils to increase the problem of waterlogging. Climate change models predict, despite decreased summer rainfall, an increase in winter rainfall in the UK. Such models also predict an increase of between 5 and 20% in the intensity of heavy winter precipitation, which currently occur every two years on average (Hulme *et al.,* 2002). These winter storms may well be of sufficient intensity to overwhelm drainage systems and clay soils naturally have a slow rate of infiltration by water, surface accumulation therefore arising as a consequence. During the winter months transpiration rates of the crop are slow, due to low temperatures, sunlight intensity and short hours of daylight, so it is more likely that rainfall is higher than the crop demand at this time of year. Already average winter rainfall is in excess of that required to maintain the soil at field capacity by between 140mm and 400mm (Smith and Trafford, 1976). The soils on our farm in Lincolnshire are mainly fairly heavy clay loams, but the worst problems with waterlogging occur at the margins of the sandy beds, which act in a similar way to the duplex soils of Western Australia.

The problem is exacerbated by the slow infiltration of water into the surrounding clays, which in turn leads to surface runoff onto the sand, which is more easily infiltrated and quickly becomes saturated, the water being prevented from travelling deeper by the clay layer below.

In addition to climate change, in the current economic climate there is a move towards larger machinery and min-till cultivation techniques, possibly increasing compaction, leaving soils more vulnerable to problems with waterlogging. Particular problems are caused by discs, which smear the soil in wet conditions, and because they depend on their weight to cut into the soil, cause compaction, especially when turning on headlands. The impact of waterlogging on wheat grain yields in the UK is less than that in some other parts of the world. Cannell *et al.* (1980) recorded grain yield losses of up to 15% using outdoor lysimeters. This is compared to losses of around 45% in the Gulf Coast region of the southern USA (Musgrave and Ding, 1998, Collaku and Harrison, 2002). The reason for this difference is twofold: the temperature and plant growth stage at which waterlogging occurs, and the predominant use in the UK of winter as opposed to spring wheat varieties. The mean distribution of UK rainfall is even across the months, so waterlogging is much more likely to occur in winter when rates of transpiration and evaporation from the crop canopy are much lower than rainfall. Vartapetian and Jackson (1997) also state that hypoxia is most likely during the winter in northerly latitudes. Therefore the soil temperature at which waterlogging occurs in the UK, a north European country, is lower. Luxmore *et al.* (1973) found that higher temperatures increased the damage caused by waterlogging substantially; 30 days waterlogging at 15-17°C reduced grain yields by 15-23% compared to 73% loss due to 30 days waterlogging at 25°C. The greatest yield losses are sustained when wheat is waterlogged at the booting stage (Boa, 1997, quoted by Setter and Waters, 2003) and plants are most likely to be killed by waterlogging between germination and emergence (Cannell *et* al., 1980). In the UK the most likely type of waterlogging is winter waterlogging which occurs during tillering, when losses are smaller. Most wheat grown in the UK - about 97% of the total hectarage of wheat - is autumn sown winter wheat, which has a longer growing season than the spring or short season wheats grown in much of the world. The longer season allows time to recover from damage and, as discussed above, the growth habit of winter wheat avoids vulnerable stages of development at waterlogging prone times

(McDonald and Gardner, 1987; Gardner and Flood, 1993). The crop is established in the autumn before the soil water table rises and ear emergence occurs well after the danger has passed in the spring. Crucially, in that it is an important mechanism in allowing the plant to recover from damage by winter waterlogging, nodal root production of winter wheat occurs in the spring, replacing the damaged seminal root system and providing for the later, yield building, stages of growth.

1.5. THE GROWTH AND DEVELOPMENT OF THE WHEAT ROOT SYSTEM

Shoot development of wheat has been extensively studied and can be described using several naming systems based on observation of the plant morphology (Feekes, 1941[quoted by Large, 1954]; Haun, 1973; Zadoks *et al.*, 1974; Klepper *et al.*, 1982). The most widely used is the decimal code described by Zadoks, but there is no universal system to describe root development. Wheat roots may be simply classified into two main types; the seminal root system initiated from the coleorhiza and the adventitious roots, also known as the nodal or crown roots, which appear from the coleoptile and stem nodes. Wheat seedlings produce 6 or 7 seminal root axes, the appearance of which is completed by early March (Gregory *et al.*, 1978a). These then branch and persist throughout the life of the crop, contrary to the earlier belief that the seminal root system was only temporary and only had to support the seedling until the permanent adventitious system appeared (Nelson, 1946 quoted by Gregory *et al.*, 1978a). There is little variation between wheat cultivars in the number of seminal root axes formed (Welbank *et al.*, 1973; Gregory *et al.*, 1978a). However the number of seminal axes may be influenced by the size and viability of the seed and its position on the ear of the parent plant (MacKey, 1973). Numbers of seminal axes varied between 3 and 6, with larger, more viable seeds producing more axes. The hierarchy of seminal root appearance was described by Wiedenroth and Erdmann (1985) and is summarised in figure 1.1, below. The first three or four seminal axes are determined in the seed, so are unable to adapt their physiology or morphology in response to stress. Also found at the seed depth is the pair of coleoptile nodal roots.

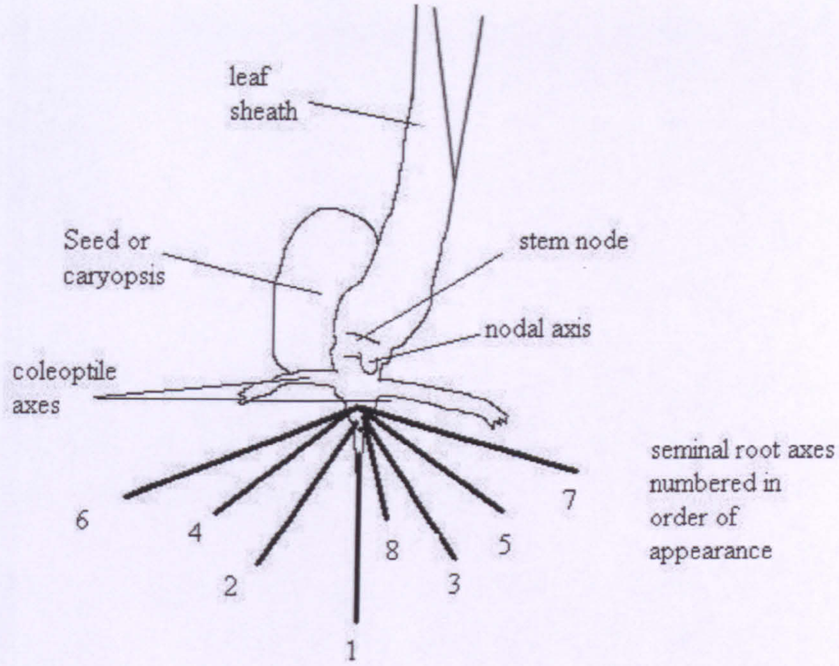

Figure 1.1. The root structure of a 16 week old winter wheat seedling, showing hierarchy of seminal roots. Adapted from Gregory *et al.,* (1978a) and Wiedenroth and Erdmann, (1985).

Wheat produces around 20 nodal axes continuously through the season from February onwards (Gregory *et al.,* 1978a). The number of nodal roots is related to the number of tillers, and therefore is determined by stress and nutritional factors. Total dry weight of roots increases exponentially from emergence to April, around the start of stem extension; thereafter the increase is linear to a maximum at anthesis (Gregory *et al.,* 1978a). After anthesis there is a decrease in dry weight, as the developing ear becomes the primary sink for photosynthates. However new growth does not cease as branches continue to be initiated and the resources from older roots are translocated (Welbank *et al.,* 1973).

A more complex, but more accurate system of naming root axes was proposed by Klepper *et al.* (1984), based on the number of the node from which the root appears. Klepper states that the terms nodal and seminal roots are inaccurate as all axes, except the primary root (R) that develops from the radicle (referred to as root 1 in the naming system by Wiedenroth and Erdmann 1985) are associated with a node. All nodes are given numbers in relation to the coleoptile node, which is 0. Therefore the scutellar node is –2, the epiblast is –1, the first foliar node is 1, the second foliar node is 2 etc.

The orientation of each root is described by dividing each node into quadrants based on the position of the midrib of the leaf associated with the node, which is in the quadrant labelled X. The opposite quadrant to the leaf was labelled Y, that to the left A and to the right, B. As shown on figure 1.2, the orientation of each successive node changes by 180^0. The positions of the first 6 or 7 axes, usually referred to as seminal roots, were R, -2A, -2B,-1A,-1B and –1X, with –2Y occasionally appearing to account for the seven seminal axes noted by Wiedenroth and Erdmann (1985) and Gregory *et al.* (1978a). The coleoptile axes were found, most commonly on 0A and 0B, after the plant had two fully developed leaves, although they were not always present. If present they always appeared together.

The AB pair of nodal roots, or crown roots, from the foliar nodes appeared three phyllochrons after the leaf from that particular node had emerged. The X axis only developed if a tiller was produced from that particular node, and if the tiller and main stem were separated, this root remained with the tiller. The Y axis was more irregular, but where present developed after the AB but before the X. At stem elongation the first four foliar nodes from the base, and usually the fifth, remained in the crown, whilst nodes 6 and 7 moved a short distance above the soil surface. Any roots these produced were short and brittle, not penetrating the soil. These are usually referred to as the basal node when growth staging plants using the Zadoks scale. Nodes 8 to 11 do not produce roots and are the first to fourth stem nodes.

Branching of the root axes could also be described using the system. Primary laterals appeared on R, -2A and –2B as leaf 2 (L2) elongated and on –1A, -1B and –1X as leaf 3 (L3) elongated.

Whilst the above system is more precise in describing root emergence in terms of plant development it is time consuming and requires a high level of skill in dissecting plants to determine the node of origin and the orientation of each root axis. Although technically inaccurate the terms seminal and nodal are used in most publications so will be used in this study, for simplicity and clarity.

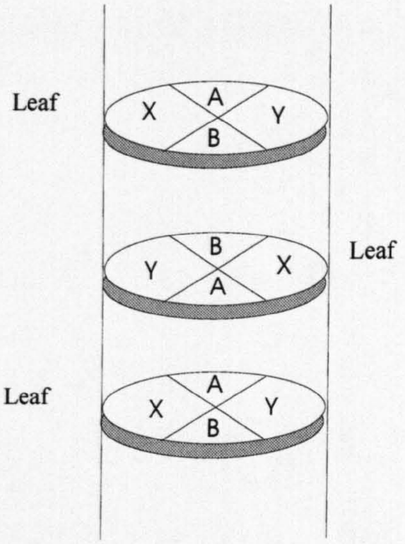

Figure 1.2. Orientation of nodal quadrants for naming of roots from Klepper *et al.* (1984).

The effects of plant nutrition on root growth and development are also much less well understood than for the shoot. Serious N deficiency was shown to delay the initiation of the nodal or crown roots by about a week, although differences in N of the magnitude likely to be found between field soils are probably not large enough to have an effect (Tennant, 1976). Welbank *et al.* (1973) reported that applying N at a rate of 100 kg ha^{-1} slightly increased root dry weight compared to controls that received no N, but the increase was small compared to the effect on shoot dry weight. Increasing the rate to 150 kg ha^{-1} had no further effect on rooting versa the 100 kg ha^{-1} treatment. In a series of factorial experiments using N, P and K it was found that the application of P and K together had a much greater effect on root dry weight than P or K alone. It is usual practice to apply P and K in the autumn, for example as 0:24:24 fertilizer, but N is now not applied until the spring, seedlings relying on soil N reserves over the winter. Autumn N applications were used in the 1970s, for example in the Letcombe lysimeter experiments, but are now discouraged for environmental reasons.

There are small differences in rooting between winter and spring crops and small differences between species. The roots of spring wheat, barley and oats accounted for a smaller fraction of total dry weight than those of winter wheat during spring but the spring cereals caught up by June, so there were no differences by harvest (Welbank *et al.,* 1973). There is very little evidence for differences in root growth between varieties of wheat, despite large differences in the shoots. A comparison between the traditional tall varieties, Cappelle Desprez and Maris Ranger and semi dwarf varieties, which were new at the time, found very little differences in root dry weight or length (Welbank *et al.,* 1973). Lucas *et al.* (2000) suggest that differences in growth, sensitivity to pH and nitrogen scavenging ability of root systems of wheat varieties exist, but concludes that there is not enough information to allow breeders to select for root characteristics, in the same way that shoot growth traits may be selected for. There is some evidence that the number of seminal axes found on wheat has increased over time in association with an increase of yield and chromosome number or ploidy. In a comparison of modern hexaploid bread wheat, (*Triticum aestivum*) and more primitive wheat species, the diploid goat grass (*Aegilops squarrosa*) had the smallest number of seminal axes, sometimes with only three axes present. The number increased through einkorn (*Triticum monococcum*), durum (*Triticum durum*), emmer (*Triticum dicoccum*) and spelt (*Triticum spelta*) to bread wheat, that had up to eight axes plus the coleoptile nodal pair (Erdman and Wiedenroth, 1986).

1.6. OBSERVATION AND MEASUREMENT OF CEREAL ROOT SYSTEMS

In comparison to the wheat shoot system there has been very little work on the roots (Monteith, 1994). This is mainly due to the difficulties in observing and sampling roots in the field, or devising an artificial system to replicate field conditions satisfactorily. Work at Rothamsted by Welbank and co workers (1973) used motorised corers to extract roots of wheat, barley and oats throughout the season, in a series of experiments investigating interactions with crop nutrition. However this method is only practicable for light, stone free soils, so useless at a site like Henfaes. Soil pits are labour intensive, especially if used through the season and are very destructive, requiring a large experimental area, and so are unsuitable for screening a large range of genetic material in small quantities. Field sampling techniques also require the roots to be washed, which is time consuming and frankly, tedious. Roots are almost impossible to separate out in soils with high organic matter, such as crop residues or weed roots. A new technique, which avoids the use of root washing, is described by Bingham *et al.* (2003). An air knife, which is a device that delivers a high velocity stream of air, is used to remove a known volume of soil from one face of a soil pit to expose the roots. These are recorded using a digital camera and image analysis software used to measure the length of roots. If the volume of soil removed by the air knife is measured the length of roots per unit volume at different depths can be calculated. The problem with the method is the time and effort needed to dig the number of pits required in a properly replicated experiment.

Root growth may be studied using hydroponics systems, which allow root structures to be observed *in situ* and easy sampling without the problems of separating the roots from the growth medium. However there is no impedance of root growth, of the type that would be caused by soil particles. Growth rates are generally higher in liquid than solid media (Abbas Al-Ani and Hay, 1983). Also sterile systems do not recreate the interactions between roots and soil flora and fauna that occur in the soil ecosystem. Soil filled rhizotron root chambers of the type described by Riedacker (1974) allow root systems to be observed *in situ* and in conditions closer to those in the field. If glass sided rhizotrons are held at an angle 30° from the perpendicular the roots will grow along the lower panel so root growth can be traced onto acetate. However harvesting roots to measure dry weight still involves root washing, and measurements of root growth are only of the portion of the roots system adjacent to the glass. Artificial systems, whether hydroponics, rhizotrons or pots, usually study the growth of single plants which are not representative of plant communities growing in a field situation. The yield of cereals is driven by the resource capture of the canopy as a whole, so it would be logical to assume that the roots systems of the plants interacted in a similar way to form an inverted canopy under the soil surface.

1.7. THE EFFECTS OF WATERLOGGING ON PLANT PHYSIOLOGY

1.7.1. Introduction

The following section describes the effect of waterlogging, hypoxia and anoxia on plant physiology, and where possible refers to work on wheat. Work on other species is considered where no equivalent exists for wheat, or for means of comparison. This section is an attempt to summarise the current knowledge and state of thinking but for in depth coverage of the subject refer to the reviews by Grable (1966), Drew and

Lynch (1980), Drew (1997), Vartapetian and Jackson (1997), Gibbs and Greenway (2003) and Greenway and Gibbs (2003).

1.7.2. Effects of oxygen deficit

Insufficient supply of oxygen creates an energy crisis in plant tissues (Hoffman *et al.* 1993). Aerobic respiration of one mole of glucose via glycolysis and the Krebs cycle can potentially create 38 mol of ATP, whereas ethanoic fermentation in anaerobic conditions yields only 2 mol of ATP. Therefore all processes in the affected plant tissue, requiring metabolic energy, are vulnerable to hypoxia. Hypoxia reduces the growth rate of the seminal root system of wheat within hours, followed by a reduction in shoot growth. The plant response to the energy crisis by the use of alternate metabolic pathways such as ethanoic fermentation is discussed in section 1.10.1, which discusses plant adaptations to hypoxia. Solution culture experiments using maize seedlings have suggested that inhibition of root growth is due to low rates of ATP regeneration rather than impaired nutrient uptake (Atwell *et al.*, 1985).

1.7.3. Effects on photosynthesis and stomatal conductance

A decrease in the rate of photosynthesis as a consequence of waterlogging or hypoxic root growth media has been reported in the results of numerous studies (Meyer and Barrs, 1988; Huang *et al.*, 1994a; Musgrave and Ding, 1998; Malik *et al.*, 2001). Although biosynthesis of chlorophyll and Ribulose bisphosphate carboxydase-oxidase (Rubisco) is indeed decreased, the decrease in the rate of photosynthesis is most likely a result of stomatal closure as the fall in photosynthesis rate occurs before the effect of waterlogging on chlorophyll concentrations is detectable (Malik *et al.* 2001). For the stomatal closure mechanism to be initiated, to maintain leaf water potential, the transpiration stream must be active; which is consistent with the hypothesis that a message of some sort is transported from the roots to the shoot via the transpiration stream (Bradford and Hsiao, 1982). In a study using tomato it was found that, although flooding did suppress the normal daily increase in hydraulic conductivity leading to a loss of synchrony with stomatal conductance, the effects were not severe enough to initiate stomatal closure (Else *et* al., 1995). Therefore the message from roots in oxygen stressed growth media to the shoot, responsible for stomatal closure is more likely chemical than hydraulic. Possible candidates for the messenger suggested were ethylene, ABA and ACC: supply in the transpiration stream of ABA decreases (Else *et al.,* 2001) and ACC increases in response to waterlogging (Else and Jackson, 1998). Jackson *et al.* (2003), working on tomato, found that the closure of stomata (within four hours of flooding) coincided with an increase in pH of the transpiration sap and a rapid decrease in delivery of some solutes (within two and a half hours of flooding), including K^+, $PO_4{}^{3-}$, $SO_4{}^{2-}$ and $NO_3{}^-$, and so it was hypothesised that a negative message in the form of decreased delivery of solutes or H^+ was responsible for stomatal closure. This hypothesis was rejected however, when the series of experiments using inhibitors and buffers failed to provide validating evidence. After ten hours of flooding cell integrity was lost, and solute uptake became deregulated, as in the experiments described in section 1.7.6.

It is also suggested that, in addition to stomatal closure, feed back inhibition of photosynthesis by increased concentrations of soluble carbohydrates, due to decreased respiration at the sink (root tissues), occurs due to waterlogging (Malik *et al.* 2001). In a study using a range of dicotyledonous crop species it was found that removing the sink caused feed back inhibition of the source, leading to a decrease in photosynthetic rate not associated with stomatal closure (Plant *et al.,* 1987). During vegetative growth the root system of wheat is the largest single sink (Gregory, 1994). However extrapolating the results to wheat is difficult, as different species had differing responses to sink removal: for example bean (*Phaseolus vulgaris*) was better able to regulate feedback inhibition following sink removal by converting sugar to starch.

1.7.4. Effects of ethylene accumulation

Hypoxia causes levels of the plant hormone ethylene to increase in affected roots and in the surrounding soil. Dowdell *et al.* (1972) reported increased ethylene in clay soils following heavy rain in winter and spring. Levels found in waterlogged field soils were high enough to inhibit root growth, although comparisons were difficult due to differences in field and laboratory conditions. It is unclear whether increased ethylene in waterlogged soil is due to a reduced rate of gas diffusion in water compared to air, leading to an accumulation of normally produced ethylene or due to increased ethylene production by the plant. Ethylene levels in the lower soil levels were lower, suggesting that the ethylene was produced by plant roots (Dowdell *et al.*, 1972). Ethylene is the plant hormone controlling senescence and fruit ripening and appears to be associated with root cortical cell death to form aerenchyma in response to waterlogging. Ethylene is also known to inhibit root growth and concentrations in root tissue can increase by x500 as a result of waterlogging (Visser *et al.*, 1997). In a comparison of the effects of hypoxia and ethylene it was found that both treatments reduced root elongation and promoted initiation of new nodal roots (Haung *et al.*, 1997b). Because ethylene and aerenchyma are linked this subject is discussed more fully in section (1.11.2.1) dealing with aerenchyma. Ethylene levels in the leaves also increase in response to hypoxia and ethylene is an inhibitor of leaf as well as root expansion. This increase may be due to enhanced foliar ethylene production as a result of increased levels of the ethylene precursor, ACC, in the transpiration stream (Bradford *et al.*, 1982; Else *et al.*, 1998), an increase in ACC-oxidase activity (English *et al.*, 1995) or a decrease in the supply of ABA from the roots (Else *et al.*, 2001). Whilst ABA can have an inhibitory effect on leaf extension it also suppresses the biosynthesis of ethylene or sensitivity of tissues to ethylene. In experiments with castor bean (*Ricinus communis*) it was found that ABA levels delivered from flooded roots via the xylem decreased within hours (Else *et al.*, 2001).

1.7.5. Effects of CO_2 accumulation

By the same mechanism of reduced gas diffusion in water that causes a decrease in soil oxygen, carbon dioxide (CO_2) in the soil increases as a result of waterlogging. Jackson (1979) reported a rise in soil atmosphere CO_2 from 1kPa to 20 kPa due to flooding. Levels of O_2 and CO_2 have been shown to have an interactive effect on root growth for pea and barley (Giesler, 1967). In a series of solution culture experiments on wheat to investigate the effects of elevated CO_2 and hypoxia it was found that increased CO_2 could alleviate the decrease in shoot growth, due to waterlogging, to some extent by enhancing photosynthesis (Huang *et al.*, 1997a). This effect was greater for the variety Savannah, which had previously being identified as being tolerant to hypoxia due to increased aerenchyma, and it was suggested that aerenchyma aided the movement of CO_2 from the roots to the shoots as well as that of O_2 in the opposite direction. Plants were grown in culture jars, with seals around the base of the shoot, so that any movement of gas nust have been along pathways inside the plants. There was no effect of elevated CO_2 in the aerobic root media on shoot growth of plants. However CO_2 enrichment of root media did decrease root growth for both cultivars tested under aerobic and hypoxic conditions, due to a change in carbon partitioning in favour of the shoot system.

1.7.6. Loss of membrane integrity

Significant leakage of K^+, Cl^-, free amino acids and soluble sugars from wheat roots grown in anoxic media has been observed (Greenway *et al.,* 1992). The rate of solute loss increases with time spent in anoxic conditions, and once 35% or more of solutes were lost the roots were not able to reabsorb K^+ and Cl^- on the restoration of aerobic conditions. This indicates that prolonged anoxia causes an irreversible breakdown in membrane integrity. It was proposed that the loss of membrane integrity and the death of apical root cells are closely related, either membrane breakdown is the cause of apical cell death or that another cause of death leads to loss of membrane integrity. After 20 hours of anoxia root tips had lost 70-90% of their solutes and their ability to resume growth. The review by Greenway and Gibbs (2003) also discussed this relationship. Some of the most important membranes are found in the mitochondria, but these can withstand up to 36 hours of anoxia before irreversible damage occurs (Vartapetian *et al.,* 1985). This is cited as evidence of the adaptive mechanisms possessed by plant cells, discussed in section 1.11.1.

1.7.7. Nutrient uptake

Leaf chlorosis and a decrease in shoot growth of barley under waterlogged conditions have been associated with reduced nitrogen uptake (Drew and Sisworo, 1977). The shortage of nitrogen in the shoot causes translocation of what is available to the young leaves, at the expense of older leaves, leading to their premature senescence. Soil nitrate did decline, but after the onset of nitrogen deficiency in the plants, so it was concluded that nitrogen deficiency was a result of decreased uptake by roots rather than denitrification by soil micro-organisms. A similar effect was found in wheat, again decreased nitrogen content of shoots lead to early senescence of lower leaves, with uptake of nitrogen being reduced within two days of the start of waterlogging

(Trought and Drew, 1980b). Application of nitrogen fertilizer countered leaf senescence, but did not have large benefits in shoot growth. This suggests that the fertilizer acted to compensate for the reduced supply of nitrogen in the soil, due to denitrification, but the plant was unable to make full use of the nitrogen as a result of restricted uptake capacity during waterlogging. Increased nitrogen had no effect on root growth when plants were waterlogged to the soil surface, but root growth above the water table increased when waterlogging was to 10cm from the soil surface. Again this suggests that roots need oxygen to utilise soil nitrogen. Interestingly when ammonia was applied to the soil surface the normal gravitropism of the roots was reversed and roots emerged from the soil surface to use the available nitrogen and oxygen. Further evidence that the decrease in plant nitrogen was more a result of decreased uptake rather than decreased availability in the soil was provided by the results of the Letcombe work, discussed in more depth in section 1.9.1. Belford *et al.* (1985) found that 42 days waterlogging in January and February or 21 days in April decreased available soil nitrate by only 2.5 kg ha^{-1} and 6.3 kg ha^{-1} respectively, a very small amount compared to subsequent fertilizer applied to the crop. Additionally nitrogen mineralisation was stimulated both by high moisture at the beginning of waterlogging when oxygen was still available and by the return of oxygen at the end of the waterlogging period. Belford therefore concluded that the effect of waterlogging on total turnover of soil nitrate over the season would be very small. The plants that had been previously waterlogged would derive a higher proportion of their total uptake from fertilizer applied in the spring. Waterlogging is most likely to occur in the UK in winter, in the early stages of plant growth. Wheat accumulates most of its nitrogen later in the season, the plot of total N uptake against thermal time being an S shaped curve (Whitmore and Addiscott, 1987). Thus waterlogging is unlikely to decrease overall nitrogen uptake by the crop appreciably over the course of the growing season.

In addition to N, uptake of P, K, Mg and Zn was found to be decreased, and the partitioning of these nutrients is altered by waterlogging; concentrations in the roots being increased and that in the shoots, decreased (Huang *et al.,* 1995). However the authors also state that waterlogging decreased root dry weight, and this would be expected to concentrate inorganic nutrients, unfortunately data is only given for nutrient concentrations per mass of root, not total uptake per root system. A decrease in the availability of N and P to the roots may also be linked with the formation of aerenchyma, discussed later. It was found that N and P-starved roots of maize were more sensitive to ethylene, promoting a more rapid and extensive initiation of aerenchyma, when supplied with exogenous ethylene, even at very low levels (He *et al.*, 1992).

The physiological reason for the decrease in nutrient uptake due to waterlogging is the need to partition ATP to essential metabolic processes to maintain the root cells' viability, rather than to the energy hungry processes of active nutrient uptake. The decrease in root growth caused by waterlogging also restricts the volume of soil that may be exploited by the root system, so decreasing nutrient availability. Additionally, as discussed in the previous section, solutes such as K^+ and free amino acids are leached out of the roots, as membrane integrity is lost (Greenway *et al.*, 1992). Nitrate is also chemically reduced by nitrate reductase to regenerate NADH, as an alternate source of energy, and this also leads to the cytosol acidification observed in waterlogged plants. Nul-mutants of tobacco, transformed to lack nitrate reductase in the roots, showed more rapid and more severe wilting, as a result of oxygen deprivation (Stoimenova *et al.*, 2003). Therefore chemical reduction of nitrate in the roots may ameliorate some of the effects of waterlogging, at the expense of decreased availability of N to the shoot. The formation of lysogenous aerenchyma, in response to waterlogging, may hinder solute transport, by decreasing the number of live cortical cells, and causing low efficiency of aerenchymatous roots (Watkin *et al.*, 1998). Restricted transport from the roots to the shoot would contribute the observation that waterlogging causes an increase in concentration of inorganic nutrients in the roots, but a decrease in the shoot (Huang *et al.*, 1995). Waterlogging tends not to decrease nutrient concentrations in the grain at harvest, because although nutrient uptake is decreased, so is yield, so inorganic nutrients are not diluted with carbohydrate (Labanauskas *et al.*, 1975).

1.7.8. Damage on return to oxygen- 'aerobic shock'

On return to aerobic conditions wheat seedlings activate their antioxidative defence mechanisms to counter the effects of increased levels of reactive oxygen species, or free radicals (Biemelt *et al.*, 1998). Defence is achieved by elevated activities of the enzymes in the ascorbate-glutathione cycle, which regenerates the antioxidants, ascorbate and glutathione to their reduced form. The activities of these enzymes are decreased during anoxia, to economise on energy demand as described by Greenway and Gibbs (2003), but restored upon re-aeration. Aerobic, or for that matter anoxic, shock is unlikely to occur in field conditions as decreases in soil oxygen due to waterlogging and the recovery of levels after drainage are gradual processes. However experiments in artificial conditions may be affected if steps are not taken to replicate the gradual change in conditions found in field soils.

1.8. EFFECTS ON ROOT GROWTH AND DEVELOPMENT

Waterlogging caused growth of the seminal root system of wheat to virtually cease within two days and breakdown of root tissue had begun after eight days (Trought and Drew, 1980a). The sensitivity of the seminal root system to waterlogging is because it lacks the ability to adapt to environmental stress, the first four axes being determined in the seed (Wiedenroth and Erdmann, 1985). Nodal axes continued to be initiated and grow, but waterlogged plants did still possess fewer axes than drained controls after 15 days, 10.3 ± 0.3 verses 13.8 ± 0.9 (Trought and Drew, 1980a). In some cases waterlogging acts as a stimulus to enhance the rate of nodal root production, especially in *Triticum aestivum*, and to a lesser extent in diploid and tetraploid *Triticum* species (Erdmann and Wiedenroth, 1986). In a study using the wetland species, *Rumex palustris* (marsh dock), it was found that adventitious root development was a response to waterlogging, under the control of ethylene and auxin (Visser *et al.*, 1996). Inhibitors of ethylene or auxin decreased the number of adventitious roots produced. The initiation of adventitious rooting was preceded by an increase in endogenous ethylene, but the concentration of auxin, a known promoter of adventitious root production remained constant. It was therefore surmised that higher ethylene levels increased sensitivity of the roots to auxin.

The apical tips of wheat roots appear more vulnerable to anoxia than older expanded tissues. For example it was found that the expanded tissues 10-20mm behind the root tip maintained the ability of their membranes to regulate solute movement when returned to aerobic conditions after 48 hours of anoxia, in contrast to the apices which had irretrievably lost nearly all solutes and elongation potential. Apical tissues are furthest from the shoot, which is source of oxygen when the soil is waterlogged, have high metabolic demand due to high rates of cell division, and are densely packed (Armstrong, 1979). The importance of the last point is unclear. It has been proposed that the schizogenous intercellular spaces, found in the expanded tissues of the root cortex, are important in supplying oxygen, and the dense packing of apical cells would therefore put them at a disadvantage. However Canny and Huang (1993) found these spaces to be mainly fluid filled, with a very small amount of gas filled pore space. The presence of the vacuole in older cells is more likely to be a factor in explaining their increased tolerance. The vacuole serves as a store for harmful molecules such as lactate (Greenway *et al.,* 1992) and has a role in regulating acidity of the cytosol (pH_{cyt}) (Greenway and Gibbs, 2003).

1.9. EFFECTS ON SHOOT GROWTH AND YIELD

Waterlogging affects shoot growth indirectly by damaging the root system, upon which the shoot depends for water and nutrients (Sojka *et al.,* 1975; Vartapetian and Jackson, 1997). Whilst the growth of wheat is determined by the resource capture of both the root and shoot systems, it is the shoot components of the plant, the grain and, to some extent the straw, that are economically valuable. Therefore the effects of waterlogging on the growth and yield of wheat are discussed in 1.9.1 below.

1.9.1. Effects of waterlogging on crop growth and yield

The most recent, and most comprehensive, work on waterlogging wheat in field conditions in the UK was done in the late 1970s at the Letcombe laboratory, Wantage. Lysimeters, of 80cm diameter and 135 cm depth, containing intact soil monoliths were buried with the tops level with the soil surface in wheat field. This was to allow the water table to be controlled whilst still allowing the plants to be part of a field crop (Cannell *et al.,* 1980). Waterlogging before emergence decreased the plant population, although compensatory growth occurred in the form of increased tiller production per plant, a greater proportion of which survived to harvest to form an ear. Flag leaves of previously waterlogged plants were also larger. These compensatory changes in plant growth patterns are characteristic of crops sown at a low seed rate, however the Letcombe experiments did not investigate any interaction effects between seed rate and waterlogging. There are no reports of any work to investigate this area, and this was a gap in our knowledge pointed out in the comprehensive review by Setter and Waters (2003). Low oxygen availability slowed germination of several cereals including wheat, but stopped completely that of several brassica and legume species, therefore wheat is more tolerant of waterlogging during germination than many other crop species (Al-Ani *et al.,* 1985).

When waterlogging occurred during tillering it did not cause death of plants and the decrease in yield was entirely due to a decrease in ear number at harvest, although the effect was less than that on the number of tillers produced, so again tiller survival increased to compensate (Cannell *et al.,* 1980; Belford *et al.*, 1985). The ability to compensate for damage caused by waterlogging may be as important as tolerance whilst waterlogged for winter cereals. Belford *et al.* (1981) commented that yield losses were much smaller than would be expected, judging by the poor appearance of the crop at the end of waterlogging. For winter oats, waterlogged during winter, shoot dry weights of waterlogged plants were 60%, 88% and 91% of controls at the end of waterlogging, anthesis and maturity, respectively (Cannell *et al.,* 1985). When waterlogging was imposed on several occasions throughout the growing season the effects were additive (Belford *et al.,* 1981). Waterlogging during stem extension decreased the number of grains per ear, and it was suggested that waterlogging interrupted the supply of inorganic nutrients to the developing spike, causing abortion of florets (Belford *et al.,* 1981). The effects of waterlogging of sand and clay soils were compared, and the damage was found to be greater on the clay soil (Cannell *et al.,* 1980). When the effects of winter waterlogging and summer drought were investigated, it was found that the depression of yield was greater for waterlogging than drought, and waterlogging did not increase the susceptibility of plants to subsequent drought (Cannell *et al.,* 1984). The return periods for the waterlogging and drought levels used in the experiments were found to be 2-3 years and 10 years respectively, thus waterlogging is the most likely stress to occur in the UK. Whilst barley was more sensitive to waterlogging than wheat, it was found to have a smaller decrease in yield due to drought (Cannell *et al.,* 1984). This was due to its earlier maturity – it was harvested 2-3 weeks before the wheat – a good example of stress avoidance rather than stress tolerance.

Yield loss in winter wheat due to waterlogging in the UK is usually associated with the reduction in tillering as waterlogging is most likely to occur during the vegetative stage of growth. When waterlogging occurs at other stages of development the effects may be more severe. In an experiment with spring wheat grown in pots, which was continuously waterlogged from emergence to just before harvest showed a small reduction in tillering but yield loss was mainly due to a reduction in the number of grains per ear and individual grain weight (Musgrave, 1994). Therefore there is some evidence that the stage of development at which waterlogging occurs determines the extent of its effects on plant growth and yield. In the case above waterlogging during stem extension was the most severe stress. Results of different experiments do not always agree however. In an another experiment on spring wheat, flooding for 96 hours had the greatest effect on growth of leaves and stems, photosynthesis and root number when the treatment was applied at anthesis rather than at stem elongation or flag leaf emergence (Meyer and Barrs, 1988). However there was no effect on grain yield at harvest and the authors suggested that waterlogging had little effect on spring wheat after tillering. This concurs with the observation that root dry weight increases exponentially in the spring, during tillering, and this rate slows to a linear rate of increase from stem extension to anthesis when accumulation of dry weight virtually ceases (Gregory *et al.,* 1978a). Therefore waterlogging during tillering would coincide with the fastest period of root growth, and thus the period of greatest metabolic demand for oxygen from the roots. Tissues are most vulnerable to damage by anoxia when growth rates are highest (Greenway and Gibbs, 2003). Yield losses due to waterlogging tend to be greatest when yields are heavy (Cannell *et al.,* 1980; Box, 1986).

As well as a decrease in grain yield waterlogging decreases straw yield (Cannell *et al.,* 1980; Belford *et al.,* 1981). The decrease was greater than that which could be explained by the decreases in shoot number and straw length alone, and it was hypothesised that waterlogging decreased the uptake of inorganic nutrients during vegetative growth leading to a decrease in thickness or dry matter content of the straw (Belford *et al.,* 1981). Decrease in straw length was most likely to have been a result of decreased shoot population producing a less dense canopy and decreased etiolation of the lower internodes. Decreased availability of nitrogen in the early spring due to waterlogging would also shorten the lower internodes, and delaying nitrogen fertilizer application is a strategy advocated by plant breeders to reduce the risk of lodging in their agronomy guidelines produced for growers of their varieties (Nickerson 1999; CPB Twyford 2000). The sparser canopy also increased the size of the flag leaves of waterlogged plants, due to less competition for light and nutrients. Despite the decrease in uptake of nitrogen, there was no decrease in grain protein at harvest, probably due to the nitrogen that was available being concentrated in the lower grain yield (Belford *et al.,* 1985).

1.10. OTHER CONSEQUENCES OF WATERLOGGING

In the UK most arable farming is intensive, with high inputs including fertilizers, pesticides and plant growth regulators (PGRs). A waterlogged soil, unable to carry a fertilizer spreader or sprayer, means that inputs can not be applied at the correct time, thus limiting their efficacy, or even preventing application at all. The consequences of this on yield may be more serious than the physiological stress imposed by soil hypoxia. For example failure to control blackgrass (*Alopercus myrosoides*), by not applying herbicide before the plant becomes too far advanced, may result in 5% yield loss for every 12.5 blackgrass plants per square metre (Lutman *et al.*, 2003). In addition to the problems of travelling over waterlogged fields, many herbicides carry the warning not to be applied to crops suffering from stress, including waterlogging (BCPC, 2003).

Waterlogging may also increase the problem of take-all (*Gaeumannomyces graminis* var. *tritici*, although it is unclear whether there is an interaction, with plants weakened by waterlogging being more susceptible to the disease, or whether the effects of the two problems are merely additive (Hornby *et al.,* 1998). Cannell *et al.* (1980) reported an increase in the amount of take-all in waterlogged lysimeters, measured as a percentage of plants showing symptoms of the disease. There is also some anecdotal evidence from farmers that problems with waterlogging may leave crops susceptible to lodging, especially stem lodging due to poor root anchorage. The decrease in K content of the shoot due to waterlogging may also cause waterlogged plants to have weaker stems (Huang *et al.,* 1995), although this effect should be countered by the shorter straw, and hence reduced shoot leverage moment.

The biological incorporation of crop residues, to achieve a healthy soil structure, is an aerobic process, and that is why exponents of min-till believe that cultivation should be shallow, so straw breaks down in the warmer, aerated upper soil layers (Townsend, 2004). Waterlogging prevents this process and could lead to problems disposing of crop residues, especially in the light of 'cross-compliance' measures that may force arable farmers to apply straw or FYM to fields.

1.11. PLANT ADAPTATIONS TO WATERLOGGING

Animals are able to move to avoid environmental stresses, whilst plants, fixed in one place throughout their life cycle have evolved to cope with environmental changes by adapting their growth, development and metabolism (Miflin, 2000). Plants attempt to cope with the effects of waterlogging either by metabolic tolerance to hypoxia by tissues or by structural adaptations of the whole plant to avoid tissue hypoxia by ensuring an adequate supply of oxygen from the aerobic portion of the plant. These mechanisms may be expressed constitutively, as in the case of wetland species, or as an adaptive mechanism, as found in crop plants. The adaptive response to waterlogging or hypoxia may be divided into three areas, differentiated by the time from the onset of stress (Dennis *et al.*, 2000). Firstly, signal transduction pathways are activated within the first four hours of waterlogging. The second stage, up to 24 hours after the start of hypoxia, is the metabolic response. This includes the induction of ethanoic fermentation as an alternative energy producing pathway, and possibly an increase in ethylene biosynthesis. The third stage is the initiation of structural adaptive changes, such as aerenchyma, possibly mediated by the metabolic changes in the second stage.

1.11.1. Metabolic tolerance

The ATP supply of a cell is only sufficient for 1-2 minutes but plant cells can survive anoxia for at least an hour. Therefore they must be able to regenerate ATP anaerobically, at least in the short term. Plants have three fermentation pathways as alternatives to oxidative phosphorylation when insufficient oxygen, the electron acceptor, is available. Plants are able to use fermentation pathways using ethanol, lactic acid and the production of alanine from glutamate and pyruvate, in contrast to animals, which are only able to use lactic acid. It appears that ethanol fermentation is the main pathway used in waterlogged plants as the acidification of the cytosol that occurs during waterlogging favours the use of the ethanoic over the lactic pathway (Drew, 1997). The possession of a more active ethanoic fermentation pathway is associated with waterlogging tolerance. Studies using ADH null mutants, unable to use this pathway, show them to be more sensitive to waterlogging. However the drop in cytosol pH may be a more serious problem than the energy deficit, killing the tissue before ATP is exhausted (Dennis *et al.*, 2000). Roberts *et al.* (1985) tested a range of plant species and found that species that had tighter cytoplasmic pH regulation during hypoxia survived longer. Cells were killed when H^+ leaked into the cytoplasm from vacuoles, as membrane integrity was lost, as discussed in section 1.7.6. Accumulation of fermentation products such as ethanol could also have a damaging effect on waterlogged plants. However when waterlogged and ethanol treated plants were compared, though responses were similar, the damage due to ethanol took longer to appear and occurred only at concentrations many times greater than would be found in waterlogged plants (Alpi *et al.*, 1984). Therefore waterlogging damage is unlikely to be as a result of ethanol accumulation. Waterlogging causes a switch in protein synthesis, reflecting the change in metabolism. Work on maize roots found that 20 new polypeptides were synthesised as a result of the switch from aerobic to anaerobic conditions (Sachs *et al.*, 1980; Sachs *et al.*, 1996). Some of these anaerobic polypeptides (ANPs) have been identified as enzymes involved in the fermentation pathways, but also present is extra expression of enzymes for glycolysis and the degradation of sugar (Dennis *et al.*, 2000). These latter enzymes would increase the flow of carbohydrates through the glycolysis and fermentation pathways to attempt to compensate for the lower energy yield per unit of carbohydrate used. This mechanism explains the observation that an exogenous supply of glucose can sometimes enhance cell survival rates in hypoxic conditions (Drew, 1997). One ANP has homology to xyloglucan endotransglycosylase, an enzyme that may be involved in lysogenous aerenchyma production (Sachs *et al.*, 1996). Changes in gene expression and protein synthesis occur both at the transcription and post-transcription level. For example levels of the LDH1 and LDH2 polypeptides of the lactate dehydrogenase both increased in response to oxygen deficit, but an increase in mRNA only occurred for *ldh1*, indicating that the regulation of LDH2 was post-transcriptional (Germaine *et al.*, 1997). A sequence, present on the promoter sequence of genes induced by hypoxia, has been identified. This anaerobic response element (ARE) has then been used to identify hypoxia-induced genes in *Arabidopsis*, such as that for alcohol dehydrogenase, an enzyme used in fermentation (Hoeren *et al.*, 1998). In addition to the changes in the polypeptides synthesised, there is a changeover in the translational material of the cell. The normal polysomes, responsible for translating aerobic proteins, dissociate and the new mRNAs for the ANPs are translated by new polysomes, which are smaller than the aerobic polysomes. Although hypoxia caused the synthesis of some proteins to be selectively enhanced, no new proteins were synthesised in anoxic conditions (Chang *et al.*, 2000). The induction of ANPs by hypoxia explains the observation that hypoxic pre-treatment allows plants to cope with subsequent anoxia and avoids the more serious consequences of anoxic shock. This phenomenon was observed by Waters *et al.* (1992), where exposure to 15-30 hours of hypoxia increased tolerance to subsequent anoxia, where tolerance was measured as the ability to resume root elongation when returned to aerated conditions. Activity of pyruvate decarboxylase increased 2-4 fold and alcohol dehydrogenase 3.3-17 fold as a result of hypoxic pre-treatment. Almost all the roots receiving aerobic pre-treatment lost their elongation potential after 21 hour of anoxia compared to only 10% of the hypoxically pretreated roots. When exogenous glucose was supplied to the hypoxically pretreated roots during anoxia all retained their elongation potential. As mentioned previously, the lower energy yield of anaerobic fermentation means that these pathways can only be a short term aid to plant survival. The phenomenon of hypoxic pre-treatment aiding apical cell survival in subsequent anoxic conditions was also observed in respect to membrane integrity (Greenway *et al.*, 1992). Hypoxic pre-treatment slowed the rate of solute leakage compared to roots grown aerobically prior to anoxia.

Enhanced fermentation by root cells, in response to oxygen stress, would be expected to decrease levels of stored carbohydrates, by increasing consumption. However, a study using wheat seedlings found that levels of fructan increased five-fold in roots and seven-fold in shoots during a period in nitrogen-flushed solution (Albrecht *et al.*, 1993). It was hypothesised that, as the enzyme responsible for fructan synthesis, sucrose : sucrose fructosyltransferase, has a low oxygen demand, fructan accumulation is an adaptation to aid survival of temporary oxygen shortage. On re-aeration the fructans were used to fuel rapid root growth. Earlier work on barley and rice also found an accumulation of sugars in waterlogged plants, but concluded that the increases were a result of decreased rates of growth during waterlogging, as sugar accumulation only occurred at oxygen concentrations low enough to reduce growth (Benjamin and Greenway 1979; Limpinuntana and Greenway, 1979). Contrary to this theory is that increased sugar accumulation occurred in shoots, where a decrease in growth rate was not recorded. Nodal roots, though, were singled out as having very high sugar levels, and this is consistent with the hypothesis of Albrecht; that sugar accumulation is an adaptation to allow a more speedy recovery in growth once the period of oxygen stress is over.

1.11.2. Structural adaptations

1.11.2.1. Aerenchyma

The internal oxygen supplies of roots are consumed within a few minutes when roots in anoxic media are detached from the shoot (Weidenroth and Jackson, 1993) so to sustain aerobic respiration in the long term plants must possess a means of transporting oxygen from the shoot to the root system. Wheat responds to low soil oxygen levels by increasing the internal porosity of the roots (Varade, 1970). Aerenchyma are tissues made up of gas filled pores called lacunae to form continuous pore spaces through the roots, stems and leaves that allow the diffusion of O_2 from the shoot into the apices of roots growing in hypoxic conditions (Gibberd *et al.*, 2001; Drew *et al.*, 2003). Those of wetland species are typically schizogenous, formed by separation of cells in the root cortex and are often constitutive (Justin and Armstrong, 1987). Those formed in response to waterlogging, such as in cereals, are formed by the death of cortical root cells and are termed lysogenous. This programmed cell death is different from cell necrosis due to anoxia in that it is a result of activation of a specific biochemical pathway in response to a stimulus and is under genetic control of the cell. Nuclear condensation and degradation of the cell's DNA occurs early in the process, the opposite of necrosis where this occurs after the degeneration of organelles. Cell death to form lysogenous aerenchyma also reduces the number of living roots cells so decreases the demand for oxygen (Armstrong, 1972; Drew *et al.*, 2000). The plant hormone responsible for programmed cell death, similar to apoptosis in animal cells is ethylene, levels of which increase in root tissue in response to waterlogging. A signal transduction pathway involving Ca $^{2+}$ and phosphokinases is induced in response to ethylene (He *et al.*, 1996a). For a review of these processes, refer to Drew *et al.* (2000). In maize ethylene biosynthesis was observed to increase in response to hypoxia, indicated by increased activities of ACC synthase and ACC oxidase (English *et al.*, 1995; He *et al.*, 1996b). Delivery of ACC from the roots to the shoots of tomato plants also increased 28-fold after 24 hours of flooding, an increase sufficient to fuel the increased ethylene production, observed in the shoot (Wang and Arteca, 1992; Else and Jackson, 1998). Ethylene biosynthesis inhibitors or inhibitors of ethylene action are known to block the formation of aerenchyma, further strengthening the case for ethylene as the plant hormone responsible for aerenchyma initiation. Both hypoxia and N starvation have been shown to induce aerenchyma formation in roots of maize, and ethylene is involved in the signalling process to stimulate cellulase activity for both stresses, demonstrated by the blocking of cellulase by ACC synthase inhibitors, the effect of which was reversed by supplying the cells with endogenous ethylene (He *et al.*, 1994). The mechanism is not identical for the two stresses however, as the study found that hypoxia increased ACC synthase activity to increase ethylene levels but N starvation depressed ethylene production. Ethylene promotes increased activity of cellulase, used to break down cell walls during aerenchyma formation, and has a greater effect on new nodal roots and on cultivars more tolerant to waterlogging due to their superior ability to form aerenchyma (Huang *et al.*, 1997b). The same authors also reported an increase in ethylene production by the roots in response to hypoxia, greater in the more tolerant variety. In barley root porosity has been observed to increase even at concentrations of oxygen not low enough to suppress growth (Benjamin and Greenway, 1979). Cells in anoxic, as opposed to hypoxic conditions, lacked the ability to respond, as the conversion of ACC to ethylene requires the presence of oxygen (He *et al.*, 1994;He *et al.*, 1996a), and the activity of ACC-oxidase is believed to be the rate limiting stage in ethylene biosynthesis under waterlogged conditions (Rijnders *et al.*, 2000). Thus hypoxic pre–treatment is required to allow the plant to respond to subsequent anoxia. In contrast, Visser *et al.* (1997) found no increase in the ethylene precursor, ACC or mRNA for ACC-oxidase, indicating no increase in ethylene production. It was hypothesised that endogenously produced ethylene built up as a result of inhibited gas transport. Therefore aerenchyma are not only initiated by ethylene, but may be essential to maintain the ethylene level below that which would be damaging, by removing endogenous ethylene.

Both seminal and nodal roots of wheat are able to form aerenchyma, providing that they are exposed to hypoxia before they reach 100mm (Thomson *et al.,* 1990). This author also reports that nodal roots may possess some aerenchyma tissue when grown in aerated media, which would explain the observation that the seminal root system is more vulnerable to waterlogging damage (Trought and Drew, 1980). Aerenchyma formation is another mechanism by which hypoxic pre-treatment allows root apices to survive subsequent anoxia; the increase in root porosity allowed hypoxically grown roots to retain elongation potential, the aerobically grown roots were unable to continue growth when returned to aerobic conditions after anoxia (Thomson *et al.,* 1990). It is the apical region of the wheat root tip that initiates the formation of aerenchyma, illustrated by an experiment where aerenchyma developed along the full length of the main axis of a nodal root, grown with only the apex in deoxygenated stagnant agar solution (Malik *et al.,* 2003). An increase in porosity of nodal roots growing above the water table was also observed, when root tips penetrated the soil water level, in wheat plants grown in soil (Malik *et al.,* 2001). This mechanism allows root tips that are growing below the water table to be supplied with oxygen from tissues growing in aerated surface soil layers.

Aerenchyma have been shown to enable wet land plants such as rice to cope with waterlogging and there is evidence to suggest that differing tolerances of wheat varieties are associated with the ability to form aerenchyma (Yu *et al.,* 1969; Haung *et al.,* 1994a, Haung *et al.,* 1997b). In the latter two sets of experiments, cultivars with more aerenchymatous nodal roots were better able to continue root growth when aeration was resumed, indicating that the supply of oxygen provided by the aerenchyma was able to maintain the viability of the root apices. In a similar experiment it was found that the adverse effects of waterlogging on leaf water potential, stomatal conductance, photosynthesis, nitrogen and chlorophyll content and growth of shoots and roots were less in the cultivar with more aerenchyma (Huang *et al.*, 1994b). In a comparison of the triticale cultivar Muir, which was selected because of observed tolerance in the field, with less tolerant wheat lines it was found that Muir had more aerenchyma, enabling the nodal roots to reach a greater length (Watkin *et* *al.*, 1998). Unfortunately the link between aerenchyma and improved crop yield when grown in waterlogged conditions is not always clear, as Muir did not have significantly better shoot growth, possibly because aerenchymatous roots are less efficient. This theme is discussed by Barrett-Lennard (2003), who asked why are aerenchyma not constitutive in crop plants if they are an advantage, and pointed out that even marsh plants that possess constitutive aerenchyma still increase their root porosity as an adaptation to hypoxia if and when it occurs. It is suggested that aerenchymatous roots are less able to take up water and nutrients due to cellular discontinuities in the root cortex. However Drew *et al* (1980), working on maize, found that aerenchyma were formed by the breakdown of the midcortex, while other parts of the root remained relatively intact. Additionally, intact cells and cell wall residues bridged the space between the outer and inner cortex. Uptake of radiolabelled Rb^+, was 'very little affected', by the presence of aerenchyma tissue. Therefore the picture is somewhat unclear.

1.11.2.2. Regulation of Radial Oxygen Loss (ROL)

If the roots, growing in a reduced soil environment, are supplied with oxygen by aerenchyma, this creates a strong diffusion gradient, to draw oxygen out of the roots. This leakage of oxygen is often referred to as radial oxygen loss or ROL. Minerals in the soil are oxidised around the roots to form a mineral plaque (Ding and Musgrave, 1995). The presence of this plaque in wheat is negatively correlated with yield in wheat, where it indicates loss of oxygen from the roots (Ding and Musgrave 1995, Musgrave and Ding, 1998). This mineral plaque has been observed in rice, where in contrast to wheat, there is a positive correlation with yield, as the presence of mineral plaque is a sign of a good oxygen supply to the roots (Chen *et al.*, 1980). The positive effect of the plaque in rice may be to oxidise toxic reduction products such as Cu and Ni outside the roots to prevent their entry into the plant (Greipsson and Crowder, 1992). In fact some degree of ROL may be essential to the survival of wetland plants to maintain an oxidised layer in the rhizosphere and form a barrier to sulphide and metal cations, so an allowance for ROL, in addition to root metabolic oxygen demands, must be made when calculating the amount of oxygen the aerenchyma must provide (Armstrong, 1972). The reddish brown plaque around the wheat roots is composed of 11 minerals, of which Fe, Mn and P were negatively correlated with yield (Ding and Musgrave, 1995). When there were differences in grain yield between varieties there was a strong negative correlation between the amount of plaque observed on the roots of a variety and its yield, but this did not occur in the first season of the experiment when all varieties used had equally poor tolerance (Musgrave 1994).

Wetland species have barriers to minimise ROL but cereal crops appear to only possess very weak barriers, even though they are able to produce aerenchyma. In a study of nine species of the Triticeae family only the wetland weed species, *Critesion marinum* (also known as *Hordeum marinum*) possessed an effective barrier to ROL in its adventitious roots, together with a high internal porosity (McDonald *et al.*, 2001). Cereals do have a weak barrier to ROL, which although ineffective compared to wetland species, is better than none. Wheat is better able to regulate ROL than barley: whilst yield of wheat varieties after waterlogging was found to be positively correlated with root porosity, there was no such relationship for barley, and it was hypothesised that the inability of barley to regulate ROL negated the advantages of increased aerenchyma (Setter *et al.*, 1999). Oilseed rape has no barrier to ROL and this explains the observation that this crop is more susceptible to waterlogging than cereals.

1.12. VARIETAL DIFFERENCES IN TOLERANCE TO WATERLOGGING

Tolerance to waterlogging has two definitions, physiological and agronomic. Physiological tolerance is plant survival or maintenance of growth rates, i.e. a tolerant cultivar will be more likely to survive waterlogging and show a smaller reduction in growth rate compared to a sensitive cultivar. The agronomic definition is the ability to maintain grain yields with as small a loss as possible compared to drained controls (Setter and Waters 2003). These definitions usual complement each other, but not in all cases. As discussed previously in section 1.4.2, the smaller decreases in yields due to waterlogging of winter wheat grown in the UK, in comparison to USA and Australia, which could be described as agronomic tolerance may be due to a lower growth rate during the most likely period for waterlogging to occur. It may not be able to maintain high growth rates whilst waterlogged, so is not physiologically tolerant but recovers in the spring, minimising yield losses and is therefore agronomically tolerant.

There has been very little recent work on waterlogging in the UK and none comparing the tolerance of winter wheat varieties currently grown. The Letcombe work described in section 1.9.1, investigated the effects of waterlogging on winter wheat and effects of waterlogging on winter wheat and winter barley were compared, finding that wheat was more tolerant than barley. However nothing was done to compare differences between wheat varieties. Additionally modern varieties may behave differently to their predecessors grown more than two decades ago, considering the advances in plant breeding in the meantime. This rate of advance can be shown by study of the 2003 Recommended List, which showed that most current varieties were first listed within the previous four years (HGCA 2003).

In the absence of work using UK germplasm studies from other parts of the world are the only source of evidence for varietal differences in waterlogging tolerance. These must be treated with caution however, due to the differences between winter and spring wheats and temperature and type of waterlogging discussed previously. In a pot study of eight spring wheat varieties grown in Louisiana, Musgrave (1994) found significant differences in grain yield between waterlogged and controls and between varieties. There was, though, no significant interaction between waterlogging and variety, suggesting that all of these commercial cultivars had an equally poor tolerance to waterlogging. In a second series of experiments it was found that yield under waterlogged conditions did not correlate with that of controls ($r^2 = 0.14$), suggesting different tolerance levels. However differences in the mean grain yield of waterlogged varieties were not significant ($P=0.1$) (Musgrave and Ding, 1998). Two lines, Coker 9877 and LA 862A16-3-3-X were picked out as possibly tolerant as they yielded over 30% above the mean.

Landraces of cereals, grown from farmer saved seed year on year, may develop tolerance, depending on the local conditions in which they are grown. Work by Davies and Hillman (1988) compared hexaploid and tetraploid wheat species and included two populations of emmer (*Triticum dicoccum*), one of European origin from the Bordeaux botanical garden and one collected from the Pontus region of Turkey.

The Pontus population had a much higher tolerance, in terms of percentage yield loss, than the Bordeaux population. The local farmers grow this emmer on their wettest fields, where no other cereal can be grown, so tolerance has been selected for over many generations. However the tetraploid emmers were out yielded by the hexaploid species tested. Of the hexaploid wheats, the most tolerant was *Triticum macha*, collected from Georgia. Unfortunately the authors had no information on the waterlogging conditions of the area this population came from, but believed it to be a high rainfall area. Another experiment found that modern hexaploid bread wheat (*Triticum aestivum*) has a greater capacity to adapt to waterlogging than more primitive diploid and tetraploid ancestors. Later appearing seminal roots had greater porosity, increased diameter and lignification as a barrier to ROL, adaptations not present to as great an extent in the primitive species (Erdmann and Wiedenroth, 1986). Of the species tested only *Triticum aestivum* was able to maintain its root/shoot ratio, but as the experiment looked at seedling growth, no grain yield data is available. This suggests that greater ability to adapt has been positively selected for as wheat has been moved from its natural environment in the semi arid Middle East.

1.13. METHODS TO COPE WITH WATERLOGGING IN AGRICULTURE

Most crop species currently grown, including wheat, are vulnerable to damage by waterlogging. Flowers and Yeo (1995), although dealing specifically with salinity, make several points that could be equally applied to waterlogging. They identify three approaches to solving the problem of yield reduction due to salinity (or waterlogging); civil engineering, for example drainage or better irrigation practice, domestication of more tolerant wild species or improvement of existing crop species by plant breeding.

1.13.1. Drainage and cultivation

On soils such as heavy clays drainage may be the only effective long term solution, for example most heavy clays in Lincolnshire have been drained over the last two centuries. However drainage is expensive, and is less effective where the problem is with soil structure, such as on silts with fine particles and a small proportion of large pore spaces. Improvement of the crop grown is therefore attractive, avoiding the expense of drainage. On some soils drainage may be impossible, due to the instability of the subsoil, such as on some duplex soils in Australia (Tennant, 1992). Where waterlogging is the result of a plough pan, deep cultivation may be effective; either using traditional subsoilers, mole ploughs, or the more recent generation of implements designed to work at a depth of around 30cm, such as the 'Flatlift'. There is some anecdotal evidence from farmers that crops with tap roots such as linseed, lupins, oilseed rape, and especially lucerne, may help break pans, by acting as biological ploughs (Gardner *et al.*, 1992). Unfortunately little conclusive scientific evidence is available. A method suggested by Gardner *et al.* (1992) uses an intercropping technique using lucerne, where cereals are direct drilled into a low-density lucerne stand, in a variation of the old practice of undersowing cereals. The lucerne lowers the water table and prevents acidity by taking up leached nitrogen at depths below the normal level of the cereal root penetration.

1.13.2. Domestication of novel species

Domestication of tolerant wetland species may be possible, as there is a better record of success in improving agronomic characteristics of plants than breeding tolerance into crop plants. For example, despite around 300 papers per annum being produced related to salinity, there are only a very small number of cultivars, tolerant to salinity, so far released (Flowers and Yeo, 1995). This contrasts to the work on Triticale, which has eliminated the undesirable characteristics associated with early cultivars, such as shrivelled grain, within forty years. Currently, food production is reliant on a handful of plant species, and these species may struggle in environments to which they are not adapted, whilst the native flora thrives (Boyer, 1982). This limitation was noticed by Darwin (1859), who pointed out that no crop species had been domesticated in areas such as Australia and the Cape of Good Hope, not because these places do not posses 'aboriginal stocks of useful plants' but because they were 'inhabited by quite uncivilised man', lacking the cultural skills to domesticate and improve these plants by selective breeding. Cultivated species were limited to those found wild in 'countries more anciently civilised', such as the Fertile Crescent of the Middle East.

1.13.3. Breeding for tolerance

For a review of this subject see that by Setter and Waters (2003), which is the most recent summary of work in this area worldwide, and includes reports on work in currently being done in China, sourced from Chinese journals.

For breeding for tolerance to be possible three criteria must be met, as described by Settter and Waters (2003). These are: 1. Genetic diversity for tolerance must exist within the crop gene pool or be able to be imported into it, for example from wild relatives or using recombinant DNA techniques. 2. The mechanisms used in achieving tolerance must be understood, so that tolerant phenotypes can be identified and selected. 3. The traits for tolerance must be heritable.

1.13.3.1. Genetic diversity for tolerance

As discussed in the previous section, the genetic diversity for tolerance to waterlogging found in commercial wheat cultivars is quite limited. This is understandable when the limited genetic diversity of all crop species is considered. The reason for the relatively small gene pool of crop plants, compared to wild plant populations, is that the early farmers who domesticated these species only had access to the wild populations in their immediate locality (Miflin, 2000). It is also unlikely that genes for waterlogging tolerance would be found in the ancestors of wheat as the wild *Triticum* and *Aegilops* species that *Triticum aestivum* was hybridised from are from the semi arid Mediterranean climatic niche (Vavilov, 1926; Hillman and Davies, 1990; Heun *et al.,* 1997). Centuries of selective breeding will have further reduced diversity in favour of more desirable agronomic characteristics.

With the diversity of knowledge available on the subject of plant adaptations to cope with waterlogging it may be possible to select plants with these traits to hybridise with crop species (Drew, 1983). Wild relatives in the Gramineae or Triticeae group therefore can be used to introduce desirable agronomic traits into commercial lines. Whilst cultivated barley, *Hordeum vulgare,* was also was derived from a species from Israel-Jordan, *Hordeum spontaneum,* (Vavilov, 1926; Badr *et al.*, 2000) 25 of the 32 wild *Hordeum* species are found in areas likely to be waterlogged (von Bothmer *et al.*, 1991 quoted by McDonald *et al.*, 2001b). Of those *Hordeum* species found in the UK *Hordeum marinum* and (sea barley or squirrel tail barley) and *Hordeum secalinum* (meadow barley) are found in waterlogging prone environments; the former around the margins of salt marsh, the latter in low lying pasture on moist heavy soils (Hubbard, 1954). As it is possible to hybridise wheat and barley to create Tritordeum, wild barley is a promising potential source of waterlogging tolerant genetic material. Taeb *et al.* (1993) and later, McDonald *et al.* (2001a) evaluated the salt marsh species, *Lophopyrum elongatum*, as a source of genetic material. This species has higher constitutive root porosity, allowing an increased supply of oxygen to the roots, but also shows a slower growth rate so has a smaller oxygen demand. In further work the wetland grass *Critesion marinum* (*Hordeum marinum*) was identified from a screen of Triticeae species, a group that includes the cereal crop species, as being waterlogging tolerant. It was shown to have high root porosity and a barrier to ROL (McDonald *et al.* 2001b; Garthwaite *et al.*, 2003). Amphiploid lines, derived from *Lophopyrum elongatum* and the commercial wheat line, Chinese Spring have also been tested, but none gave a substantial improvement in tolerance (McDonald *et al.*, 2001a). Slow growth rates are an adaptive feature of wild plants that may help cope with stress (Grime and Hunt, 1975, Lambers and Poorter, 1992) but this is not a desirable feature of a crop plant, where high growth rates are needed to give good yields and compete with weeds. A major obstacle to wide hybridisations between crop and wetland species is that they belong to very differing groups in terms of growth habit, even if they are genetically related, as in the case of *Hordeum vulgare* and *Hordeum marinum*. Grime and Hunt (1975) categorised species into three groups based on relative growth rate (RGR) under controlled, optimum conditions, so to measure the maximum genetic potential (RGR_{max}). The first group have high RGR_{max} and are found in highly productive but stable environments, such as rain forest, and tend to be tall perennials that produce leaf litter. The second type are found in productive but disturbed environments and have high RGR_{max} but a short life span, and tend to partition most of their energy to seed production. Cereal crop species, their weedy ancestors and arable weeds fall into this group. Slow growing, stress tolerant species with a low RGR_{max}, are found in stable but poor environments such as wetlands. The fast growing species from the second group have high rates of respiration per unit organ weight and higher nutrient demand and uptake. The slow growing species have a lower concentration of organic nitrogen and minerals, due to having more cell wall material and plant secondary compounds, leading to a lower rate of photosynthesis but greater leaf longevity (Lambers and Poorter, 1992). These characteristics would allow these species to be more tolerant of waterlogging but be of little use in a crop plant. In view of the fact that ecological and agronomic characteristics of crop and wild species may be mutually exclusive it may be a better strategy to try to find more modest tolerance in closer relatives (Flowers and Yeo, 1995). For example, tolerance may be found in land races of cereal crops from waterlogging prone regions, rather than wide hybridisation with marsh species.

If the range of genetic material found in the crop gene pool and that of wild relatives is insufficient, or the desired trait is unavailable biotechnology may be used. Genetic transformation allows a vast range of genes to be utilised, regardless of the organism they were isolated from (Miflin, 2000). This method may avoid some of the work needed to subsequently remove undesirable traits from the wild parent. However genes from a close relative, such as a wild grass species, are more likely to successfully integrate into the wheat genome, so species from the *Triticeae* tribe still provide the best option as a donor, even with the use of genetic recombination technology.

1.13.3.2 Understanding of the mechanisms of tolerance

As discussed previously, the mechanisms of plant tolerance are quite well understood, from studies on a variety of plant species. For example, aerenchyma have been identified as a possible mechanism of tolerance to waterlogging and varietal differences in ability to form aerenchyma may account for different levels of tolerance between these varieties (Huang *et al.*, 1997), so why not select for aerenchyma? Unfortunately, from a breeding point of view, waterlogging tolerance appears to be a composite of several diverse physiological and morphological traits, including aerenchyma formation, nodal root initiation, fermentation, control of cytosol pH, regulation of ROL, low RGR during waterlogging and high RGR afterwards, to speed recovery. When these must be combined with desirable agronomic traits such as high yield, disease and pest resistance and high endosperm quality it is very unlikely that a commercial wheat line, tolerant to waterlogging is possible in the near future.

1.13.3.3. Heritability of traits

To attempt to breed a waterlogging tolerant cultivar, selection traits are required. The most obvious method is to select for the best yield or smallest yield decrease after waterlogging. However grain yield itself is a complex trait, and using one complex trait to select for another is unlikely to succeed (Flowers and Yeo, 1995). In respect to salinity tolerance Barrett-Lennard *et al.* (1999) suggest using ion accumulation rates of leaf senescence as selection criteria. The problem is finding marker traits that always associate with tolerance during recombination. When simple traits, such as disease resistance, which may involve only a single resistance gene, are incorporated into crop plants from wild relatives by wide hybridisation it is relatively easy to select for them in subsequent backcrosses. In the case of a complex trait, involving many genes, such as waterlogging tolerance, selection would be virtually impossible. There is some work however to suggest waterlogging tolerance may be controlled by a small number of genes, and so could be simply heritable. Boru *et al.* (2001) found that waterlogging tolerance in wheat, measured by lower leaf chlorosis and higher yields can be inherited, and identified four genes by a series of crosses with sensitive and tolerant parents. These were dominant traits named *Wt1, Wt2, Wt3* and *Wt4.* Tolerance was additive with *Wt1*, which all tolerant lines had in common, in combination with any one of the other three, giving what was described as a high level of tolerance.

1.13.4. Breed for yield not tolerance

Richards (1983, 1995) argued, for salinity, that as tolerance is a complex trait and soils are variable, even in the same field, in the extent of the problem it is better to breed for maximum yield potential under non-stressed conditions. This is applicable to waterlogging also. As the salinity was patchy, like waterlogging, it was found that a high yield in non-stressed conditions, was able to compensate for yield loss on the poor patches (Richards, 1983). In a comparison of crop plants and tolerant wild species, it was found that the crop plants were still more productive in saline conditions, due to their faster growth rates (Richards, 1995).

1.14. REASONS FOR UNDERTAKING THIS RESEARCH

The effects of waterlogging on plant physiology and plant adaptations, both metabolic and structural are fairly well understood. However there is much less information about how affected plants interact as part of a crop canopy. The leaf architecture of cereals such as wheat is designed so that a stand of plants acts as a single canopy in resource capture, a principle articulated by the work of Scott and Monteith thirty years ago (Monteith, 1994). The study of single plants, therefore gives only a limited picture, although useful in studying plant physiology. The second major gap in knowledge is the lack of work on winter wheat varieties grown in the UK, both in looking at the effects of waterlogging and at tolerance. The most recent UK work is at least twenty years old and did not compare varieties. Therefore a series of experiments, using varieties currently available in the UK and using current agronomic practices, such as fertilizers and pesticides, is required. These experiments need to be conducted in field conditions, or as near as possible, whilst still allowing control of the waterlogging treatment imposed.

1.15. AIMS AND OBJECTIVES OF THIS PROJECT

The aims and objectives of this project were as follows:

- Investigate the effects of waterlogging on plant growth and development, with special emphasis on the effects on crop plant population. This is because many studies use single plants, whereas the yield of wheat is a result of resource capture by the canopy as a whole.

- Determine if differences in response and tolerance to waterlogging exist between varieties currently grown in the UK.

- Explain any varietal differences in response and identify characteristics to allow farmers and breeders to select more tolerant varieties.

- Study the patterns of root growth under waterlogged conditions, as wheat root systems are a neglected area of study compared to the extensive knowledge available on the shoot system.

1.16. EXPERIMENTS TO ACHIEVE THESE OBJECTIVES

Variety screening experiments in large outdoor containers and in the field reported in Chapter 2. In these experiments plants were allowed to reach maturity, and the long term effect of winter waterlogging was studied, along with the response of a range of winter wheat varieties currently grown in the UK.

Variety screening experiments at the vegetative stage in tubes in the glasshouse, reported in Chapter 3. These experiments allowed the effects of waterlogging on shoot and root growth to be studied, and compared the response of varieties during the stress period.

An experiment in lysimeters in the glasshouse to investigate the interaction between the effects of winter waterlogging and subsequent summer drought, reported in Chapter 4. Additionally the interaction with seed rate was investigated in the first season, and with variety in the second.

The interaction between the effects of delayed sowing and waterlogging was investigated in the experiment reported in Chapter 5.

A detailed study of growth and development of the root system and the effect of waterlogging on this, was made using mini-rhizotrons, reported in Chapter 6.

Chapter 2: THE TOLERANCE OF CURRENT UK WHEAT VARIETIES TO WINTER WATERLOGGING

2.1. INTRODUCTION

There has been very little recent research on the effects of waterlogging on the growth and yield of winter wheat in the UK, the last being done by Cannell, Belford and co workers at Letcombe in the late 1970's, using lysimeters buried in field plots, which described the effects of waterlogging on winter wheat (discussed in section 1.9.1). The effects of waterlogging on winter wheat and winter barley (Cannell *et al.*, 1984) and winter oats (Cannell *et al.*, 1985) were investigated, but little was done to compare differences between varieties of wheat. Additionally modern varieties may behave differently to their predecessors grown more than two decades ago, considering the advances in plant breeding in the meantime. As discussed in the literature review there is some evidence from studies in other parts of the world that differences in tolerance to waterlogging exist between varieties (Haung *et al.*, 1997; Musgrave and Ding, 1998). This suggests that it may be possible to find more tolerant varieties amongst those grown in the UK. In addition to tolerance whilst waterlogged, the ability of wheat to recover subsequently may be just as important. Some current wheat varieties are already known to possess characteristics that may allow them to do this. For example Deben has a high tillering potential, Hyno Esta and Hyno Quinta have high growth rates, associated with their hybrid nature, and Soissons has a fast development rate, due to its lower photoperiod sensitivity to switch from the vegetative to the reproductive phase of growth.

The experimental strategy was to screen as much genetic material as possible in the first season, then follow up any interesting varieties with a larger scale trial under field conditions. For this purpose an experiment was set up using plastic bins; in effect a large out-door pot experiment. All plots were waterlogged, as including drained controls would have halved the number of varieties that could be tested with the available resources. A second experiment, to investigate the effect of waterlogging at the seedling stage was also set up in tubes in the glasshouse. The results of this experiment are presented in chapter 3. The bin experiment would give information on agronomic tolerance, measured by the ability to provide the highest grain yield after waterlogging, and the tube experiment would look at the ability to sustain the highest rate of dry matter accumulation compared to drained controls, which is physiological tolerance (Setter and Waters, 2003). The results of these two experiments were then used to select five varieties, with possibly different levels of tolerance to be grown in a fully replicated trial under field conditions, including drained controls.

2.2. MATERIALS AND METHODS

2.2.1. 2001-2002 Variety screen – Experiment 1

Sixty plastic dustbins of seventy litre capacity, and 42 cm surface diameter, were filled with local sandy loam topsoil (see section 2.2.2.1) from the same location as that used in the glasshouse lysimeter experiment, described in chapter 4. Bins were 64 cm deep, to allow a reasonable volume of soil for root exploration. The experiment was set up outside, but within an area surrounded by a windbreak, which provided some shelter. This area was netted in June to exclude birds and prevent damage to the maturing ears. The soil was worked by hand to achieve a seedbed with fine tilth and seeds sown by hand using a template. The target plant population was 300 plants m^{-2}, which equated to thirty-six plants per bin. Two seeds were sown in each position and the seedlings later thinned to ensure a uniform plant population. Twenty varieties, of which seventeen were from the 2001 NIAB Recommended List, plus Xi19 and two hybrids, were used, each replicated three times. All varieties were sown on 18 October 2001. The experimental design was a randomised block design, with three blocks, with each variety represented once within each block. A summary of the varieties used is given in table 2.1 below; all are winter varieties which require vernalisation. Particular attention has been paid to growth rate, as this has been shown to affect stress tolerance in wild plants (Lambers and Poorter, 1992). Further agronomic details of the varieties are given in the 2001 NIAB list, a copy of which is included in Appendix 1.

Table 2.1. Winter wheat varieties used in the 2001-2002 variety screen experiment.

Variety	**Comments on characteristics likely to affect performance in the experiment**
Biscay	High yield potential, weak straw
Buchan	Soft endosperm, feed variety, recommended for the north of UK.
Charger	Hard endosperm, milling variety. Fast development rate
Claire	Most popular variety, good yields, good disease resistance- except mildew
Consort	Poor disease resistance, good as a 2nd wheat
Deben	High yield potential, good disease resistance, weak straw. Very high tillering, able to compensate for damage, described as a 'Stress Buster' in the farming press.
Equinox	Good yield potential.
Hereward	Lower yield, high grain protein
Hyno Esta	Fast developing hybrid
Hyno Quinta	Fast developing hybrid
Madrigal	Soft feed variety, becoming outclassed
Malacca	Milling variety, better yield but lower protein than Hereward
Napier	High tillering rate – recommended in 'second wheat' situations
Option	Group 2 milling variety, average yield.
Riband	Older variety, poor disease resistance
Savannah	High yield potential, poor disease resistance
Shamrock	Low yield potential. Waxy 'Irish green' leaves- hence name
Soissons	Fast developing, unlike all other varieties does not require >14 hours daylight to switch from vegetative to reproductive growth
Tanker	High yield potential, short stiff straw, moderate disease resistance
Xi-19	High yield potential, but also milling quality. Fast development rate (parentage includes Cadenza spring wheat). Tall straw

Sources: The Recommended Lists of Cereals 2001-4 (NIAB and HGCA).

2.2.1.1. Management

All seeds were supplied treated with 'Sibutol Secur' seed dressing containing bitertanol, fuberidazole and imidacloprid. P and K were applied at the rate of 40 kg ha^{-1} in the form of 0:24:24 fertilizer worked into the soil immediately before sowing. All crop management operations are listed below. Application rates are expressed per hectare to allow comparison, although the actual area of each bin was 0.1385 m^2. Although some varieties had slightly different rates of development crop management operations were all carried out on the same calendar date. Weeds were controlled by hand weeding. A total of 175 kg ha^{-1} of nitrogen was applied, by hand, in the form of ammonium nitrate prills (34.5% N) in two splits. The first application (2/5 split) was made on 13 March during spring tillering (approx GS25) and the second (3/5) on 23 April when the plants were approaching first node stage (GS31). BASF 3C chlormaquat was applied on 12 April using a hand sprayer at a rate equivalent to 2.25l ha^{-1} in 200-400l water at the pseudostem-erect stage (GS30). Landmark (epoxiconazole + kresoxim-methyl) was applied at the T1 timing (GS 31) on 2 May at a rate of 1L ha^{-1} along with 0.67 kg ha^{-1} Unix (cyprodinil). This was followed by 1L ha^{-1} Landmark at T2 (GS 39) on 21 May. Some eyespot (*Pseudocercosporella herpotrichoides*) lesions were noted on the stem base, forming a complex with *Fusarium,* before the application of Unix, but no white heads had appeared by harvest, indicating that the disease was controlled. Powdery mildew (*Erysiphe graminis*) was also a problem in the early spring, due to wet weather and the sheltered nature of the experimental site. However the disease did not infect the yield forming upper leaves later in the season.

2.2.1.2. Waterlogging Treatment

Two drainage holes were drilled in each bin, one at 10 cm below the soil surface and one 1cm above the soil surface. Bins were watered individually using a hose until water flowed from the lower hole, indicating that the soil water table was at 10cm below the soil surface. The upper hole was to prevent flooding by heavy rain, as the purpose of this experiment was to investigate soil waterlogging, not flooding which usually causes plant death. All other holes were sealed with rubber bungs and silicon sealant. Water was applied to all bins daily during the treatment period which was from December 14, 2001 to March 11, 2002. At the end of the waterlogging period a hole was drilled 2cm above the base of each bin to allow water to drain.

2.2.1.3. Measurements

Chlorosis of the first four leaves to emerge was measured *in situ* using a Minolta SPAD meter between January 22 and March 25, this period included the end of waterlogging and the first application of nitrogen fertilizer. Readings were taken once the leaf had fully emerged, indicated by the presence of the ligule, until the leaf had senesced, when leaves became too shrivelled to take readings. A random sample of five plants from each pot was used; each measurement was taken one third of the length from the ligule, on the upper surface.

Plots were harvested between July 19 and July 29 as each variety matured, starting with Soissons. Soissons was harvested on 19 July, Hyno Esta and Hyno Quinta on 22 July and the others between 25 and 29 July, beginning with Xi-19, Shamrock and Charger. At harvest plants were counted and cut with shears 2cm above the soil surface. All plant material was bagged and taken to the laboratory for growth analysis. Aborted tillers and small green ears from secondary tillers, not likely to produce grain by harvest, were separated out and counted. The mature ears were cut from the stems at the collar immediately below the ear and counted. A random subsample of five stems was measured to determine straw length. The ears were divided into two subsamples; the first was threshed by hand and the fresh weight of the grain measured to allow the grain moisture content to be calculated, and a 'grab sample' of 10-15 ears from the second was used for a spikelet count. The plant fractions were all bagged and dried for 48 hours in an oven at 80°C. The grain moisture subsample was weighed, the dried ears hand threshed and the grain and chaff fractions of subsamples added together. The dry weight of grain, straw, chaff and aborted/green tillers was measured. Dried grain samples were milled and the grain nitrogen content measured using the Kjeldahl method. Crude protein content of the grain was calculated by multiplying percentage nitrogen content by a factor of 5.83 (Sylvester-Bradley *et al.*, 1997).

2.2.2. 2002-2003 Field Trial - Experiment 2

Five varieties were chosen, for their differing responses to waterlogging from the previous season's variety screen; these were Claire, Deben, Hereward, Riband and Xi-19. Deben was chosen because it had the highest grain yield after being waterlogged in the bin experiment, so may be agronomically tolerant, due to its high tillering rate allowing it to compensate for damage caused by waterlogging. Claire was chosen as a control variety as its yield was the average of the twenty varieties, both mean and median, it was used in the first lysimeter experiment and it was the most widely grown variety in the UK, at the time of setting up the trial. Riband and Xi-19 yielded higher and lower respectively than expected, according to NIAB rankings, and the differences in their appearance during waterlogging suggested that they may have different levels of tolerance. Finally Hereward was selected as a variety with a low grain yield, following waterlogging. Three varieties did have lower yields; Soissons the lowest, then Shamrock and Hyno Esta. Soissons was rejected as its NIAB recommendation is only for the South and poses extra problems for crop management, due to its faster development, meaning fertilizer and agrochemical inputs could not be applied to all varieties on the same calendar date. Shamrock and Hyno Esta were not popular varieties in the UK, Shamrock subsequently losing its recommendation, and the hybrid Hyno Esta requires a lower seed rate, an extra factor that was undesirable in a comparison of varieties.

2.2.2.1. Experimental design and crop management

The site was a gentle slope running south to north, facing the Menai Strait. The previous crop was an established grass ley of several years. The soil is a fertile alluvial loam with a high content of stones (Rheidol series) classified as a Dystric Cambisol in the FAO system (Teklehaimanot and Sinclair, 1993). The topsoil is approximately 70 cm deep and overlays stones, sand and gravel, making this a well-drained site. This factor is important because achieving fully drained controls, alongside waterlogged areas, is one of the major difficulties in investigating the effects of waterlogging in a field setting (Musgrave and Ding, 1998). Plots were sown at a seed rate of 325 seeds m^{-2} using a Wintersteiger 1.2m plot drill on 30

September 2002. Plots were 10.5m long by 1.2m wide, ten rows per plot, with 12cm between rows. Plots were aligned north to south, and arranged in six randomised blocks. All varieties were treated with Sibutol-Secur seed dressing. The seedbed was prepared using a plough, followed by a Kverneland tine cultivator, and plots were rolled after drilling. Fertilizer and agrochemical applications are shown in the table below; herbicide, PGRs and fungicides were applied using a knapsack sprayer with a 1.2 m boom with four fan nozzles using recommended volumes of water, to ensure even coverage.

Table 2.2. Field trial agronomy inputs. Rates are expressed per hectare; all agrochemicals (see footnote) were applied with a knapsack and were diluted in water equivalent to 200-400 l/ha.

Calendar Date	**GS**	**Description**	**Application**
14/10/02	12/13	2nd/3rd leaf	P and K fertilizer, 40 kg/ha
15/11/02	21	Autumn tillering	Lexus herbicide (20 g/ha) to control wild turnip/charlock
12/3/03	29	Spring tillering	1st nitrogen split 2/5 of 175 kg/ha to encourage tiller survival
8/4/03	30/31	Beginning of stem extension	Unix (0.67 kg/ha) to control eyespot and powdery mildew. 3C Chlormaquat 720 (1.25 l/ha) and Moddus (0.2 l/ha) PGR
9/4/03	30/31	Beginning of stem extension	2nd nitrogen split 3/5 of 175 kg/ha to fuel grand growth phase beginning in May
6/5/03	31/32	T1 1st node, 2nd node	Landmark (1l/ha) fungicide and Moddus (0.2 l/ha) PGR
23/5/03	39	T2 flag leaf	Landmark (1 l/ha)
4/6/03	59	T3 End of ear emergence	Folicur (0.5 l/ha) ear wash to control *Alternaria* and *Fusarium* ear blight

Lexus (Dupont) contains 50% w/w Flupyrsufuron methyl
Unix (Novartis) contains 75% w/w cyprodinil
BASF 3C Chlormequat 720 (BASF) contains 720g/l chlormequat chloride
Landmark (BASF) contains 125 g/l epoxiconazole and 125 g/l kresoxim-methyl
Moddus (Syngenta) contains 250 g/l trinexapac-ethyl
Folicur (Bayer) contains 250g/l tebuconazol

2.2.2.2. Waterlogging treatment

Waterlogging treatment was applied using a watering system to irrigate areas 1.2 x 1.2 m enclosed by a bund. The watering system was made from garden hose, held in place by wooden stakes, with three 2mm holes positioned to apply water to each waterlogged plot. Bunds were made from four 1.2m lengths of 110.1 mm x 2.5 mm wooden planks wrapped in polythene sheet to ensure waterproofing. The polythene was cut longer than the length of the planks to leave an excess at each end. The planks were held together with wood screws and the excess polythene folded and stapled to waterproof the corner of each box. These boxes were partially buried so that a bund with a height of 20mm above the soil surface was formed around the waterlogged plots. Plots were considered waterlogged when standing water held by the bund at the lower side of the slope was observed. As discussed in the literature review, waterlogging may be from the bottom upwards, such as where a pan has formed, and as reproduced in closed container experiments such as the bins or the Letcombe lysimeters; alternatively it may be from top downwards, where infiltration of water into the soil is slow. It was this latter type of waterlogging that was recreated artificially, by applying water at a faster rate than it could infiltrate into the soil and by using the bunds to prevent surface runoff. Waterlogging from the bottom upwards could not be achieved, without instillation of closed lysimeters, due to the well-drained nature of the experimental site. The waterlogging period was from 17 December 2002 to 4 March 2003, although the system was turned off for a week, beginning on 6 January due to frost.

2.2.2.3. Measurements

Plots were sampled for growth analysis on 5 March 2003 just after the end of the waterlogging period. All plants in an area 15cm x 3 rows (36cm) wide were dug up and the number of plants counted. The small sample size was dictated by the need to leave enough plants inside the waterlogged boxes for another growth analysis sample at anthesis and a larger harvest sample. In the laboratory tillers were counted and all the shoot material bagged and dried in an oven at 80 °C for 48 hours. Once weighed the dried samples were milled and analysed for nitrogen content using the Kjeldahl method.

A second growth analysis was done on 6 June 2002 at anthesis. The sample size was the same as previously and plants were cut at the basal node and bagged. Green tillers with ears were separated from the dead or senescing tillers and the percentage of shoots with ears calculated. A tiller was counted as dead or dying if the youngest leaf was yellowing. A subsample of ten stems was taken and separated into ears, stems/leaf sheath and lamina. These ears were used to count spikelets, the stems to measure straw length and the lamina to measure GAI with a leaf area meter. The fractions were then bagged and dried in an oven at 80 °C for 48 hours before being weighed to calculate the partitioning of dry weight. The bulk samples were dried in the same way to calculate total biomass.

Immediately before harvest straw length from the basal node to the collar was measured as the crop was standing. Measurements were made on five stems chosen at random in each plot, and the mean of five measurements was used as a replicate when the results were analysed. Harvest was carried out between August 1 and August 6, starting with Xi-19, then Claire, and then the remaining three varieties as one block. All remaining plant material in the waterlogged boxes was harvested, along with 1m long samples across the whole width of the control areas. Waterlogging did not delay harvest. Ears were cut at the collar, bagged, weighed fresh and dried at 80°C for 48 hours, then weighed dry, a small subsample being held back to allow Hagbergs to be measured later if necessary. This subsample was also used to count spikelet number, both the total number of spikelets initiated and the number of these that had filled. Ear number per unit area was calculated by weighing a subsample of dried ears, counting the ears within it, and then multiplying by total ear DW m^{-2}/ subsample DW. Straw was cut 20mm above the soil surface and weighed fresh. A subsample was taken, weighed and dried to calculate straw moisture content and total straw dry weight. The dried ears were threshed using a Wintersteiger threshing machine. Samples of grain were weighed and run through a Tecator numigral seed counter to allow the TGW to be calculated. Dried grain and straw subsamples were milled and analysed for nitrogen content using the Kjeldahl method. The remaining portions of the plots, all grown under control conditions, were harvested using a Hege plot combine harvester. The fresh weight of grain was measured and a subsample taken and dried to calculate grain moisture content.

2.2.3. Statistical analysis

All experiments were analysed using Genstat 6. Experiment 1 was analysed using a single factor ANOVA in randomised blocks with 38 residual degrees of freedom. Experiment 2 was analysed using a two factor ANOVA without blocking with 50 residual degrees of freedom. Although the experiment was designed and sown with three randomised blocks, crow and rabbit damage to some plots at establishment meant that they were discarded, and some plots had two waterlogged boxes and control areas, maintaining the original six replicates but unbalancing the block design.

Where the appropriate ANOVA found there to be significant differences between means, the LSD was calculated based on t with P = 0.05, to compare means. LSD(t) (P = 0.05) is used in this chapter and throughout the thesis. Where there is a large number of means to compare (>10), it may be appropriate to use Q (Tukey test), to avoid type one errors. However in this thesis, where there were larger numbers of means to compare, these tend to refer to interactions, which were often not significant by ANOVA, for example the interaction between waterlogging and variety in the field experiment (10 means) was not significant, whilst the effects of waterlogging (2 means) and variety (5 means) were. In the variety trial in the bins reported in this chapter, 20 varieties were used, but there were only three replicates, so using LSD(Q) would not be sensitive enough to pick up differences between varieties, likewise the first tube experiment (chapter 3). As these two experiments were planned to identify varieties for further testing, it was thought better to have a test that was too sensitive, with the opportunity to confirm or disprove the results in later experiments, than to risk discarding potentially important data at too early a stage.

Whilst it is common practice not to present non significant interactions, these have been included in this thesis where the data fits a general trend or is otherwise interesting, for example compare the yield data in Table 2.15 to the significant trend shown in Figure 3.12.

In experiment 1 relationships between variables were analysed using simple linear regression with Genstat. For experiment 2, where there were two factors –

waterlogging and variety – simple linear regression with groups was used. First waterlogging was used as the group term, then variety.

2.3. RESULTS

2.3.1. 2001-2002 Variety Screen

2.3.1.1. SPAD Readings

The readings of leaf greenness taken with a Minolta SPAD 501 meter on the first four leaves are given in the following section. A lower reading indicates lower leaf chlorophyll and chlorosis either due to waterlogging or natural senescence. Results for the five varieties selected for the later field trial (Claire, Deben, Hereward, Riband and Xi-19) are shown graphically together with the mean for all twenty varieties. Where there were significant differences between varieties ($P<0.05$), the least significant difference (LSD) at the 5% level is shown by a vertical bar. The means of all varieties are shown in table form, as there are too many to show clearly graphically.

The first and second leaves senesced during the period of measurement as indicated by the falling readings, whilst leaf four was still emerging and so darkened as chlorophyll content increased. Differences between varieties were significant or almost significant at several sampling dates, and these are indicated by the presence of LSD bars on the graphs. The ranking of varieties was not always consistent over all leaves and sampling dates. However there appears to be a trend that Xi-19 had less greenness in the lower leaves (leaves 1 and 2) than Claire. Varieties had different rates of development, and this would affect the rate of senescence of the lower leaves. As senescence progressed, achieving accurate SPAD readings became more difficult, due to shrivelling of lamina. Additionally readings decrease very rapidly during the final stages of senescence, with completely dead lamina giving a reading of zero. The increased variation between replicates of the same variety explains the decrease in significance level of the differences between varieties; for leaf 1 (Table 2.3) differences between varieties were significant ($P = 0.001$) on the first sampling date, becoming non significant ($P = 0.095$) by the second and further decreasing in significance (P = 0.174) by the third and last sampling. The bins were drained on 11 March and the first nitrogen fertilizer application was made on 13 March, and the senescence of leaf 3 appears to be checked in response to this (Figure 2.3). This observation suggests that decreased nitrogen uptake may be the cause of senescence of the lower leaves due to waterlogging. Leaves 1 and 2 were already too far senesced by this time for the nitrogen to have an effect (Figures 2.1 and 2.2).

Table 2.3. Readings taken with a SPAD meter recording the senescence of the first leaf of twenty wheat varieties during the waterlogging period.

Variety	22/1/02	11/2/02	27/2/02
Biscay	30.3	22.0	11.5
Buchan	27.8	24.1	6.8
Charger	25.9	26.5	9.0
Claire	31.9	25.3	12.8
Consort	28.9	27.7	6.1
Deben	36.2	18.3	8.5
Equinox	29.3	19.0	13.8
Hereward	31.6	20.9	15.0
Hyno Esta	37.5	28.0	10.1
Hyno Quinta	36.5	21.3	12.5
Madrigal	33.4	28.4	13.7
Malacca	27.6	27.8	4.4
Napier	27.0	18.5	6.2
Option	34.4	22.3	8.6
Riband	35.4	29.6	6.9
Savannah	28.1	18.4	3.6
Shamrock	31.5	25.4	10.4
Soissons	24.3	15.6	10.5
Tanker	35.4	14.8	8.5
Xi 19	24.0	15.8	7.8
P	0.001	0.095	0.174
SED	3.33	5.22	3.76
LSD	6.74	ns	ns

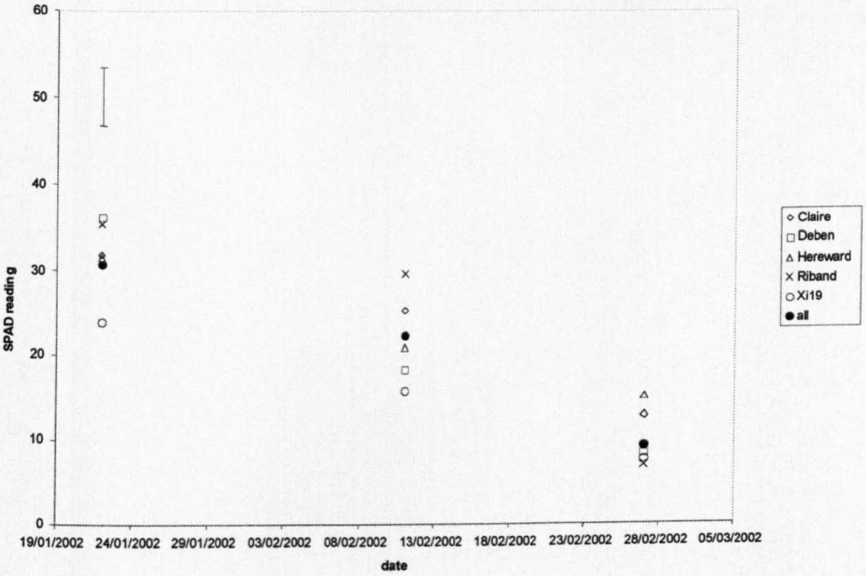

Figure 2.1. Readings taken with a SPAD meter recording the senescence of the first leaf of five selected varieties of winter wheat and the mean of all 20 varieties during the waterlogging period. The LSD(t) is shown as a bar when differences between variety were shown to be significant by ANOVA.

Table 2.4. Readings taken with a SPAD meter recording the senescence of the second leaf of twenty wheat varieties during, and after the waterlogging period.

Variety	22/1/02	11/2/02	27/2/02	12/3/02
Biscay	35.9	40.6	22.7	11.1
Buchan	38.5	33.6	15.9	10.3
Charger	41.0	31.7	33.1	13.0
Claire	37.9	36.4	27.6	16.5
Consort	36.8	30.3	16.4	6.1
Deben	41.0	36.8	24.5	6.8
Equinox	36.9	28.8	14.5	7.0
Hereward	38.7	33.7	22.5	7.5
Hyno Esta	43.8	38.4	22.0	9.6
Hyno Quinta	40.4	37.4	22.1	9.7
Madrigal	41.2	37.8	34.2	22.4
Malacca	32.0	31.0	18.7	8.4
Napier	36.6	31.6	15.5	10.0
Option	38.3	36.1	20.7	10.6
Riband	38.0	32.6	22.0	10.4
Savannah	42.1	31.4	5.8	1.9
Shamrock	40.4	36.3	26.3	18.0
Soissons	37.3	32.6	14.4	4.0
Tanker	38.0	40.4	14.7	4.7
Xi 19	34.4	33.7	13.4	11.4
P	0.003	0.064	<0.001	<0.001
SED	2.32	3.59	5.34	3.19
LSD	4.69	ns	10.81	6.56

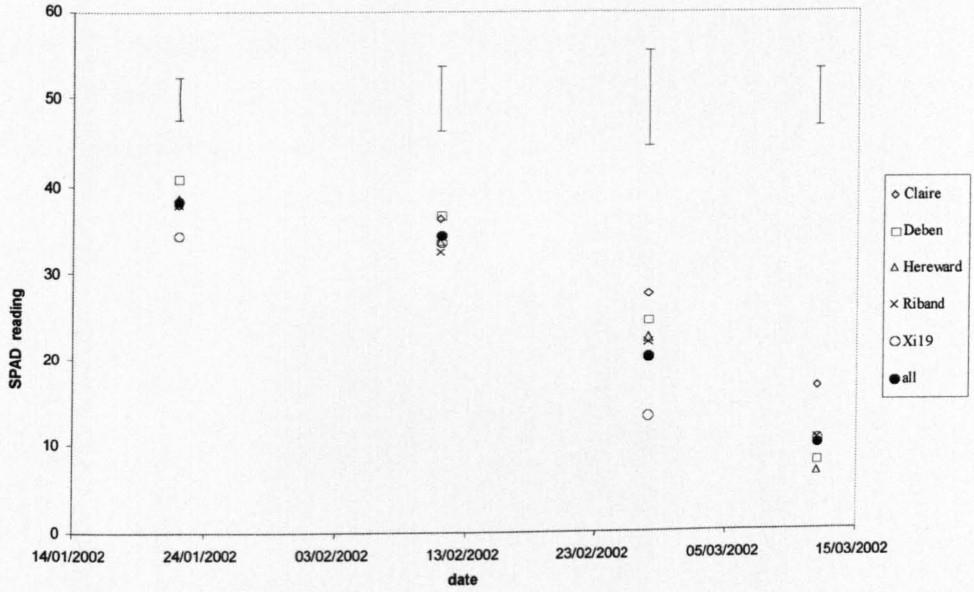

Figure 2.2. Readings taken with a SPAD meter recording the senescence of the second leaf of five selected varieties of winter wheat and the mean of all 20 varieties during and after the waterlogging period. The LSD(t) is shown as a bar when differences between variety were shown to be significant by ANOVA.

Table 2.5. Readings taken with a SPAD meter recording the senescence of the third leaf of twenty wheat varieties during, and after the waterlogging period. Waterlogging ceased on 11 March 2002.

Variety	22/1/02	11/2/02	27/2/02	12/3/02	25/3/03
Biscay	40.2	33.8	34.2	27.3	28.9
Buchan	43.1	36.4	25.0	25.5	25.4
Charger	43.4	38.9	37.7	28.3	32.3
Claire	39.9	35.7	37.9	30.9	28.3
Consort	42.9	37.3	37.8	30.0	24.6
Deben	39.0	34.7	38.3	33.6	32.4
Equinox	42.6	34.3	35.9	29.5	30.3
Hereward	39.5	37.0	34.4	27.5	30.6
Hyno Esta	43.5	34.6	36.9	24.9	24.3
Hyno Quinta	39.4	39.2	34.0	31.1	32.1
Madrigal	43.5	37.6	37.0	34.3	35.1
Malacca	38.8	34.6	27.7	26.1	27.3
Napier	39.1	34.9	32.2	22.4	28.7
Option	37.7	36.9	29.6	25.5	26.0
Riband	43.1	34.7	34.4	27.4	25.9
Savannah	41.0	36.5	31.6	28.8	31.5
Shamrock	37.6	37.5	37.5	31.0	31.3
Soissons	44.3	41.7	35.2	23.6	23.4
Tanker	46.2	38.9	34.0	28.9	25.3
Xi 19	39.0	35.2	31.9	26.5	27.8
P	0.155	0.057	0.001	0.297	0.199
SED	2.88	2.15	2.89	4.00	3.97
LSD	ns	ns	5.85	ns	ns

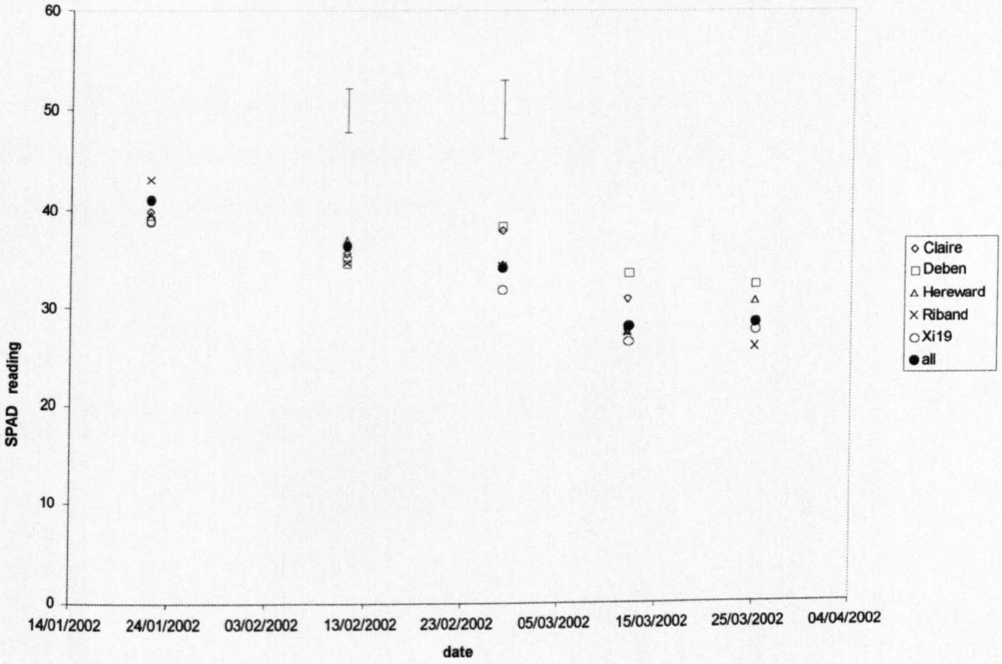

Figure 2.3. Readings taken with a SPAD meter recording the senescence of the third leaf of five selected varieties of winter wheat and the mean of all 20 varieties during and after the waterlogging period. Waterlogging ceased on 11 March 2002. The LSD(t) is shown as a bar when differences between variety were shown to be significant by ANOVA.

Table 2.6. Readings taken with a SPAD meter recording the senescence of the fourth leaf of twenty wheat varieties during, and after the waterlogging period. Waterlogging ceased on 11 March 2002.

Variety	27/2/02	12/3/02	25/3/02
Biscay	34.1	37.9	40.1
Buchan	37.7	38.8	42.1
Charger	38.3	37.1	37.8
Claire	37.5	38.6	41.5
Consort	37.9	37.7	41.6
Deben	38.4	36.1	42.9
Equinox	39.6	39.6	45.6
Hereward	36.8	35.5	36.7
Hyno Esta	35.9	34.7	37.9
Hyno Quinta	34.4	35.2	38.1
Madrigal	38.5	36.6	42.5
Malacca	36.3	36.0	38.7
Napier	32.6	35.2	37.7
Option	33.7	32.7	32.9
Riband	36.5	37.2	41.1
Savannah	37.5	36.8	42.4
Shamrock	35.9	37.7	37.3
Soissons	37.7	38.2	41.0
Tanker	37.5	39.7	40.8
Xi 19	35.4	36.5	40.1
P	<0.001	0.285	<0.001
SED	1.13	2.23	2.07
LSD	2.29	ns	4.19

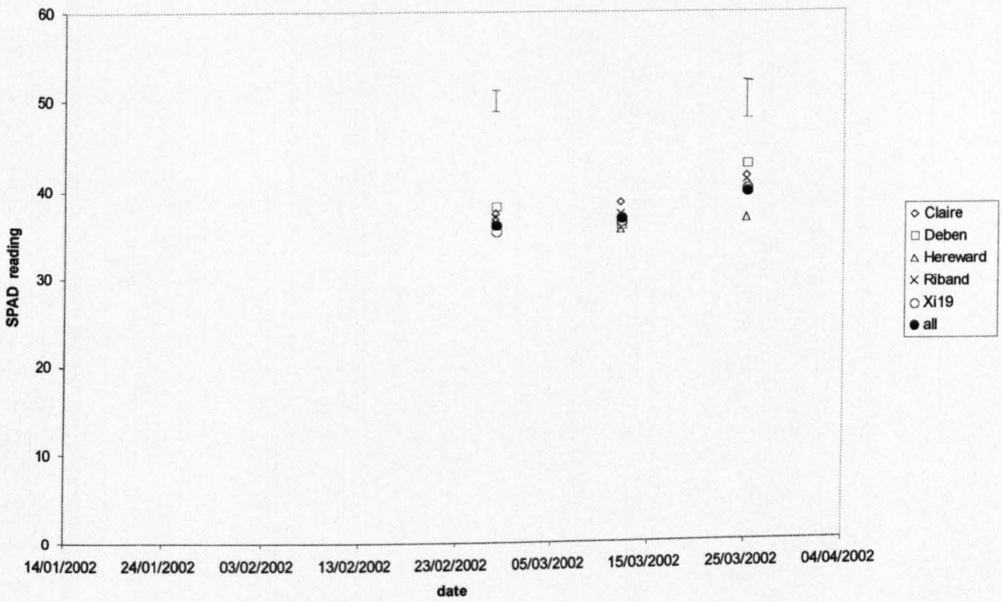

Figure 2.4. Readings taken with a SPAD meter recording the senescence of the fourth leaf of five selected varieties of winter wheat and the mean of all 20 varieties during and after the waterlogging period. Waterlogging ceased on 11 March 2002. The LSD(t) is shown as a bar when differences between variety were shown to be significant by ANOVA.

2.3.1.2. Harvest measurements

As all bins were waterlogged only the relative performance of the varieties compared with each other was measured. Varieties in bold type were selected for testing in the 2002-2003 field trial. Deben gave the highest yield and Soissons the lowest. There were significant differences between varieties in grain yield and in all yield components (Table 2.7). In general the fast developing varieties Soissons, Xi-19 and the hybrids, Hyno Esta and Hyno Quinta yielded less than would be expected.

Table 2.7. Grain yield and yield components from the variety trial, July 2002. Varieties are ranked in descending according to grain yield. Those highlighted in bold type were selected for inclusion in the field trial.

Variety	Grain DW (g/m^2)	NIAB yield rating 2002	Ears m^{-2}	Grains ear^{-1}	TGW (g)	Harvest Index %
Deben	1324	104	484	51.2	59.9	57.4
Savannah	1254	103	388	61.8	62.9	64.3
Biscay	1243	103	455	55.4	56.3	57.2
Riband	1239	99	402	59.1	59.3	58.8
Tanker	1225	104	392	63.6	56.1	58.7
Buchan	1223	99	426	63.3	51.7	56.3
Charger	1195	98	428	62.4	51.3	58.3
Madrigal	1189	101	424	60.9	52.6	58.5
Option	1182	102	479	59.0	47.8	55.4
Claire	1159	101	407	62.4	52.3	55.1
Equinox	1153	100	402	60.0	55.2	47.7
Consort	1152	101	400	61.3	53.5	57.9
Hyno Quinta	1130	-	412	53.7	58.4	52.0
Xi 19	1129	104	395	54.9	57.1	53.3
Napier	1125	104	443	54.4	53.6	55.6
Malacca	1096	98	421	57.0	52.2	56.3
Hereward	1036	90	450	50.8	51.8	51.1
Hyno Esta	1010	-	402	54.9	52.4	48.7
Shamrock	1001	94	433	52.6	50.4	52.3
Soissons	992	89	400	55.8	51.0	53.3
P	0.001		0.020	0.005	0.016	0.008
SED	71.6		6.0	3.55	3.54	3.46
LSD	144.9	4	27.4	7.18	7.17	7.00

NIAB yield data is expressed as a percentage of that for five control varieties and refers to fungicide treated from the Recommended List of Cereals 2002, LSD is quoted as 4%, P and SED are not given – see Appendix 1 (NIAB, 2002).

Of all the characteristics tested, yield potential under optimum conditions, expressed as the NIAB treated yield score, had the highest correlation with the grain yield of the varieties tested (Figure 2.5). This broad agreement with the NIAB rankings on the 2002 Recommended List suggests little interaction between waterlogging and variety, although comparisons should be treated with caution due to different growing conditions. However Riband yielded much better than expected and Xi-19 worse, and their appearance during waterlogging (Riband had low levels of leaf senescence and Xi-19 high, see SPADs) indicates this deviation from the expected may have been due to waterlogging. The weakest relationship was between ear population and yield, where the linear regression was not significant (P = 0.364). This was surprising, as waterlogging during tillering would have the greatest effect on this characteristic, and high tillering varieties might be more able to compensate. The linear regression between yield and grain number per ear was not quite significant and the correlation was weak (P = 0.007, percentage of variation accounted for = 12.5). The positive correlations between harvest index and yield (Figure 2.6), and thousand grain weight (TGW) and yield (Figure 2.7) were weak but the linear regressions were significant. Deben, Savannah and Riband had high TGW and yields, and Hereward, Shamrock and Soissons were low yielding, with small TGWs. The TGW of the varieties in this experiment were generally higher than those on the 2002 NIAB list but the relative values were in agreement, shown by the good correlation (Figure 2.8). Deben, Savannah and Riband also had high harvest indices and yields, whereas Hereward and Hyno Esta had significantly lower harvest indices and grain yields.

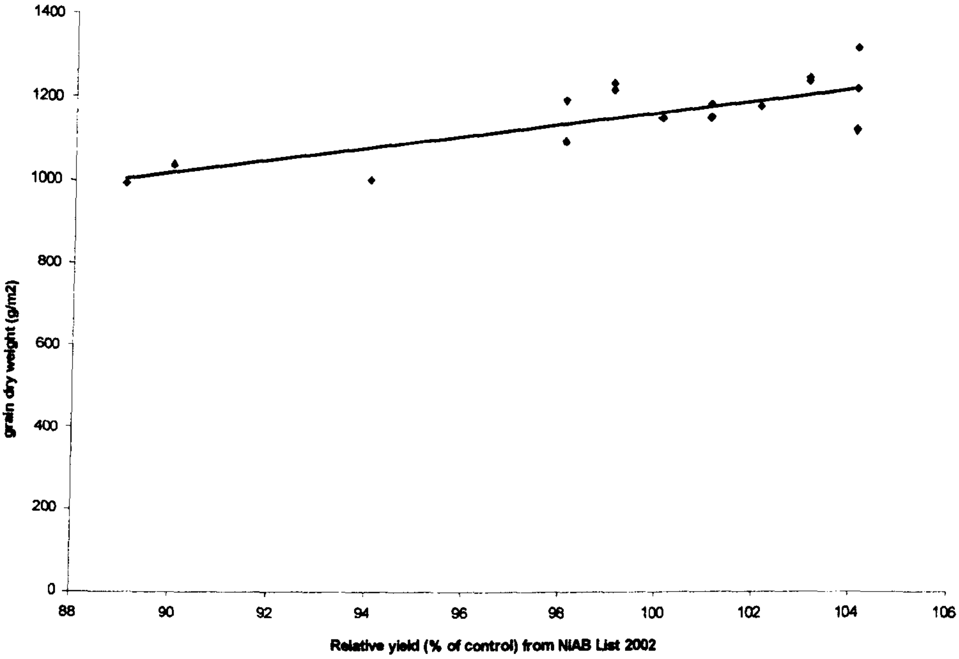

Figure 2.5. The relationship between grain yield (grain DW g/m^2) of varieties grown under waterlogged conditions during the winter months and yield potential as measured by the NIAB 2002 treated yield rating. $P<0.001$, Percentage variation accounted for by linear regression = 54.3. Fitted line $y = 14.708x - 303.64$.

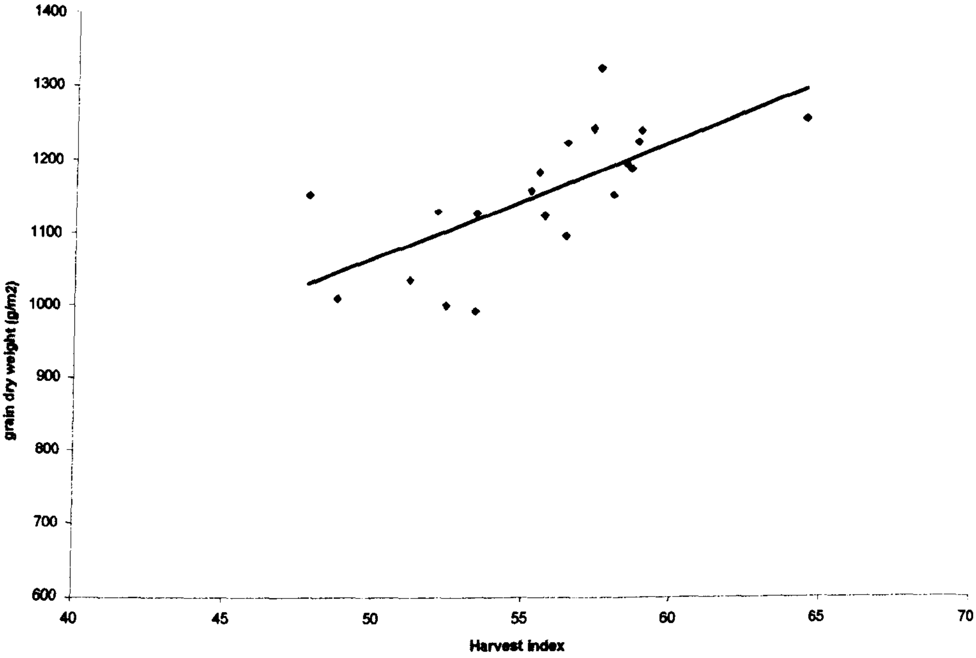

Figure 2.6. The relationship between grain yield of varieties (grain DW m^{-2}) grown under waterlogged conditions during the winter months and harvest index. $P = 0.010$, Percentage variation accounted for by linear regression = 43.1. $y = 15.85x + 275$

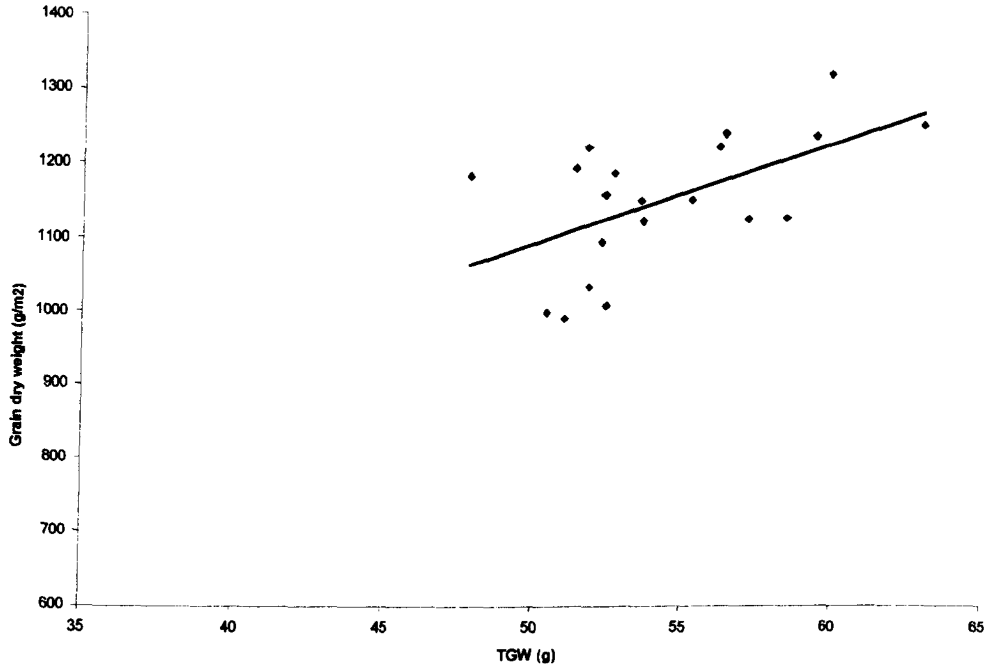

Figure 2.7. The relationship between grain yield of varieties (grain DW m^{-2}) grown under waterlogged conditions during the winter months and thousand grain weight. $P = 0.010$, Percentage variation accounted for by linear regression = 27.5. $y = 13.53x + 419$

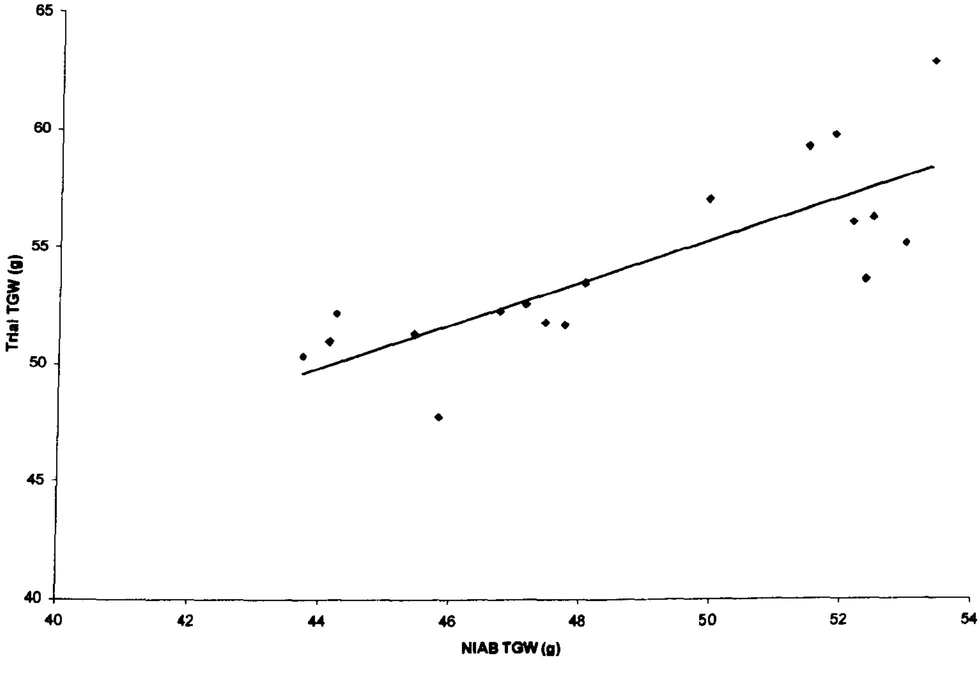

Figure 2.8. The relationship between TGW of varieties grown under waterlogged conditions during the winter months and TGW from NIAB 2002 list. $P<0.001$, Percentage variation accounted for by linear regression = 62.0. $y = 0.892x - 2.76$

There were significant differences between varieties in the number of fertile spikelets per ear, as would be expected, due to the different genotypes. There were also significant differences between varieties in straw length, with the hybrids and Xi-19 having the longest straw (Table 2.8). Tall strawed varieties also tended to have the lowest harvest index (see table 2.7). There were no significant differences between varieties in the total amount of nitrogen taken up by the crop over the season. There was a strong negative relationship between grain yield and grain crude protein percentage content (Figure 2.9). This suggested that the significant differences between varieties in grain protein were a result of dilution of nitrogen with carbohydrate in the endosperms of the higher yielding varieties. The regression between grain protein and TGW was significant but the negative relationship was not as strong (Figure 2.10), suggesting that whilst nitrogen dilution did occur in some varieties with large, starchy endosperms such as Deben, other factors were involved. For example bread making wheats such as Hereward have a genetic propensity to have higher grain protein due to the possession of more protein storage bodies in the endosperm. Grain protein was strongly correlated with the expected values from the NIAB list (Figure 2.11), but all varieties had much lower grain protein content than would be expected (NIAB, 2002). This was most likely due to the low nitrogen fertilizer input (175 kg ha^{-1}) and the high yield (mean for all varieties was the equivalent of 13.25 t ha^{-1}). The differences between varieties in protein content were not as great as would be expected, suggesting that waterlogging or some other factor, for example the low nitrogen application, had a levelling effect.

Table 2.8. Number of fertile spikelets per ear, straw length, grain protein content and total uptake of nitrogen of twenty winter wheat varieties at harvest, July 2002.

Variety	Filled spikelets ear^{-1}	Average straw length cm	Grain protein % (= %N of DW x 5.83)	N uptake g m^{-2}
Deben	20.4	59.5	6.86	15.6
Savannah	19.3	61.5	7.25	15.6
Biscay	19.8	62.8	7.01	14.9
Riband	19.4	62.3	7.28	15.4
Tanker	20.4	52.9	7.80	16.4
Buchan	19.6	57.6	7.81	16.4
Charger	18.6	58.3	7.85	16.0
Madrigal	20.1	56.0	7.57	15.4
Option	20.5	61.9	7.73	15.7
Claire	25.0	58.9	7.78	15.4
Equinox	22.1	56.7	7.96	15.7
Consort	19.6	58.1	8.18	16.1
Hyno Quinta	18.0	72.9	7.97	15.4
Xi 19	21.2	67.5	8.22	15.9
Napier	21.5	55.7	8.04	15.5
Malacca	18.8	59.9	8.17	15.4
Hereward	21.5	60.9	8.72	15.4
Hyno Esta	19.1	73.3	7.78	13.4
Shamrock	17.9	53.6	9.19	15.7
Soissons	17.5	65.7	8.83	15.0
P	<0.001	<0.001	0.001	0.700
SED	0.72	2.61	0.439	0.99
LSD	1.45	5.27	0.889	ns

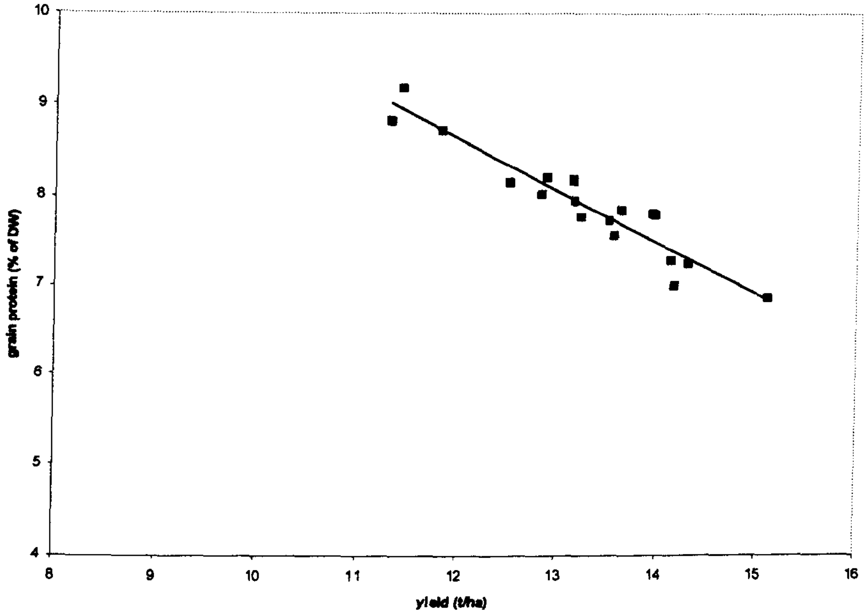

Figure 2.9. The relationship between grain protein concentration of winter wheat varieties grown under waterlogged conditions during the winter months, and grain yield. P < .001, Percentage of variation accounted for by linear regression = 90.0%. y = -0.5731x + 15.496

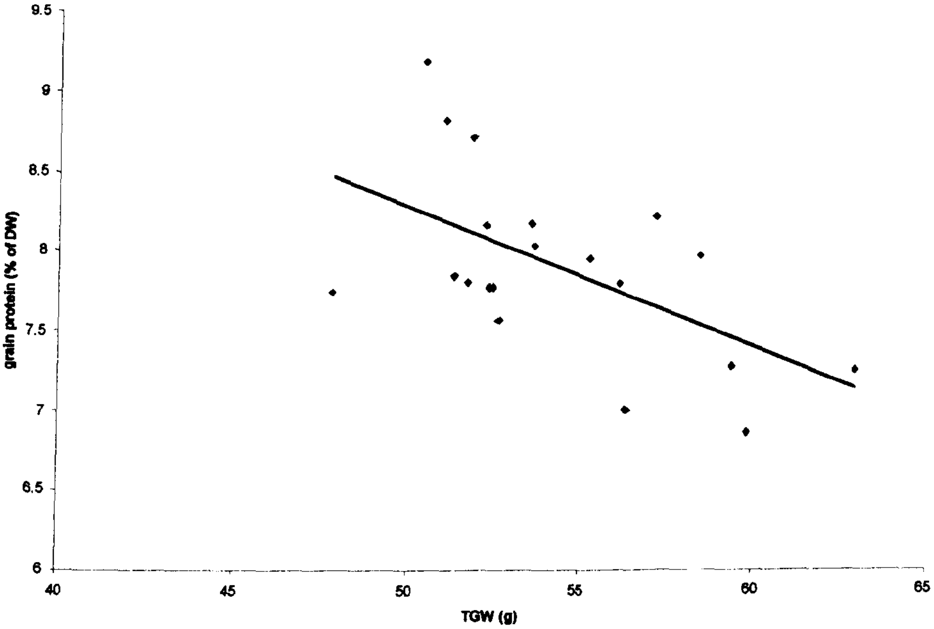

Figure 2.10. The relationship between grain protein concentration of winter wheat varieties grown under waterlogged conditions during the winter months, and TGW. P = 0.008, Percentage of variation accounted for by linear regression = 29.5 %. y = -0.0886x + 12.71

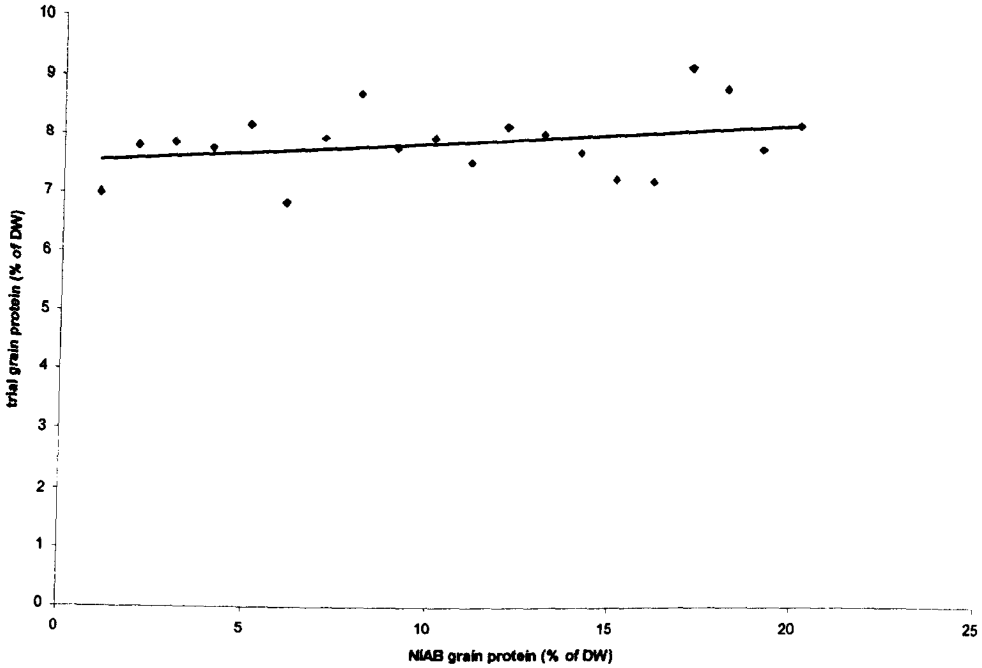

Figure 2.11. The relationship between grain protein concentration of winter wheat varieties grown under waterlogged conditions during the winter months, and their potential grain protein value in the 2002 NIAB Recommended List. $P < 0.001$, Percentage of variation accounted for by linear regression = 61.9%. $y = 0.892x - 2.76$

2.3.2. Field experiment

The experiment was sown during a dry spell in early autumn 2002. The first significant rainfall was on 11 October 2002. Thereafter the remainder of October and November were exceptionally wet. There was a prolonged dry spell during February, March and April 2003, but increased rainfall in May (Figure 2.12). This much-needed rain prevented the plants suffering from drought during ear emergence so spikelet fertility was not affected. Very dry, hot weather in August speeded ripening, but plants did not show drought symptoms (leaf curling) during grain filling. Indeed the plants appeared to cope well with the dry conditions late in the season, possibly because the dry spell in spring had encouraged deep rooting.

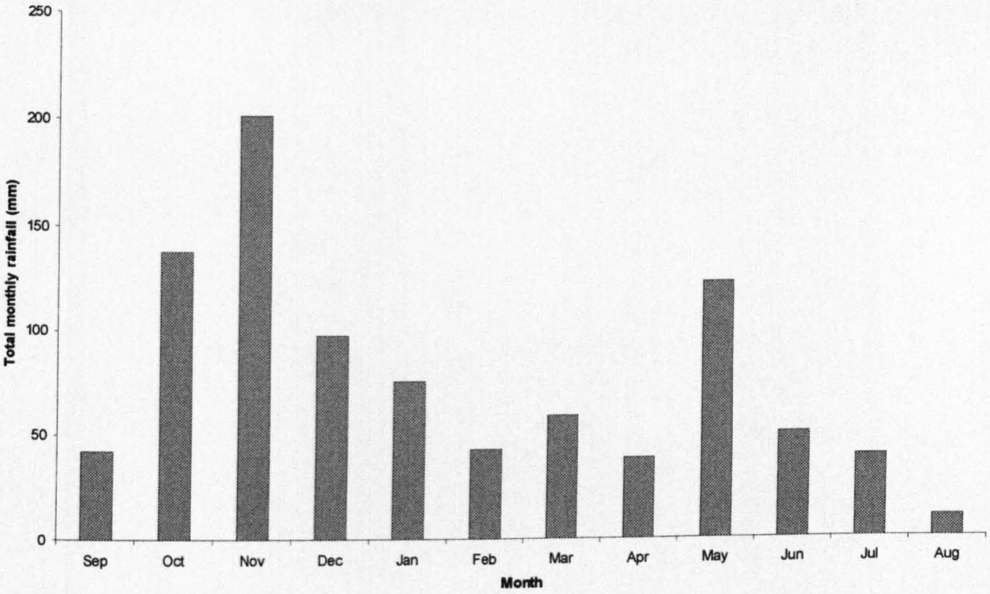

Figure 2.12. The total rainfall for each month of the 2002-2003 growing season. The experiment was sown on 30 September 2002 and harvested between 1 and 6 August 2003.

2.3.2.1. Growth analysis at the end of waterlogging 4/3/03

Waterlogging significantly decreased the post winter plant population. Whilst there were no significant differences between the varieties, Xi-19 and Hereward had the highest surviving plant population post waterlogging, and Deben the smallest number of plants. Both Hereward and Xi-19 have an erect growth habit, hence less inter plant competition, whilst Deben has a planoform growth habit. Waterlogging decreased the number of shoots per square metre by a significant decrease in the plant population, but had no effect on the number of tillers per plant. There were significant differences between the varieties in both the number of shoots per area and per plant; Riband had the most and Xi-19 the least in both cases. Waterlogging decreased the total shoot biomass per unit area by almost half, as a result of the decrease in plant and shoot populations and a significant decrease in the dry weight per plant and per shoot. Although there was no significant interaction between variety and waterlogging, Xi-19 had the smallest percentage reduction in biomass but appeared least healthy, that was in agreement with increased senescence of lower leaves observed using a SPAD meter in the 2001-2002 variety screen (see Tables 2.3 and 2.4 and Figures 2.1 and 2.2).

Table 2.9. The effect of winter waterlogging on plant measurements taken at the end of the waterlogging period.

	Plants m^{-2}	Shoots m^{-2}	Shoots $plant^{-1}$	Shoot DW g m^{-2}	DW g $plant^{-1}$	DW mg $shoot^{-1}$
Waterlogging						
Control	302	1625	5.5	136.5	0.46	90
Waterlogged	241	1290	5.5	77.3	0.32	62
Variety						
Claire	261	1299	5.1	97.0	0.37	74
Deben	239	1309	5.6	108.5	0.44	82
Hereward	295	1559	5.4	106.9	0.36	67
Riband	272	1935	7.3	110.9	0.40	56
Xi-19	292	1185	4.3	111.5	0.39	99
Interaction						
Claire C	284	1485	5.3	118.7	0.42	79
Claire W	238	1114	4.8	75.4	0.32	68
Deben C	272	1454	5.5	140.4	0.53	97
Deben W	207	1164	5.6	76.5	0.36	67
Hereward C	330	1744	5.4	140.8	0.43	82
Hereward W	259	1374	5.4	72.9	0.29	53
Riband C	306	2228	7.6	149.7	0.50	68
Riband W	238	1642	7.1	72.0	0.31	44
Xi-19 C	318	1216	4.0	133.1	0.43	122
Xi-19 W	265	1154	4.5	89.8	0.34	77
P						
Waterlogging	<0.001	<0.001	0.929	<0.001	<0.001	<0.001
Variety	0.219	<0.001	<0.001	0.279	0.279	<0.001
Interaction	0.988	0.313	0.869	0.666	0.666	0.546
SED						
Waterlogging	16.8	76.6	0.33	693	0.025	6.1
Variety	26.6	120.7	0.53	10.96	0.040	9.7
Interaction	37.6	170.7	0.75	15.5	0.057	13.7
LSD						
Waterlogging	33.8	153.3	ns	13.92	0.051	12.3
Variety	ns	242.4	1.06	ns	ns	19.4
Interaction	ns	ns	ns	ns	ns	ns

Waterlogging significantly decreased the percentage nitrogen content of the shoot system, causing chlorosis of older leaves. There were also significant differences between varieties. Xi-19 and Deben had the lowest nitrogen content after waterlogging, probably as these larger plants (Table 2.9) had a higher demand for N, which could not be met by the restricted root system. In contrast Riband and Claire produced smaller plants after waterlogging so there was less dilution of N. Waterlogging decreased the total uptake of nitrogen by half, but there were no significant differences between varieties or a significant interaction.

Table 2.10. The effect of winter waterlogging on the nitrogen percentage content and total uptake of samples taken at the end of the waterlogging period.

	% N content of shoots	Uptake of N gm^{-2}
Waterlogging		
Control	3.74	5.11
Waterlogged	3.47	2.67
Variety		
Claire	3.64	3.59
Deben	3.55	3.88
Hereward	3.59	3.84
Riband	3.84	4.35
Xi-19	3.39	3.79
Interaction		
Claire C	3.85	4.59
Claire W	3.44	2.58
Deben C	3.64	5.11
Deben W	3.46	2.65
Hereward C	3.56	5.06
Hereward W	3.62	2.63
Riband C	4.05	6.07
Riband W	3.64	2.63
Xi-19 C	3.57	4.75
Xi-19 W	3.20	2.84
P		
Waterlogging	<0.001	<0.001
Variety	0.006	0.478
Interaction	0.193	0.395
SED		
Waterlogging	0.074	0.266
Variety	0.117	0.420
Interaction	0.165	0.594
LSD		
Waterlogging	0.149	0.534
Variety	0.235	ns
Interaction	ns	ns

2.3.2.2. Growth analysis at anthesis

Waterlogging significantly decreased the number of ears per unit area, but there was no effect on the number of ears per plant (Table 2.11). Differences in ear number per unit area were significant between varieties but there was no significant interaction between treatment and variety, with Deben and Xi19 having the highest and lowest ear numbers, respectively, for both treatments. There was some compensation by increased tillering efficiency of waterlogged plants, with a smaller proportion of the total number of tillers initiated being aborted. There was a significant interaction between treatment and variety (P=0.014), with Riband (control) having a particularly poor efficiency. It was the highest tillering variety in March but only the fourth highest in terms of ear number in June. There was a significant decrease due to waterlogging in total dry matter accumulated (Table 2.11); a result of the lower shoot number, a reduction in resource capture by the smaller canopy, and the reduction in straw length. The measurement of green area at anthesis was based on green leaf area only. Although excluding green ears (they would not fit through the machine) does not give an accurate absolute measurement, a relative comparison between treatments and varieties could still be made. Waterlogging significantly reduced GAI and there were significant differences between varieties (Table 2.12). Deben had the largest GAI and Riband the smallest. Riband was badly affected by *Septoria tritici* whilst Deben has good resistance in addition to waterlogging tolerance and high tillering. The reduction due to waterlogging can partly be explained by the reduction in shoot number and partly due to decreased leaf area per shoot. (The latter was only significant when Riband was excluded from the analysis as *Septoria* had more severely affected the denser control canopy, falsely suggesting that waterlogging increased green area per shoot. The results of the analysis excluding Riband are included in brackets). The reduction in green leaf area per shoot can be explained in relation to the decreased uptake of nitrogen caused by waterlogging. There was no effect of waterlogging on dry weight per plant or per surviving shoot (Table 2.12), in contrast to the samples taken just after waterlogging. There was a significant shortening of straw caused by waterlogging but no differences between varieties. Whilst Xi19 and Deben would be expected to be taller, a robust PGR programme appears to have evened out varietal differences. There was an increase in the dry weight per unit length of straw due to waterlogging (Table 2.12).

Table 2.11. The effect of winter waterlogging on shoot biomass and tiller production of five winter wheat varieties at anthesis. Analysis was done on transformed values for tilling efficiency, measured as the percentage of shoots to have formed an ear.

	Total DW m^{-2} (g)	Ears $plant^{-1}$	Total shoots m^{-2}	Ears m^{-2}	% shoots with ears (sq rt)
Waterlogging					
Control	1999	2.70	903	781	86.9 (9.31)
Waterlogged	1525	2.69	657	602	92.0 (9.59)
Variety					
Claire	1631	2.65	741	659	89.0 (9.43)
Deben	1933	3.52	903	818	90.6 (9.52)
Hereward	1876	2.61	833	747	90.4 (9.50)
Riband	1651	2.40	770	631	84.1 (9.16)
Xi-19	1718	2.29	654	603	93.0 (9.64)
Interaction					
Claire C	1899	2.86	870	769	88.2 (9.38)
Claire W	1363	2.45	611	549	90.0 (9.49)
Deben C	1997	3.17	951	855	90.3 (9.50)
Deben W	1870	3.86	855	781	91.0 (9.54)
Hereward C	2235	2.66	997	873	88.2 (9.39)
Hereward W	1518	2.57	670	620	92.5 (9.62)
Riband C	1900	2.47	954	731	76.3 (8.73)
Riband W	1402	2.32	586	531	92.0 (9.59)
Xi-19 C	1966	2.35	744	676	91.5 (9.56)
Xi-19 W	1470	2.23	565	531	94.6 (9.72)
P					
Waterlogging	<0.001	0.934	<0.001	<0.001	0.001
Variety	0.223	0.005	0.004	0.002	0.006
Interaction	0.457	0.557	0.221	0.555	0.014
SED					
Waterlogging	99.9	0.210	40.5	36.0	0.080
Variety	158.0	0.332	64.0	56.9	0.127
Interaction	223.4	0.470	90.5	80.4	0.179
LSD					
Waterlogging	200.7	ns	81.3	72.3	0.161
Variety	ns	0.667	128.5	114.3	0.254
Interaction	ns	ns	ns	ns	0.359

Table 2.12. The effect of winter waterlogging on green area, straw growth and dry weight of five winter wheat varieties at anthesis. Data in parentheses are means excluding Riband (see text for explanation).

	GAI Leaves only	Green leaf area /shoot (cm^2) (*-Riband*)	Straw Length cm	Straw DW mg cm^{-1}	DW g $plant^{-1}$	DW per Viable tiller
Waterlogging						
Control	6.10	78.7(*79.8*)	62.4	27.4	6.87	2.5
Waterlogged	4.51	74.9(*74.4*)	56.6	29.9	6.78	2.5
Variety						
Claire	4.95	74.6	57.7	28.1	6.50	2.4
Deben	6.49	79.8	57.7	27.2	8.31	2.3
Hereward	5.45	73.1	59.9	27.8	6.45	2.4
Riband	4.73	75.6	61.2	29.1	6.28	2.5
Xi-19	4.89	80.9	61.1	31.2	6.51	2.8
Interaction						
Claire C	5.91	76.3	59.2	27.4	6.97	2.4
Claire W	3.99	72.8	56.2	28.7	6.02	2.4
Deben C	7.12	84.3	61.6	24.8	7.34	2.3
Deben W	5.87	75.3	53.8	29.5	9.28	2.3
Hereward C	6.37	73.3	61.5	28.2	6.84	2.5
Hereward W	4.53	72.9	58.3	27.4	6.24	2.4
Riband C	5.35	74.5	66.3	26.2	6.43	2.5
Riband W	4.10	76.6	56.1	32.0	6.13	2.6
Xi-19 C	5.73	85.1	63.5	30.6	6.79	2.9
Xi-19 W	4.05	76.8	58.6	31.8	6.24	2.7
P						
Waterlogging	<0.001	0.117(*0.036*)	<0.001	0.008	0.868	0.84
Variety	0.003	0.192(*0.078*)	0.129	0.056	0.141	0.00
Interaction	0.921	0.518(*0.553*)	0.205	0.128	0.488	0.65
SED						
Waterlogging	0.229	2.41 (*2.46*)	1.13	0.89	0.555	0.07
Variety	0.473	3.81 (*3.48*)	1.78	1.40	0.877	0.11
Interaction	0.669	5.39 (*4.91*)	2.52	1.99	1.240	0.16
LSD						
Waterlogging	0.601	ns (*4.97*)	2.27	1.78	ns	n
Variety	0.950	ns (*ns*)	ns	ns	ns	0.14
Interaction	ns	ns (*ns*)	ns	ns	ns	n

There was no significant decrease in nitrogen percentage of the leaves and stems, unlike the previous growth analysis, just after the end of waterlogging period. There was a small but significant decrease in the nitrogen percentage content of the ears.

Table 2.13. The effect of winter waterlogging on nitrogen content of anthesis samples

	N content as % of lamina DW	N in lamina (gm^{-2})	N content as % of stem DW	N in stems (gm^{-2})	N content as % of ear DW	N in ears (gm^{-2})	N uptake (kg /ha)
Waterlogging							
Control	2.76	8.36	0.79	10.32	1.47	5.27	239
Waterlogged	2.71	6.12	0.76	7.40	1.39	4.07	174
Variety							
Claire	2.72	6.84	0.84	8.98	1.42	4.44	203
Deben	2.61	8.46	0.69	8.64	1.42	4.74	215
Hereward	2.54	7.01	0.69	8.45	1.36	4.84	203
Riband	3.09	7.00	0.93	10.01	1.49	4.45	215
Xi-19	2.71	6.86	0.74	8.23	1.47	4.89	200
P							
Waterlogging	0.510	<0.001	0.471	<0.001	0.019	<0.001	<0.001
Variety	<0.001	0.177	0.006	0.402	0.064	0.713	0.897
Interaction	0.499	0.982	0.691	0.887	0.879	0.805	0.988
SED							
Waterlogging	0.065	0.481	0.046	0.616	0.031	0.264	12.27
Variety	0.103	0.760	0.073	0.974	0.048	0.418	19.40
Interaction	0.145	1.075	0.103	1.378	0.068	0.591	27.43
LSD							
Waterlogging	ns	0.966	ns	1.237	0.061	0.531	24.65
Variety	0.206	ns	0.146	ns	ns	ns	ns
Interaction	ns	ns	ns	ns	ns	ns	ns

The percentage of the final above ground biomass at maturity, which had been accumulated at each of the growth analysis timings, was calculated. The total biomass accumulated by final harvest at maturity is underestimated, due to the loss of aborted tillers and dead lower lamina, which slough off and rot on the soil surface. Additionally the smaller size of the sampling areas in the two pre-harvest growth analyses tends to lead to an overestimation. Hereward had a 'leafy' growth habit and a poor efficiency in converting green area into grain yield (see Figure 2.15), and all these factors appear to have combined to falsely suggest that this variety actually loses biomass between anthesis and maturity. Data for Hereward that is misleading in this way is presented in italics (Table 2.14). The data in table 2.14 suggests that the reductions in dry weight of waterlogged plants noted at the end of waterlogging and at anthesis were at least partly due to delayed development as seen in the lysimeter (Chapter 4) and sowing date (Chapter 5) experiments, as the waterlogged plants had achieved a smaller proportion of their final biomass. Plants in the previously waterlogged areas appeared to begin anthesis 2-3 days after the controls of the same variety. As growth during the grand growth phase may be between 20 g/m^2 and 50 g/m^2 per day (Sylvester-Bradley *et al.*, 1997) a delay in development of only a couple of days could cause there to be a significant reduction in dry weight of waterlogged plots compared with controls. The effect of waterlogging in delaying development is shown by the shift to the right of the growth curve (Figure 2.13). Although there are not enough data points to fit a curve, the accumulation of dry matter in wheat has been previously established by numerous workers.

Table 2.14. The effect of winter waterlogging on dry matter accumulation during the growing season

	DW g m^{-2} at harvest	% accumulated by end water-logging	% accumulated by anthesis
Waterlogging			
Control	2161	6.4	94.8
Waterlogged	1943	4.0	78.5
Variety			
Claire	2134	4.5	76.8
Deben	2247	4.8	86.2
Hereward	1885	5.7	*102.0*
Riband	1988	5.5	83.1
Xi-19	2007	5.5	85.1
Interaction			
Claire C	2193	5.4	87.8
Claire W	2076	3.6	65.8
Deben C	2387	5.9	83.9
Deben W	2106	3.6	88.6
Hereward C	1948	7.5	*120.8*
Hereward W	1822	4.0	83.2
Riband C	2165	7.0	88.7
Riband W	1811	4.0	77.6
Xi-19 C	2113	6.3	92.9
Xi-19 W	1900	4.8	77.4
P			
Waterlogging	<0.001	<0.001	0.007
Variety	0.001	0.204	0.095
Interaction	0.593	0.459	0.234
SED			
Waterlogging	0.1	0.385	5.77
Variety	0.1	0.609	9.12
Interaction	0.1	0.862	12.9
LSD			
Waterlogging	0.109	0.774	11.6
Variety	0.172	ns	ns
Interaction	ns	ns	ns

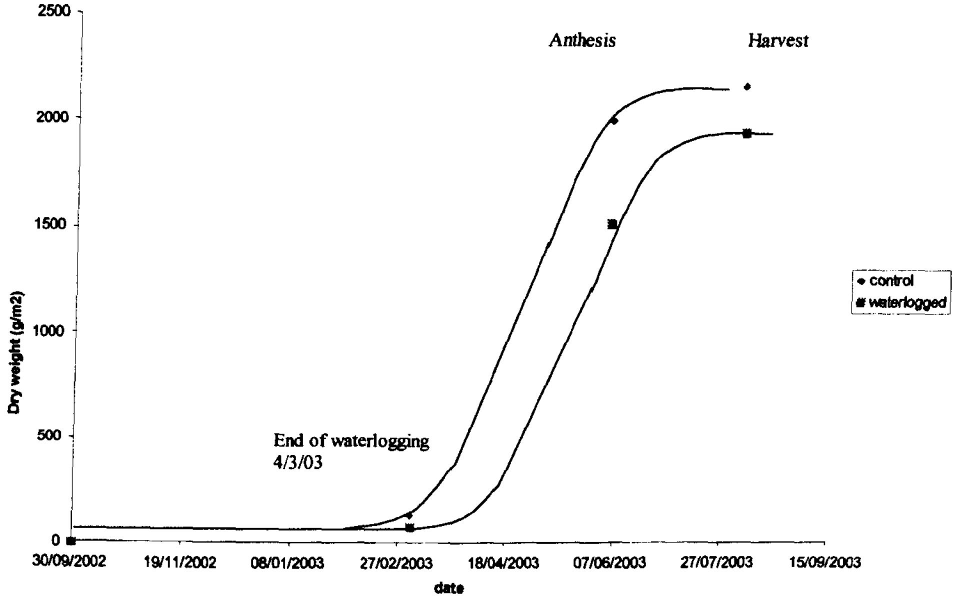

Figure 2.13. Mean dry weight accumulation during the growing season of five varieties of winter wheat, grown under waterlogged or control conditions. The curves were fitted by eye. The percentage decrease in total dry weight at the end of waterlogging, anthesis and maturity respectively were: mean of all varieties = 43.4, 23.8, 10.1, Claire = 36.5, 28.2, 5.3, Deben = 45.5, 6.2, 11.8, Hereward 48.7, 32.1, 6.4, Riband = 51.9, 26.2, 16.4 and Xi-19 = 32.6, 25.3, 10.1.

2.3.2.3. Harvest results

Waterlogging significantly (P = 0.001) decreased grain yield at harvest. There were significant differences in grain yield between varieties, with Deben having a significantly greater yield than all varieties except Claire, and Hereward having a significantly smaller yield than all other varieties. There was no significant interaction between waterlogging and variety, but Hereward showed a much smaller decrease in yield due to waterlogging than all the other varieties. Of the yield components waterlogging decreased ear number per area but had no effect on TGW or the number of grains per ear. There were significant differences between varieties in all these characteristics, but no significant interaction between waterlogging and variety. Deben and Claire had a significantly higher ear population than the other three varieties, and Deben and Xi-19 had a significantly larger TGW. Riband and Xi-19 had significantly more grains per ear than Deben or Hereward. The linear regression between ear population at harvest and grain yield at harvest was significant ($P < 0.001$), and the addition of waterlogging treatment to the model did not result in a significant increase in the variation accounted for by the model. This was to be expected, given that waterlogging did not significantly affect the other yield components – TGW and grain number per ear. The addition of variety improved the model significantly ($P<0.001$) and increased the variation accounted for by the model from 53.1% to 73%, with the relationship for Hereward being significantly different from the other varieties. For Hereward the relationship between ear number and yield appeared stronger than the other varieties, possibly because of its low TGW and fewer grain sites per ear meant that this variety had less potential to compensate for lower ear populations by increasing the yield of grain per ear. The regressions between TGW, grain number per ear and yield were not significant, and so were not plotted.

Table 2.15. Yield and yield components of five winter wheat varieties grown in drained or waterlogged conditions during the winter months.

	Yield (t/ha)	Ears m^{-2}	TGW (g)	Grains /ear
Waterlogging				
Control	13.3	542	54.2	40.5
Waterlogged	12.2	478	54.6	41.7
Variety				
Claire	13.4	562	51.6	41.2
Deben	14.2	578	57.2	37.9
Hereward	10.7	473	52.1	39.1
Riband	12.6	485	52.8	43.5
Xi-19	12.8	453	58.3	43.6
Interaction				
Claire C	13.9	584	51.3	41.3
Claire W	13.0	540	51.8	41.1
Deben C	15.1	614	56.8	38.2
Deben W	13.3	542	57.6	37.6
Hereward C	10.9	481	52.8	39.2
Hereward W	10.6	465	51.3	39.0
Riband C	13.3	520	52.5	42.8
Riband W	11.9	449	53.1	44.3
Xi-19 C	13.5	512	57.7	40.9
Xi-19 W	12.0	395	59.0	46.4
P				
Waterlogging	0.001	0.003	0.472	0.404
Variety	<0.001	<0.001	<0.001	0.048
Interaction	0.690	0.588	0.475	0.655
SED Waterlogging				
Variety	0.33	20.0	0.50	1.44
Interaction	0.52	31.7	0.79	2.27
	0.73	44.8	1.12	3.21
LSD				
Waterlogging	0.66	40.3	ns	ns
Variety	1.04	63.7	1.59	4.56
Interaction	ns	ns	ns	ns

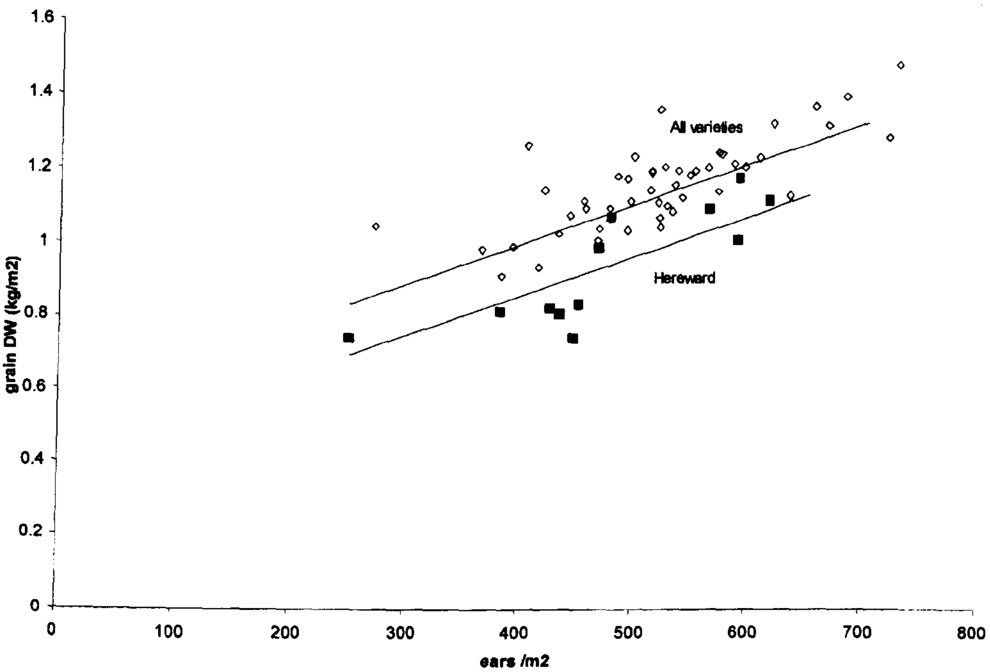

Figure 2.14. The relationship between grain yield and ear number m^{-2} of five varieties of winter wheat grown in drained and waterlogged conditions. $P < 0.001$, percentage of variation accounted for by single linear regression = 53.1 %. Addition of variety to model was significant ($P < 0.001$) and accounted for 73% of variation. Hereward $y = 0.00192x + 0.4245$, other varieties $y = 0.001092 + 0.5646$

Waterlogged plants had a slightly higher dry weight of grain per plant, as compensation for the lower plant population. There was no significant effect of waterlogging on grain dry weight per ear, therefore the increase was due to a higher number of ears of waterlogged plants. This did appear to occur, although the difference was not quite significant ($P = 0.077$). There were significant differences between varieties; Deben had the largest grain dry weight per plant due to it having the most ears per plant, Hereward had the smallest grain yield per plant, the smallest grain weight per plant and the least ears per plant. There was no significant interaction between waterlogging and variety. Waterlogging had no effect on the number of spikelets initiated per ear or the number of these that produced grain. There were significant differences between varieties, and Claire had the greatest number of spikelets per ear. It was observed that whilst Claire had evenly sized ears, with a consistent number of spikelets, the ears of Xi-19 fell into two discrete groups.

Primary tillers produced in autumn had up to 28 spikelets per ear, in contrast to the secondary tillers, which appeared in spring, which had 14/16 spikelets. There was no significant effect of waterlogging or variety on the number of fertile florets that produced a grain, per spikelet.

Table 2.16. The effect of winter waterlogging on grain dry weight per plant, per ear, ear number per plant, and spikelet counts.

	Grain DW g/plant	Grain DWg/ear^{-1}	Ears /plant	Filled spikelets	Initiated spikelets	Grains /filled spikelet
Waterlogging						
Control	4.06	2.19	1.9	20.5	23.7	1.99
Waterlogged	4.73	2.28	2.1	20.4	23.6	2.06
Variety						
Claire	4.71	2.12	2.3	22.6	25.4	1.82
Deben	5.40	2.17	2.5	18.8	21.4	2.03
Hereward	3.38	2.04	1.7	20.6	24.8	1.93
Riband	4.36	2.30	1.9	19.5	21.8	2.24
Xi-19	4.18	2.54	1.7	20.9	24.6	2.12
P						
Waterlogging	0.026	0.286	0.077	0.824	0.799	0.467
Variety	0.001	0.002	<0.001	<0.001	<0.001	0.080
Interaction	0.953	0.436	0.627	0.790	0.655	0.814
SED						
Waterlogging	0.290	0.081	0.13	0.418	0.451	0.097
Variety	0.459	0.127	0.20	0.661	0.713	0.153
Interaction	0.649	0.180	0.30	0.935	1.008	0.216
LSD						
Waterlogging	0.583	ns	ns	ns	ns	ns
Variety	0.922	0.256	0.41	1.328	1.432	ns
Interaction	ns	ns	ns	ns	ns	ns

Waterlogging decreased straw length and there was also a significant interaction between waterlogging and variety, Xi-19 having the greatest decrease. Waterlogging increased the weight per length of the straw. The effect of waterlogging on moisture content of the crop was not significant, although the straw of waterlogged plants appeared to contain higher moisture content. The straw of Hereward had a high moisture content, explained by a characteristic of this variety observed in the field, which is to retain green areas of the lamina and at the stem nodes, even when the grain is mature.

Table 2.17. The effect of winter waterlogging on straw measurements at harvest and moisture content of ears and straw.

	Straw length /cm	Straw density mg/cm	Ear % moisture	Straw % moisture
Waterlogging				
Control	72.4	19.7	13.4	21.5
Waterlogged	64.1	21.8	13.9	24.3
Variety				
Claire	66.8	19.6	15.1	17.3
Deben	69.5	19.5	11.8	22.9
Hereward	66.9	22.6	11.3	32.6
Riband	69.4	20.0	11.6	20.1
Xi-19	68.5	21.7	18.4	21.6
Interaction				
Claire C	69.7	18.6	14.9	17.2
Claire W	64.0	20.7	15.2	17.4
Deben C	72.6	18.7	11.7	22.2
Deben W	66.4	20.3	11.9	23.6
Hereward C	70.4	22.5	11.2	29.2
Hereward W	63.3	22.6	11.4	35.9
Riband C	75.2	19.3	10.8	20.6
Riband W	63.5	20.7	12.5	19.5
Xi-19 C	73.8	18.7	18.1	18.1
Xi-19 W	63.1	24.6	18.7	25.1
P				
Waterlogging	<0.001	0.028	0.177	0.227
Variety	0.028	0.213	<0.001	0.002
Interaction	0.020	0.434	0.798	0.711
SED				
Waterlogging	0.68	0.99	0.42	2.31
Variety	1.08	1.56	0.66	3.66
Interaction	1.52	2.21	0.94	5.17
LSD				
Waterlogging	1.37	1.99	ns	ns
Variety	2.16	ns	1.33	4.64
Interaction	3.06	ns	ns	ns

Waterlogging had no significant effect on grain protein content, but as would be expected there were significant differences between the varieties, with Hereward having the highest grain protein content. There was no significant interaction between waterlogging and varieties, although varieties appeared to show different responses. Waterlogging increased grain protein of Claire and Hereward, decreased that of Xi-19, and had no effect on Riband and Deben.

Table 2.18. Nitrogen content of grain and straw at harvest, and the total uptake by the crop.

Treatment	Level	Grain protein concentration %	Straw N %	Total uptake by crop $kgha^{-1}$
Waterlogging	Control	9.52	0.34	19.7
	Waterlogged	9.49	0.42	18.2
Variety	Claire	8.94	0.34	18.7
	Deben	8.99	0.37	19.9
	Hereward	11.06	0.38	18.8
	Riband	9.33	0.48	18.6
	Xi-19	9.20	0.33	18.5
Waterlogging x Variety	Claire C	8.69	0.27	18.7
	Claire W	9.20	0.40	18.8
	Deben C	9.01	0.40	21.2
	Deben W	8.97	0.34	18.7
	Hereward C	10.91	0.29	18.7
	Hereward W	11.21	0.48	18.9
	Riband C	9.44	0.43	19.8
	Riband W	9.22	0.53	17.5
	Xi-19 C	9.54	0.30	19.7
	Xi-19 W	8.87	0.36	17.0
P				
Waterlogging		0.918	0.021	0.058
Variety		<0.001	0.065	0.773
Interaction		0.596	0.256	0.533
SED				
Waterlogging		0.246	0.035	0.781
Variety		0.389	0.056	1.234
Interaction		0.550	0.079	1.745
LSD				
Waterlogging		ns	0.071	1.568
Variety		0.780	0.113	ns
Interaction		ns	ns	ns

2.3.2.4. Effects of waterlogging on resource capture

When linear regression analysis was used there was a strong, significant positive relationship between the total amount of nitrogen taken up by the crop up to anthesis and the green area at anthesis (Figure 2.15). When waterlogging treatment was introduced to the analysis, this did not result in a significant improvement (change P = 0.208) in the variation accounted for by the model and the lines for the control and waterlogged plots were not significantly different. This indicates that waterlogging did not affect the ability of the plant to use captured nitrogen to produce green leaf area, although waterlogging decreased both the total nitrogen uptake and green area at anthesis. Adding variety to the model produced a significant improvement ($P<0.001$), and the variation accounted for increased from 63.9% to 77.3%, with the constant of the regression line fitted for Deben being significantly different from that for the other varieties. Figure 2.15 below suggests that Deben is better able than the other varieties to convert the higher nitrogen uptake to green area, as a result of its larger shoot population at anthesis, and better resistance to foliar disease.

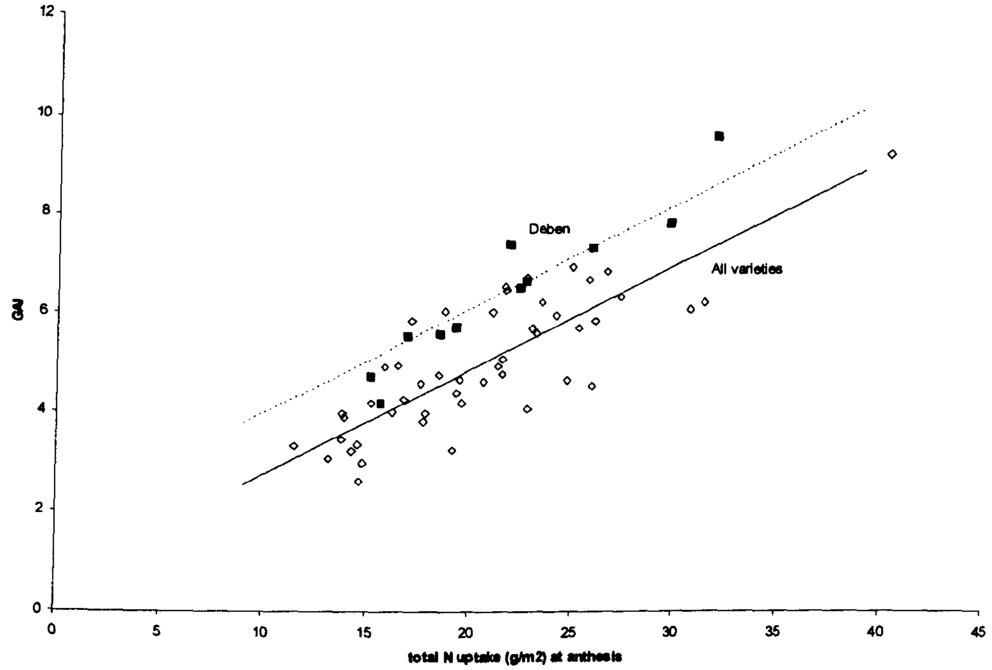

Figure 2.15. The relationship between green leaf area at anthesis and total nitrogen uptake by the crop. $P < 0.001$, percentage of variation accounted for by linear regression = 63.9%, the addition of variety to the model, $P < 0.001$, percentage of variation accounted for by the model = 77.3. Deben $y = 0.2137x + 1.85$, other varieties $y = 0.2137x + 0.618$

The linear regression fitted to describe the relationship between green area at anthesis and final grain dry weight at harvest was a significant ($P = 0.015$), although the correlation was weak (Figure 2.16). Adding waterlogging treatment to the model did not result in a significant improvement ($P = 0.121$), indicating that previous waterlogging did not effect the source – i.e. the rate of photosynthesis – or the sink – i.e. the number or ability of the grain sites to accept photosynthates – during the grain filling period. However waterlogging did significantly decrease both green area and grain yield. Adding variety to the model produced a significant improvement ($P < 0.001$), and increased the variation accounted for from 8.3% to 44.5 %. Only the regression line fitted for Hereward was significantly different from the other varieties. In this case the correlation appeared to be weaker than for the other varieties, indicating that Hereward was unable to convert extra green area into extra yield. Hereward had the lowest TGW, a small ear population at harvest and low number of grains per ear, indicating that yield was sink limited. Although the difference between the regression line for Xi-19 and the other varieties was not significant (P = 0.230) and so the line was not plotted, there was a much stronger correlation between green leaf area and yield for this variety, indicating that unlike Hereward, the sink was not limiting, as Xi-19 had a higher TGW and more grains per ear, and so was able to utilise the increased resource capture of the larger canopy.

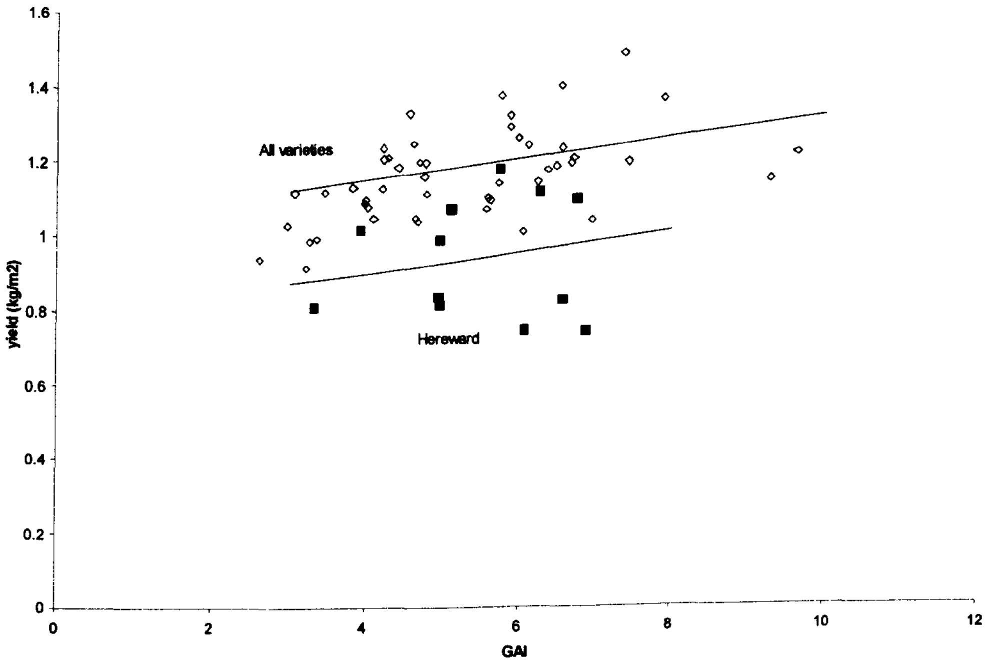

Figure 2.16. The relationship between grain dry weight at harvest and leaf green area at anthesis. $P < 0.015$, percentage of variation accounted for = 8.3%, the addition of variety to the model, $P < 0.001$, percentage of variation accounted for = 44.5. Hereward $y = 0.0277x + 1.0411$, other varieties $y = 0.0277x + 0.7897$

2.4. DISCUSSION

2.4.1. Effects of waterlogging

The reduction in shoot population at the end of waterlogging in experiment 2 was due to the reduction in plant population. Previous experiments had suggested that reduction in shoot population was due to a reduction in tillering per plant. However, under normal conditions, the effect of reducing plant population would be to increase tiller production and survival. Under control conditions the increased tillering per plant would be expected to compensate for the lower plant population, as happened in the 2001-2002 lysimeter experiment (Chapter 4). Indeed the ear number per waterlogged plant was slightly higher than the controls for four of the five varieties. A decrease in plant population over winter of the size measured, from 302 plants m^{-2} to 231 plants m^{-2}, would not normally cause the decrease in yield found at harvest, as increased tillering would compensate. For example there was no significant difference between the grain yields of the control lysimeters (chapter 3) sown at 264 and 132 plants m^{-2}. Therefore waterlogging had decreased the plant population and then inhibited tillering to prevent the plants making full use of the more open canopy to tiller and compensate. The significantly reduced shoot population shows that waterlogging still had an effect on tiller number per plant in not allowing this compensation to take place. No death of plants waterlogged after emergence was found in the glasshouse lysimeter experiment, discussed in chapter 4, or in the work at Letcombe (Cannell *et al.* 1980). However both these experiments were hand sown, so the even spacing of plants would minimise competition. Although differences between varieties in plant population were not significant, Xi-19 and Hereward, which have erect leaves and thus decreased interplant competition when compared to varieties with prostrate or planoform leaves, had the highest plant populations after waterlogging. The high tillering, prostrate and more aggressive seedlings of Deben had the lowest plant population, suggesting that inter plant competition was responsible for death of waterlogged plants in the field experiment, which did not occur in the hand sown lysimeter experiments. Additionally it was observed that glasshouse grown wheat plants tend to have a more erect growth habit than their equivalents, grown outdoors. This is possibly a result of the sheltered conditions in the glasshouse, which appeared to produce 'softer', less competitive plants. Due to their high winter growth rate Xi-19 plants were also larger, and the results of the sowing date and waterlogging date interaction experiment in the bins (see chapter 5) suggested that the larger early sown plants were better able to survive waterlogging, possibly due to higher carbohydrate and amino acid reserves in the larger shoot system.

The reduction in biomass per unit area by waterlogging at the end of the waterlogging period was not only due to decreased plant and shoot populations but also lower dry weight per plant and shoot. The decreased tiller weight also means these tillers were much less likely to survive, explaining why the reduction in shoot number persisted to harvest. There is some debate in the published literature as to whether a reduced growth rate is a sign of sensitivity or tolerance to waterlogging. Boru *et al.* (2001) used reduction in dry weight as a measure of sensitivity together with leaf chlorosis. However Hoffmann *et al.* (1993) stated that hypoxia causes an energy crisis in the plant and that the ability to shift limited resources away from growth of parts of the plant by slowing growth rate to maintain the plant as a whole is a sign of tolerance. Observations made in this experiment seem to support the latter hypothesis.

Uptake of nitrogen over winter was reduced from 5.1gm^{-2} to 2.7gm^{-2}, and this should be considered keeping in mind work by Sylvester-Bradley *et al* (1997) that showed that 3g of N are needed to produce one unit of green area. Canopy size is primarily determined by shoot population (Sylvester-Bradley *et al.*, 1990), and to achieve a pre stem-extension shoot population of 1200/m^2 the crop is required to take up 24 kg/ha N, as shoot N content is at least 2 mg per shoot (Sylvester-Bradley *et al.*, 2001). As the N uptake (27 kg/ha) and shoot population (1290/m^2) of waterlogged plots did not fall below these critical values, this may explain why the decrease in grain yield due to waterlogging was relatively minor. The variety with largest green leaf area per shoot was Xi19, a partial compensation for the lower shoot number. Interestingly the next highest was Deben which also had the largest shoot number, making a very dense canopy (GAI = 7.1 control, 5.9 after waterlogging), which would partially explain this variety's poor resistance to lodging (HGCA, 2004). Dense canopies cause etiolation of the lower internodes, and also increase the area exposed to wind and rain. Deben also took up the largest amount of nitrogen by harvest, and the observation that Deben is ranked as the highest yielding variety on light soils (HGCA,

2003) suggests that this variety has a good ability to scavenge available nitrogen from the soil.

As both the total shoot dry weight and the nitrogen content as a percentage of total dry weight were significantly decreased by waterlogging it was to be expected that uptake, measured as the total nitrogen in the crop, was also decreased significantly. The lack of difference between varieties in total nitrogen uptake is because varieties with high dry weight had low percentage nitrogen due to dilution with carbohydrate. The results show that the uptake of nitrogen is equally restricted for all varieties, suggesting loss of nitrogen through denitrification in the soil, or equally poor root growth and active uptake in all the varieties. The latter is more likely as previous work has found that the total amount of nitrate lost due to denitrification during a similar period of waterlogging in the winter was only 2.5kg ha^{-1} (Belford *et al.,* 1985), which is a very small amount when it is considered that the difference between the drained and waterlogged crops in plant nitrogen uptake in this experiment was equivalent to 24 kg ha^{-1}.

There may be a tenuous link between tolerance to waterlogging and grain protein. Considering that total nitrogen uptake was significantly decreased by waterlogging, it would be expected that varieties with the smallest decrease in yield would have the greatest decrease in grain protein due to dilution, but the reverse was the case. Hereward and Claire had the smallest percentage decrease in biomass production and grain yield and a small, but not significant, increase in grain protein due to waterlogging, whereas Xi-19 had a decrease in grain protein and appeared to be the most intolerant variety in terms of chlorosis of lower leaves and inhibition of tillering. Also greater numbers of ears per plant in response to the lower plant population after waterlogging would be expected to decrease the nitrogen partitioned to each ear. This did not happen either, as Xi-19 was the only variety not able to increase tillering per plant. Waterlogging significantly increased straw nitrogen content. This may have been due to delayed development; meaning translocation from the straw was not complete. However this would be indicated by increased grain and straw moisture content as the crop was less ripe, and although there was a small increase it was not significant for grain or straw. The answer may lie in the observation of increased straw density. The plant perhaps laid down extra reserves of nitrogen and carbohydrate in the stem in response to exposure to stress. However previous experiments have found the opposite to be true, where straw dry weight of waterlogged plants was decreased by a greater extent than could be accounted for by the decrease in stem number or stem length, indicating that the straw was less dense (Belford *et al.,* 1985).

2.4.2. Effects of variety

Whilst there were significant differences in yield between varieties under waterlogging in experiment 1, there was no significant interaction between waterlogging and variety in experiment 2. This suggests that no variety is more tolerant than any other, so the best strategy to deal with waterlogging is to select the highest yielding variety under control conditions. As stated above the cause of yield loss is a reduction in ears m^{-2} due to plant death so the choice of a variety with a high tillering potential, such as Deben counters this. There were significant interactions, however, between waterlogging and variety in the tube experiment. Previous work that had taken plants to yield (Musgrave and Ding, 1998) also found no interaction between variety and waterlogging whilst pot or solution experiments did find interactions, where tolerance was measured by the decrease in dry weight or leaf chlorosis. This suggests that varietal yield potential and ability to recover from stress plays a more important part in determining yield than tolerance to hypoxia.

The results also cast doubt on the wisdom of assuming that a low total dry weight or a large decrease in dry weight compared to a control is a sign of poor tolerance to hypoxia. Deben and Claire, which highest grain dry weights after waterlogging, had low shoot dry weights in March and had accumulated a smaller percentage of their final dry weight than the other varieties. Both these varieties also had lower observed levels of lower leaf senescence suggesting that the ability to reduce growth rates to conserve limited resources may be a mechanism of tolerance to hypoxia. The slowing of the rate of development may also be part of this conservation mechanism. Interestingly the best two varieties, Deben and Claire, are products of the Nickerson breeding programme, both including the variety Wasp in their parentage. Following survival of waterlogging, it is important for the crop to undergo vigorous compensatory growth to maintain yield potential, and this appears to be a characteristic of Deben especially.

There was a significant interaction between waterlogging and variety in the effects on straw length. Xi-19 had the largest decrease in straw length due to waterlogging and this variety also has the greatest response to PGR, according to HGCA Recommended List 2003 (HGCA, 2003). Resistance of Xi-19 to lodging increases from 5 without PGR to 8 with PGR. As well as causing the straw to be shorter waterlogging also appears to have increased the density of the straw, and although the interaction is not significant, the difference between waterlogged and control is greatest for Xi-19.

As previously stated, waterlogging reduced yield by reduction in ear number at harvest. This was due to the continuing effect of the lower plant population. All varieties except Xi-19 increased ears per plant slightly to compensate for the loss of plants over the winter. There was no significant effect of waterlogging on grain weight per ear, TGW or number of grains per ear, but Xi-19 showed an increase in these in waterlogged plants. This may be an alternative compensation mechanism, as Xi-19 was unable to compensate for plant loss by increasing tiller number per plant, as the other varieties appear to have done. Alternatively, waterlogging, by decreasing the number of tillers per plant for Xi-19, decreased the number of small secondary tillers which are a characteristic of this variety and when present decrease the average ear size. There was no effect on the number of spikelets initiated or the proportion of these that filled. These findings agree with those at Letcombe, where waterlogging during tillering reduced yield by a reduction in ear number as opposed to during stem extension, which reduced grain weight per ear. There were significant differences between varieties with Deben and Claire yielding the most due their higher tiller number. The results broadly agreed with those from the previous trial in the bins although Riband was badly affected by *Septoria* when grown under field conditions, and hence did not perform as well. There was no significant interaction between waterlogging and variety. However Hereward had a much smaller reduction in yield than the other varieties and the lowest yield, again in agreement with previous work which suggested smallest reductions in yield due to waterlogging occur when yield potential is lowest. Hereward's lack of yield response to waterlogging may be explained by the relationship between green area at anthesis and final yield. Whilst there was a positive relationship between green area during grain filling and yield for the other varieties, and so the decrease in green area due to waterlogging decreased yield, Hereward was unable to make use of extra green area. This was probably due to sink limitation, as this variety had fewer ears and smaller and fewer grains in each ear. Waterlogging acted as a source limitation, in decreasing the green area and thus decreasing the availability of photosynthates to the developing grain. This result shows the need for caution when assuming that a small response to an environmental stress is a sign of tolerance, it may merely be because yield is already limited by some other factor. Claire yielded second best when waterlogged, with a smaller percentage yield loss than Deben, indicating the best all round package of good yield and tolerance.

Chapter 3: TOLERANCE OF WHEAT VARIETIES TO WATERLOGGING AT THE VEGETATIVE STAGES OF GROWTH

3.1. INTRODUCTION

In the UK autumn sown winter wheat is most likely to experience waterlogging during the winter, due to the low transpiration rates at this time of year, and the increased likelihood of winter storms, as discussed in the literature review. At this time plants will be in the vegetative phase of growth, and so experiments to study the effects of waterlogging on wheat plants during the seedling and the tillering phase would be appropriate. The first tube experiment, reported in this chapter, was planned to complement the variety trial in the bins (see Chapter2). As plants were not grown to maturity they could be grown in small tubes. Many of these could be set up in a small area, allowing drained controls and a sufficient amount of replication. As the root systems of individual plants were confined to the tubes, they could be studied more easily than field or container grown plants. The small surface area of the bins meant that no destructive sampling could be undertaken before maturity, so the information about the responses of plants during the vegetative phases of growth was limited. Therefore a comparison with the tube experiment could be used to fill in some of the gaps in the overall picture, for example root growth was not measured in the bin experiment. It was also hoped that the results of these experiments would allow the identification of traits that could be used to screen varieties for waterlogging tolerance at the seedling stage, thus facilitating a faster breeding programme.

The results of the variety trials in the bins, field (Chapter2) and the first tube experiment suggested that varieties with a faster development rate over winter such as Xi-19, Soissons, and the hybrids Hyno Esta and Hyno Quinta were possibly more vulnerable to damage by winter waterlogging. A slower growth rate during periods of physiological stress has been identified as a characteristic associated with stress tolerance in plants (Grime and Hunt, 1972; Lambers and Poorter, 1992). Conversely Deben and Claire, which had the highest grain yields after waterlogging in the 2003 field variety trial, may be able to tolerate waterlogging by reducing their growth rate during the stress period and then tiller rapidly in the spring to compensate for plant losses. A second tube experiment was therefore planned to investigate the interaction between growth rate and waterlogging. For this experiment seven varieties of wheat, currently grown in the UK were chosen: four conventional winter wheat varieties, Deben, Claire, Xi-19 and Hereward, as these were grown in the 2003-4 field experiment; the autumn sown hybrid Hyno Esta; the fast developing, day-length insensitive winter wheat Soissons; and Paragon, a spring variety with no vernalisation requirement.

Previous research by suggested that seminal and nodal roots had different responses to waterlogging (Trought and Drew, 1980; Erdmann and Wiedenroth, 1985) and that some varieties have better tolerance to waterlogging as a result of their ability to initiate nodal roots (Haung *et al.,* 1994; Haung *et al.,* 1997). Hence an aim of this experiment was to find if there were varietal differences in patterns of root initiation in response to waterlogging and if any varieties demonstrated evidence of aerenchyma by having roots that penetrating below the water level.

3.2. METHOD

3.2.1. 2002 experiment

Plastic drainage tubing of 32mm diameter was cut into 250mm lengths, the bottom of each length plugged with insulation fleece and filled with silver sand (horticultural grade, lime free silica sand, particle size <1mm). The tubes were arranged in rows in eight plastic boxes, 25 in each, with sand packed between the tubes to hold them upright. The base of each box was first filled with fine gravel (horticultural grade, lime free, washed quartzite grit, particle size = 4mm) to a depth of 20 mm to allow free drainage underneath the tubes. Each variety was planted, one seed to each tube, in rows of five tubes, with five varieties to each box, on March 25, 2002. Seeds were sown approximately 20 mm deep. The varieties used were the same as the bin experiment; Biscay, Buchan, Charger, Claire, Consort, Deben, Equinox, Hereward, Hyno Esta, Hyno Quinta, Madrigal, Malacca, Napier, Option, Riband, Savannah, Shamrock, Soissons, Tanker and Xi-19. Further details are given in table 2.1. The boxes were duplicated to allow a waterlogging treatment. Boxes were arranged on benches in an unheated glasshouse, with no supplementary lighting. Boxes had holes drilled in the side 1cm above the base to allow drainage. Once emerged plants had two to three leaves the holes in the waterlogging treatment boxes were closed with rubber bungs and the water level raised to 40mm below the top of each tube. Plants were watered daily with tap water from sowing, and after April 1, Phostrogen solution was applied weekly until harvest at a rate of 2 ½ 10ml scoops in 50l *aq*, increasing to 5 scoops in 50l *aq* on April 19 to supply the nutrient demands of the growing plants. Phostrogen contains nitrogen (14 %), phosphate (10%), potassium (22.4%), magnesium (2.5 %), sulphate and trace elements (boron, copper, iron, manganese, molybdenum, zinc and calcium). Waterlogging treatment began on 1 April 2002, after the plants had began to tiller. Any plants that had failed to emerge by this time, or which had grown abnormally, were treated as missing values in the analysis. Once a week the bungs were removed from the waterlogged boxes to allow them to drain, then these were flushed with tap water to prevent build up of excess nutrients in the sand. Waterlogging continued for four weeks and plants were harvested at the end of this period, on April 25; none of the plants had reached the pseudostem erect stage (GS 30) by the time of harvest.

At harvest, 31 days after sowing, all plants were removed from the tubes, washed and photographed. Green tillers and dead or dying tillers were counted. A tiller was regarded as dead or dying if the youngest leaf was yellowing. Each plant was then separated into the following fractions; roots, green lamina, dead or dying lamina and stem or leaf sheath. These were bagged, labelled and dried for 48 hours in an oven at 80°C before being weighed.

3.2.2. 2004 experiment

Prior to starting this experiment germination tests were carried out as a precaution because the seed was of different ages (but no older than three years and had been cold stored). For these germination tests, twenty-five seeds of each variety were arranged on filter paper on Petri dishes, watered to begin imbibition, and placed in an incubator at 18 °C. Each variety was replicated three times. Germination was counted after 24 and 48 hours. A seed was counted as having germinated if it possessed a radicle of 2mm or more. The thousand grain weight (TGW) of each variety was measured by counting the number of seeds in a sample of known weight using a seed counter. Again each variety was replicated three times. After establishing that the germination of all varieties was close to 100% after 48 hours a second batch of seeds was placed on moist filter paper in Petri dishes and put in an incubator at 18 °C for 24 hours so that they had already imbibed, and so that germinated seeds could be selected for sowing. The same 250 mm long 32 mm diameter tubes as used in the 2002 experiment were filled with a growth medium of five parts sieved soil to one part sand, by volume. The soil was the same as that used in the lysimeter experiments in the previous two seasons (See chapter 4). It was decided to substitute this mixture for the sand used in the earlier experiment (2002) to avoid the use of nutrient solution, as this had lead to an accumulation of algae. The same plastic boxes as before were used, four with drainage holes and four with all holes blocked. A layer of coarse sand, 25 mm deep, was laid in the bottom of each box, the tubes arranged upright and soil packed around them. One germinating seed was sown, 20mm deep, in the centre of each tube on 27 January, 2004. Spare tubes of each variety were also prepared at this time, to replace any plants that failed, a lesson learned from the first experiment. The seven varieties used were Claire, Deben, Hereward, Hyno Esta, Paragon, Soissons and Xi-19. Eight boxes were set up, so that a pair, one waterlogged and one control box, could be harvested at four timings after the beginning of waterlogging. Three replicates of each variety were sown in the first three pairs of boxes and four replicates in the last pair, to be the final harvest.

Emergence began on February 3 and emerged plants were counted daily. Nearly all plants had emerged by February 9 and any that had not done so by this date were recorded as failures and replaced by the spares. Waterlogging began on February 10; achieved by closing all drainage holes and raising the water level to 40mm below the soil surface.

Harvests were carried out on 23 February, 5 March, 16 March and 31 March, at 28, 39, 50 and 65 days after imbibition, respectively. Plants were removed from the tubes and the roots washed to remove all soil. Leaves were counted as either emerged if a ligule had been formed or emerging if not. Tillers were counted if visible without peeling back the leaf sheath, and described; for example T0 for the coleoptile tiller, T1 for the first foliar tiller, etc. The length of emerged leaf lamina was measured for both emerging and emerged leaves. The health of the lamina was also noted, with regard to any chlorosis or senescence. The number of seminal and nodal root axes initiated was counted, and the length of the longest nodal and seminal root measured. The plants were then bagged and dried in an oven at 80 °C for 48 hours. The shoot and root system were separated and weighed after drying. At the first harvest on February 23 the caryopsis was separated and weighed separately, but in subsequent harvests was weighed together with the roots as seed reserves were exhausted by this time. On the final harvest plants from one row from each box were photographed before analysis.

2.2.3. Statistical analysis

Statistical analysis in both experiments was by a two factor ANOVA, without blocking, using Genstat 6 in 2002 and Genstat 7 in 2004. Percentage values were transformed using the square root function before analysis. In the 2002 experiment there were 145 residual degrees of freedom, as a result of 15 missing values, where seed either failed to germinate or grew abnormally. Planting spare tubes eliminated such missing values in 2004, where there were 28 residual degrees of freedom for the first three sampling dates, and 42 for the final sample, as a result of increasing the number of replicates from three to four. Regression analysis was done using simple linear regression in Genstat. It is usual not to present *non-significant* regressions. However in cases where the absence of a significant relationship between two variables makes a pertinent point (e.g. Figure 3.10) these have been presented.

3.3. RESULTS

3.3.1. 2002 tube experiment

Waterlogging significantly decreased total plant dry weight, shoot dry weight, and root dry weight, but the effect of waterlogging was greatest on the roots, so that the root dry weight as a percentage of the total dry weight decreased (Table 3.1). Waterlogging also decreased the total number of shoots per plant and the mean dry weight per shoot. The very high shoot number of the controls was possibly because these plants were sown too late to be vernalised. Weekly applications of Phostrogen nutrient solution would also mean that plant nutrition was not a limiting factor to tillering. Waterlogging increased the amount of dead material, expressed as a percentage of total plant dry weight. There were significant interactions between waterlogging and variety for all characteristics except total plant dry weight, indicating that there were varietal differences in response to waterlogging. Varieties could be divided into groups determined by their differing responses to waterlogging. Claire, Consort, Deben, Hyno Esta, Hyno Quinta and Xi-19 had a high shoot dry weight under control conditions, but suffered a large decrease due to waterlogging. A similar pattern occurred for root dry weight, with some varieties with high control dry weights showing a large decrease. Some varieties did not fit this trend, such as Tanker, which had a small decrease in shoot dry weight due to waterlogging, but a large decrease in root dry weight. Madrigal stands out has having a low shoot and root dry weight both for drained and waterlogged treatments, but only suffered small decreases in shoot and root dry weight. As can be seen in figures (3.1,3.2 and 3.5), Riband was around the median for shoot and root dry weight and shoot number per plant. Shoot dry weight was decreased by waterlogging but root dry weight and shoot number of this variety were almost unaffected. The linear regression fitted to relationship between plant dry weight under waterlogged and control conditions, shown in Figure 3.3, was not significant (P = 0.180), indicating that there were differences in the response to waterlogging between varieties, also shown in Figures 3.1 and 3.2. Therefore performance under stressed conditions was not correlated with performance under unstressed conditions. There was a significant linear relationship (P < 0.001) between the percentage decrease in dry weight due to waterlogging and the plant dry weight under control conditions. Varieties with the highest control plant dry weights had a tendency to suffer the largest decrease in dry weight when waterlogged (Figure 3.4).

Table 3.1. P and SED from analysis at the end of waterlogging, for means see over.

	Total Plant DW (g)	Shoot DW (g)	Roots DW (g)	Root DW as % of Total DW	Shoots plant^{-1}	Dead material l% DW
P						
Waterlogging	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Variety	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Interaction	0.059	0.043	0.001	0.007	0.014	<0.001
SED						
Waterlogging	0.087	0.044	0.053	1.45	0.47	1.00
Variety	0.276	0.140	0.168	4.57	1.48	3.15
Interaction	0.391	0.198	0.237	6.46	2.10	4.45

Table 3.1. Dry weight of plants and plant fractions and numbers of shoots of 31 day old winter wheat seedlings, grown in waterlogged or drained sand.

Table 3.1a. Total plant dry weight (g)

	Biscay	Buchan	Charger	Claire	Consort	Deben	Equinox	Hereward	Hyno Esta	Hyno Quinta	Madrigal	Malacca	Napier	Option	Riband	Savannah	Shamrock	Soissons	Tanker	Xi 19	mean
C	2.18	1.96	1.31	2.22	2.45	2.73	1.69	1.69	2.53	2.13	0.80	2.57	1.53	2.03	1.43	2.53	2.07	2.33	2.14	2.81	2.06
W	1.30	0.94	1.03	1.75	1.07	1.13	1.02	1.04	1.10	0.91	0.79	1.23	1.38	1.42	1.20	1.23	1.46	1.15	1.31	1.21	1.18
mean	1.74	1.45	1.17	1.98	1.76	1.93	1.35	1.37	1.81	1.52	0.79	1.90	1.45	1.73	1.32	1.88	1.77	1.74	1.73	2.01	

Table 3.1b. Shoot dry weight (g)

	Biscay	Buchan	Charger	Claire	Consort	Deben	Equinox	Hereward	Hyno Esta	Hyno Quinta	Madrigal	Malacca	Napier	Option	Riband	Savannah	Shamrock	Soissons	Tanker	Xi 19	mean
C	0.82	0.83	0.48	1.26	1.01	0.98	0.64	0.71	1.24	1.32	0.44	0.94	0.61	0.74	0.75	0.62	0.74	1.10	0.93	1.48	0.88
W	0.76	0.55	0.50	0.62	0.46	0.64	0.50	0.47	0.70	0.60	0.42	0.54	0.76	0.73	0.62	0.44	0.63	0.73	0.87	0.77	0.75
mean	0.79	0.69	0.49	0.94	0.73	0.81	0.57	0.59	0.97	0.96	0.43	0.74	0.69	0.74	0.68	0.53	0.69	0.92	0.90	1.12	

Table 3.1c. Root dry weight (g)

	Biscay	Buchan	Charger	Claire	Consort	Deben	Equinox	Hereward	Hyno Esta	Hyno Quinta	Madrigal	Malacca	Napier	Option	Riband	Savannah	Shamrock	Soissons	Tanker	Xi 19	mean
C	1.70	1.13	0.82	0.96	1.45	1.75	1.05	0.98	1.28	0.81	0.45	1.63	1.14	1.29	0.68	1.91	1.33	1.23	1.21	1.33	1.21
W	0.54	0.39	0.53	1.13	0.61	0.49	0.52	0.58	0.40	0.32	0.36	0.69	0.62	0.69	0.58	0.79	0.83	0.41	0.45	0.44	0.57
mean	1.12	0.76	0.68	1.05	1.03	1.12	0.78	0.78	0.84	0.56	0.41	1.16	0.88	0.99	0.63	1.35	1.08	0.82	0.83	0.89	

Table 3.1d. Root dry weight as a percentage of total plant dry weight

	Biscay	Buchan	Charger	Claire	Consort	Deben	Equinox	Hereward	Hyno Esta	Hyno Quinta	Madrigal	Malacca	Napier	Option	Riband	Savannah	Shamrock	Soissons	Tanker	Xi 19	mean
C	61.9	58.2	63.9	46.6	58.9	63.3	59.7	57.3	47.8	38.3	47.6	62.9	61.1	62.3	48	75	64.4	49.8	58.2	49.8	56.8
W	39.5	44.1	50.8	63.3	56.7	42.8	50.2	56.3	36.4	35	48.6	55.7	44.4	47.7	47.3	63.5	54.6	36.8	34.2	36.7	47.2
mean	50.7	51.2	57.3	55	57.8	53	55	56.8	42.1	36.7	48.1	59.3	52.8	55	47.6	69.2	59.5	43.3	46.2	43.3	

Table 3.1e. Number of shoots per plant

	Biscay	Buchan	Charger	Claire	Consort	Deben	Equinox	Hereward	Hyno Esta	Hyno Quinta	Madrigal	Malacca	Napier	Option	Riband	Savannah	Shamrock	Soissons	Tanker	Xi 19	mean
C	22.8	17.5	12.4	9.0	14.6	16.2	14.8	13.0	15.2	19.0	9.3	19.2	14.0	12.6	10.6	11.7	15.0	12.2	16.0	9.4	14.2
W	13.8	9.0	10.3	7.6	8.8	13.3	9.6	8.2	11.6	9.8	10.0	13.0	12.5	12.2	10.6	8.2	12.6	11.0	13.0	7.2	10.6
mean	18.3	13.3	11.3	8.3	11.7	14.7	12.2	10.6	13.4	14.4	9.6	16.1	13.3	12.4	10.6	9.9	13.8	11.6	14.5	8.3	

Table 3.1f. Dry weight of dead material as percentage of total plant dry weight

	Biscay	Buchan	Charger	Claire	Consort	Deben	Equinox	Hereward	Hyno Esta	Hyno Quinta	Madrigal	Malacca	Napier	Option	Riband	Savannah	Shamrock	Soissons	Tanker	Xi 19	mean
C	0.0	0.0	0.0	0.0	0.0	3.4	0.0	0.0	7.6	0.0	0.0	0.0	0.0	4.5	0.0	0.4	0.0	2.6	0.0	1.7	1.0
W	17.1	9.4	6.2	16.1	18.2	11.9	13.5	4.3	22.4	24.3	4.6	26.4	6.0	20.0	1.8	22.0	4.5	10.0	5.7	24.1	13.4
mean	8.5	4.7	3.1	8.1	9.1	7.6	6.8	2.2	15.0	12.1	2.3	13.2	3.0	12.3	0.9	11.2	2.3	6.3	2.9	12.9	

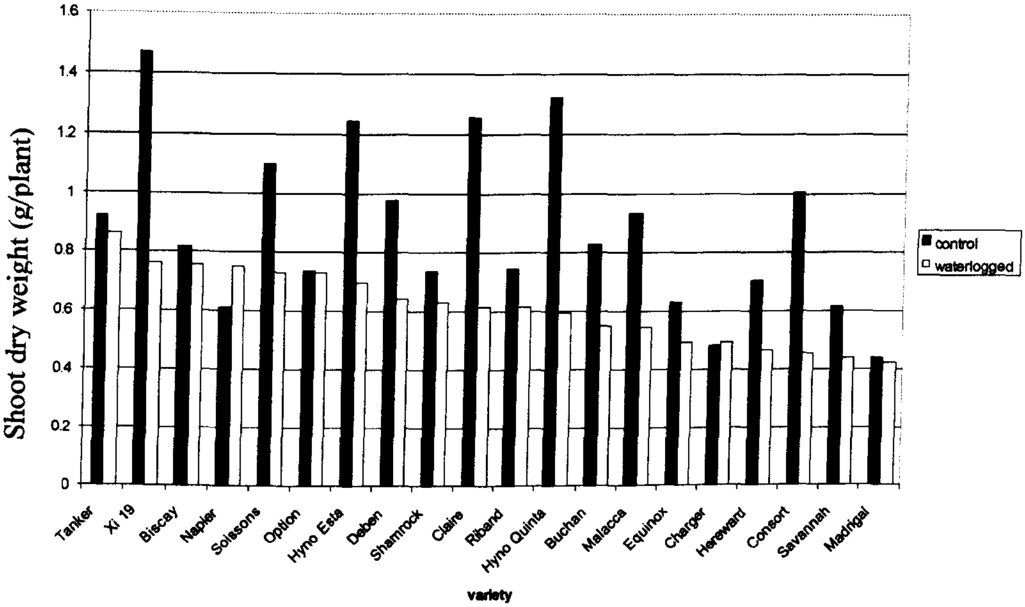

Figure 3.1. Shoot dry weight of 31 day old seedlings of 20 UK winter wheat varieties grown in drained or waterlogged sand. Varieties are ranked by their performance under waterlogged conditions, best to worst from left to right.

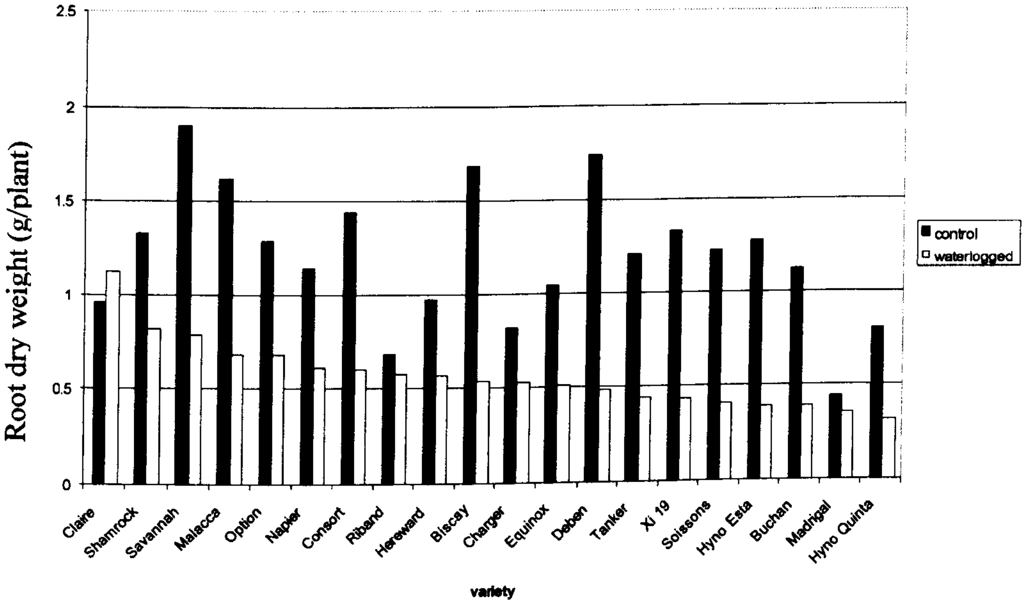

Figure 3.2. Root dry weight of 31 day old seedlings of 20 UK winter wheat varieties grown in drained or waterlogged sand. Varieties are ranked by their performance under waterlogged conditions, best to worst from left to right.

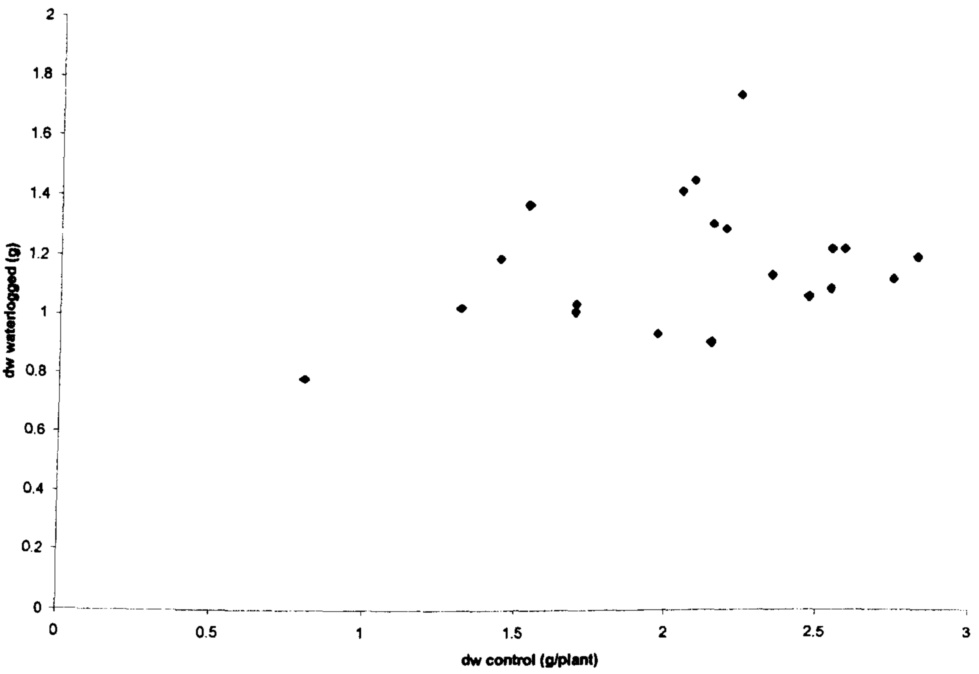

Figure 3.3. The relationship between mean dry weight per plant of 20 winter wheat varieties grown in waterlogged sand and mean dry weight when grown in drained control conditions. P = 0.180, percentage of variation accounted by linear regression for = 4.7.

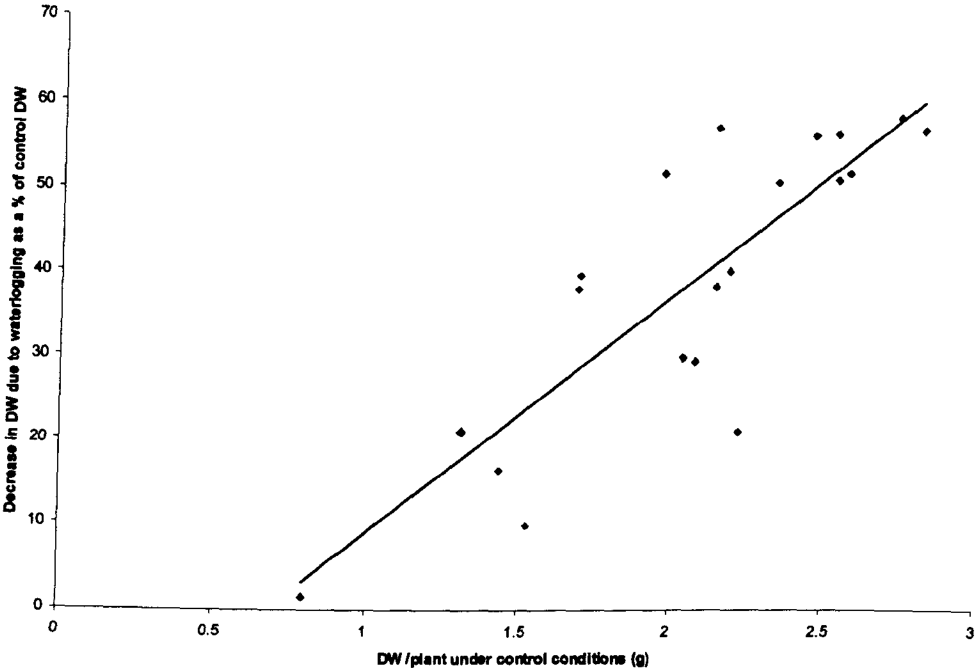

Figure 3.4. The relationship between mean percentage decrease in total dry weight of 20 wheat varieties and the mean plant dry weight when grown in control conditions. $P < 0.001$, percentage of variation accounted for by linear regression = 68.7. $y = 28.36x - 19.39$

Whilst there was a significant interaction between waterlogging and variety for the number of shoots per plant, the interaction is not as marked as that for root and shoot dry weight, in terms of altering the performance of varieties relative to each other. The most prolifically tillering varieties under control conditions, such as Deben, Biscay and Tanker, tended to have the most shoots when waterlogged. Likewise Claire and Xi-19 had fewer shoots than other varieties for both treatments. The correlation between drained and waterlogged shoot number was weak, but the regression was significant, which concurs with the previous observation. However Buchan, Consort, Equinox, Hyno Esta, Hyno Quinta and Malacca all fell from having some of the highest shoot numbers under control conditions to having some of the lowest when waterlogged. In contrast the shoot numbers of Madrigal, Option and Riband were unaffected by waterlogging.

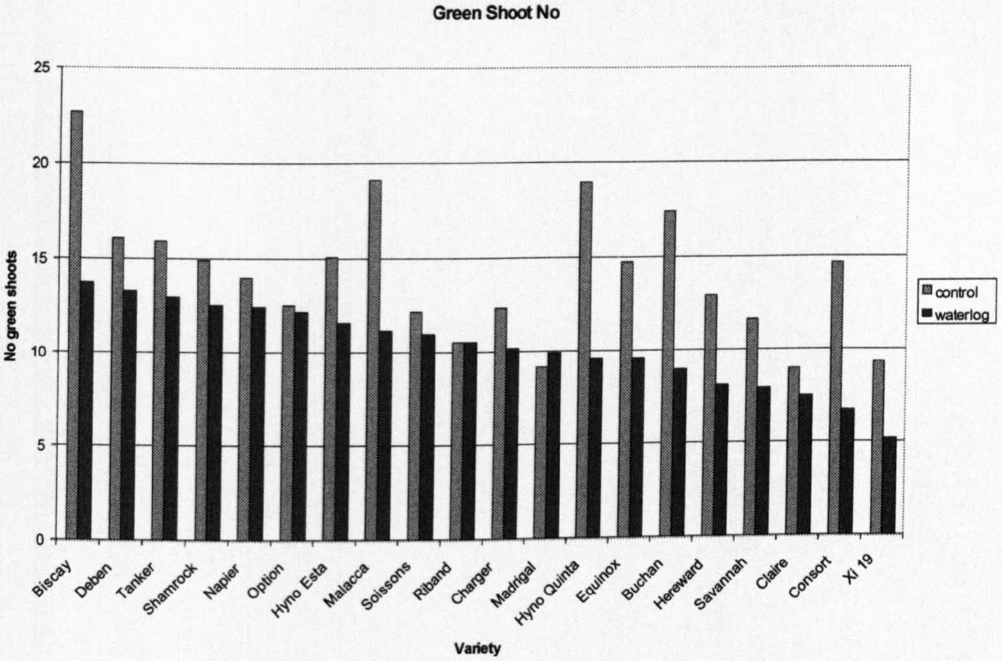

Figure 3.5. Total number of green shoots per plant of 31 day old seedlings of 20 UK winter wheat varieties grown in drained or waterlogged sand. Varieties are ranked by their performance under waterlogged conditions, best to worst from left to right.

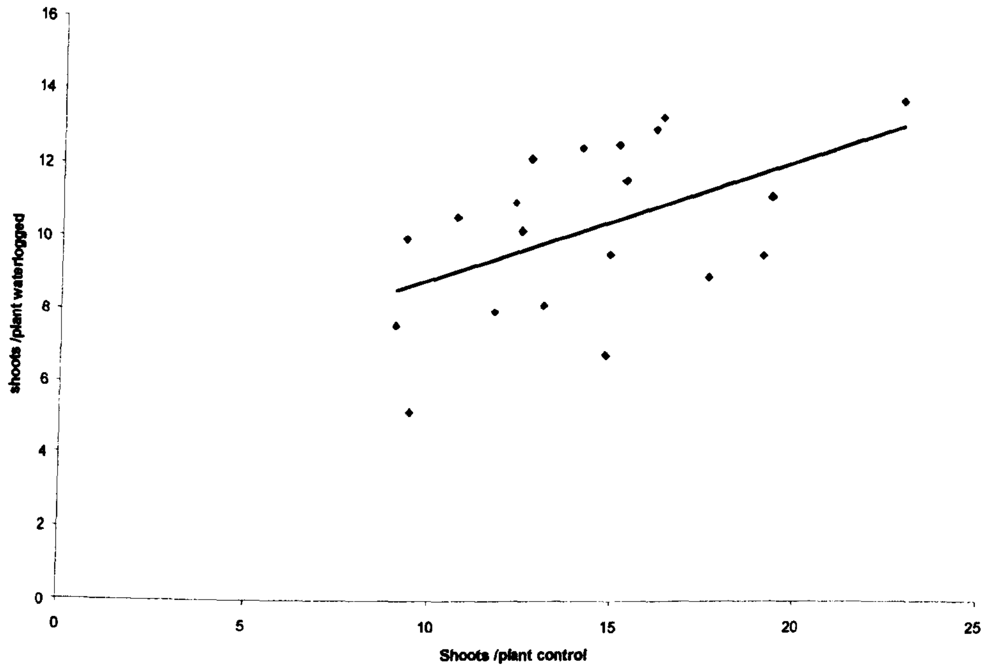

Figure 3.6. The relationship between the number of shoots per plant of 20 winter wheat varieties when grown in drained or waterlogged conditions. P = 0.023, percentage of variation accounted for by linear regression = 21.5. y = 0.328x + 5.64

3.3.2. 2004 experiment

3.3.2.1. Thousand grain weight, germination and emergence

There were significant differences in thousand grain weight between the varieties, with Deben and Xi-19 having significantly larger seed than the other varieties and Claire significantly smaller seed than the others. There was no difference in the final germination after 48 hours, but some varieties germinated and emerged faster than others, notably Paragon, the spring wheat and Xi-19, which includes a spring variety in its parentage. Seed vigour does not appear to be related to seed size for these varieties, but rather to growth habit, determined by genotype. Spring wheat varieties are usually more vigorous during emergence than their autumn sown equivalents to overcome poorer seedbed conditions.

Table 3.2. The TGW, % germination after 24 and 48 hours - as tested in the germination test on moist filter paper - and the time taken from imbibition to emergence in the tubes. The figures in brackets are the square roots of the percentage figures and statistical analysis was done on the transformed data, so the SED and LSD refer to this.

Variety	TGW g	% germination after 24 hours	% germination after 48 hours	Time from inbibition to emergence (days)
Claire	46.6	48.0 (6.92)	96.0 (9.80)	10.28
Deben	53.9	16.0 (3.98)	96.0 (9.80)	10.54
Hereward	51.0	30.7 (5.53)	98.7 (9.93)	9.64
Hyno Esta	49.3	49.3 (7.02)	100.0 (10.00)	10.12
Paragon	48.7	90.7 (9.51)	96.0 (9.80)	9.25
Soissons	49.6	52.0 (7.21)	98.7 (9.93)	9.42
Xi-19	60.8	69.3 (8.31)	100.0 (10.00)	9.50
P	<0.001	<0.001	0.343	<0.001
SED	0.66	0.357	2.364	0.229
LSD	1.42	0.7660	ns	0.453

3.3.2.2. Caryopsis weight

The data in table 3.3 suggests that waterlogging slowed the rate of use of seed reserves by the growing plants, probably by decreasing the amount of oxygen available for respiration. However the differences were very small when compared to the original carypsis weight of approximately 50mg (see table 3.2).

Table 3.3. Dry weight of caryopsis (mg) of 28 day old seedlings of seven wheat varieties, grown in drained or waterlogged conditions, 13 days after the start of waterlogging.

	Claire	Deben	Hereward	Hyno Esta	Paragon	Soissons	Xi-19	mean
C	3.53	6.63	5.77	2.90	5.27	4.13	4.57	4.69
W	6.53	8.50	5.40	3.77	8.10	7.67	8.37	6.90
mean	5.03	7.57	5.58	3.33	6.68	5.90	6.47	

	Treatment	Variety	Interaction
P	0.028	0.362	0.899
SED	0.959	1.794	2.538
LSD	1.965	ns	ns

3.3.2.3. Root growth and development

Differences in root growth between varieties were significant only at the first two harvests, when Deben, Xi-19 and Soissons had more seminal axes than the other varieties (Table 3.4). Deben and Xi-19 had high thousand grain weight (see table 3.2), a characteristic that has been associated with the production of a larger number of seminal roots (MacKey, 1973). The effect of waterlogging was only significant at the second harvest, when waterlogging decreased the number of seminal axes initiated. There was no significant interaction between waterlogging and variety at any time.

Table 3.4. Effects of variety and waterlogging on the mean number of seminal root axes initiated per plant.

Date		23/02/2004	05/03/2004	16/03/2004	31/03/2004
Days after imbibition		28	39	50	65
	C	4.1	4.8	4.9	4.8
	W	4.1	4.2	4.6	4.9
		23/02/2004	05/03/2004	16/03/2004	31/03/2004
	Claire	4.2	4.7	4.7	5.0
	Deben	5.2	5.0	5.0	4.8
	Hereward	3.0	4.0	4.3	4.5
	Hyno Esta	3.7	3.7	4.7	5.1
	Paragon	3.0	4.2	4.2	4.1
	Soissons	5.3	5.0	5.0	5.3
	Xi-19	4.3	5.0	5.3	5.1
P	treatment	0.692	0.002	0.247	0.479
	variety	<0.001	<0.001	0.34	0.198
	interaction	0.954	0.089	0.627	0.544
SED	treatment	0.24	0.18	0.28	0.25
	variety	0.45	0.33	0.53	0.47
	interaction	0.63	0.47	0.75	0.66
LSD	treatment	ns	0.37	ns	ns
	variety	0.91	0.69	ns	ns
	interaction	ns	ns	ns	ns

The differences in the number of nodal root axes initiated, due to waterlogging, were significant at the second and subsequent harvests (Table 3.5). Waterlogged plants initiated more nodal axes in response to waterlogging. Differences between the varieties were significant at the second and third harvest, when the fast developing Paragon and Soissons had more nodal axes than other varieties. There was no significant interaction at any time. At the second harvest the longest nodal roots of the waterlogged plants were longer than those of the controls for Claire, Hereward, Soissons and Xi-19 (Figure 3.7). This was a result of the nodal roots of waterlogged plants being initiated earlier. By the final harvest, when the plants were 65 days old, both the seminal and nodal roots of the controls were longer (Figure 3.8). The seminal roots of the waterlogged plants had begun to senesce and the tips had shrivelled by the final harvest and were restricted to above the water level; in fact they were shorter than those of waterlogged plants at earlier harvests. At this time the nodal roots of the waterlogged plants were longer than the seminal roots, but no variety had roots able to penetrate more than 150mm below the water line. Waterlogging significantly decreased the dry weight of the root system at all sampling dates (Table 3.6). There was only a significant varietal effect on the second harvest, which also gave the only varietal effect on seminal root number.

Table 3.5. Effects of variety and waterlogging on the mean number of nodal root axes initiated per plant.

Date		23/02/2004	05/03/2004	16/03/2004	31/03/2004
Days after imbibition		28	39	50	65
	C	0.14	1.38	2.29	3.04
	W	0.38	2.76	3.90	4.50
		23/02/2004	05/03/2004	16/03/2004	31/03/2004
	Claire	0.17	1.50	3.00	2.62
	Deben	0.17	1.50	2.83	4.25
	Hereward	0.17	1.33	2.33	3.62
	Hyno Esta	0.17	3.00	3.00	3.62
	Paragon	0.00	3.00	3.83	4.00
	Soissons	0.67	2.17	3.67	4.12
	Xi-19	5.00	2.33	3.00	4.12
P	treatment	0.143	<.001	<.001	<.001
	variety	0.315	<.001	0.019	0.253
	interaction	0.241	0.259	0.485	0.438
SED	treatment	0.158	0.191	0.218	0.364
	variety	0.296	0.356	0.408	0.680
	interaction	0.418	0.504	0.577	0.962
LSD	treatment	ns	0.390	0.447	0.734
	variety	ns	0.730	0.836	ns
	interaction	ns	ns	ns	ns

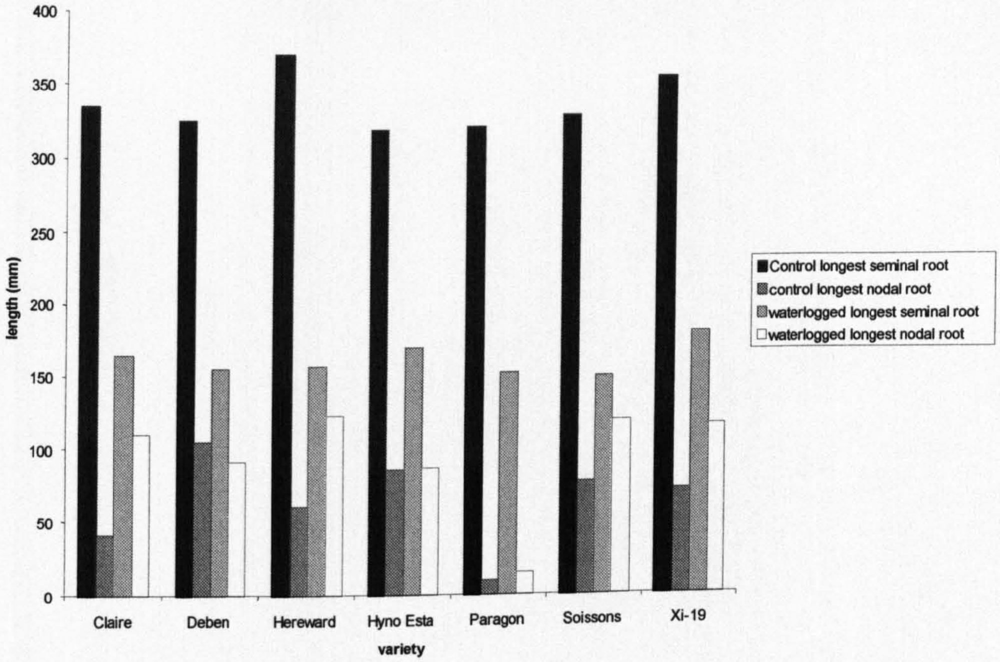

Figure 3.7. The mean length of the longest seminal and nodal roots of 39 day old plants of seven wheat varieties, grown under waterlogged and drained control conditions, 24 days after the start of waterlogging.

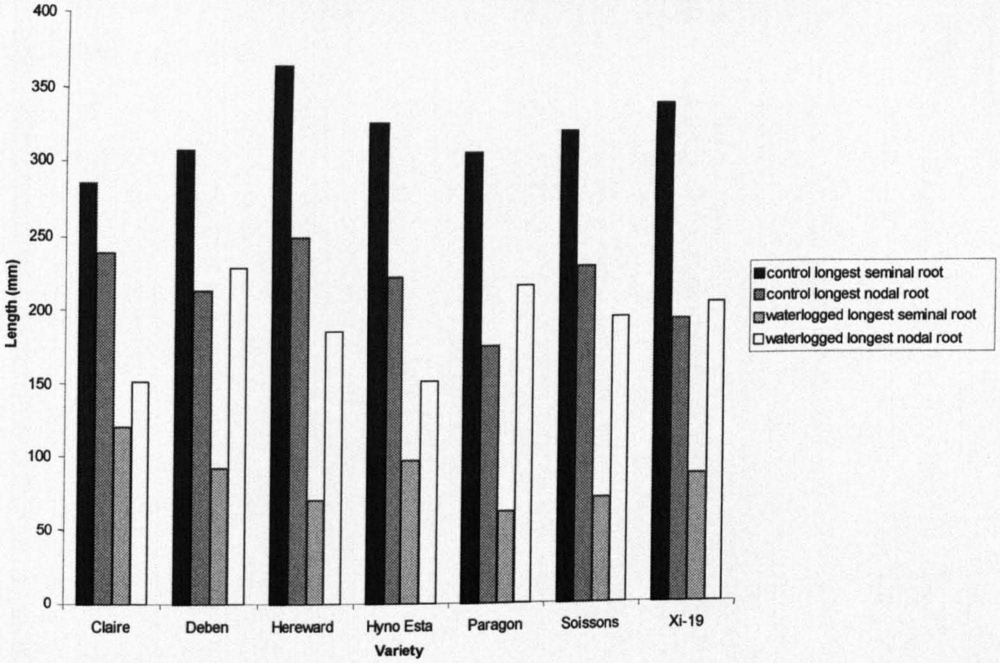

Figure 3.8. The mean length of the longest seminal and nodal roots of 65 day old plants of seven wheat varieties, grown under waterlogged and drained control conditions, 50 days after the start of waterlogging.

Table 3.6. Effects of waterlogging on the dry weight (mg plant^{-1}) of the root systems of 7 varieties of wheat.

	23/02/2004	05/03/2004	16/03/2004	31/03/2004
C	35	141	223	224
W	26	51	71	83

	23/02/2004	05/03/2004	16/03/2004	31/03/2004
Claire	27	66	128	160
Deben	23	77	133	141
Hereward	31	95	143	152
Hyno Esta	34	125	166	168
Paragon	29	91	149	114
Soissons	36	107	167	179
Xi-19	35	111	146	161

Variety	Treatment	23/02/2004	05/03/2004	16/03/2004	31/03/2004
Claire	C	30	90	190	196
Claire	W	24	42	65	124
Deben	C	33	110	190	204
Deben	W	12	45	77	78
Hereward	C	37	151	228	231
Hereward	W	25	38	57	74
Hyno Esta	C	37	170	260	267
Hyno Esta	W	31	80	73	70
Paragon	C	34	140	218	160
Paragon	W	24	42	80	69
Soissons	C	37	159	257	261
Soissons	W	36	55	77	97
Xi-19	C	37	165	221	251
Xi-19	W	33	58	71	71
P	treatment	0.002	<0.001	<0.001	<0.001
	variety	0.065	0.003	0.203	0.181
	interaction	0.444	0.155	0.264	0.101
SED	treatment	2.5	6.9	9.2	12.7
	variety	4.7	13.0	17.1	23.8
	interaction	6.6	18.4	24.2	33.7
LSD	treatment	5.1	14.2	18.8	25.7
	variety	ns	26.6	ns	ns
	interaction	ns	ns	ns	ns

Figure 3.9 shows that whilst waterlogging did slow the growth of the root system it did not stop completely. By the final harvest the nodal root system must have constituted the greater part of the dry matter of the waterlogged roots as the seminal root system was virtually dead, in contrast to the control plants, which possessed an

extensive and highly branched seminal root system. For an illustration of this, refer to the photographs in Appendix III. There appeared to be no further increase in the root dry weight of the controls between the penultimate and final harvests. This is a result of these larger plants becoming 'pot bound' in the small tubes.

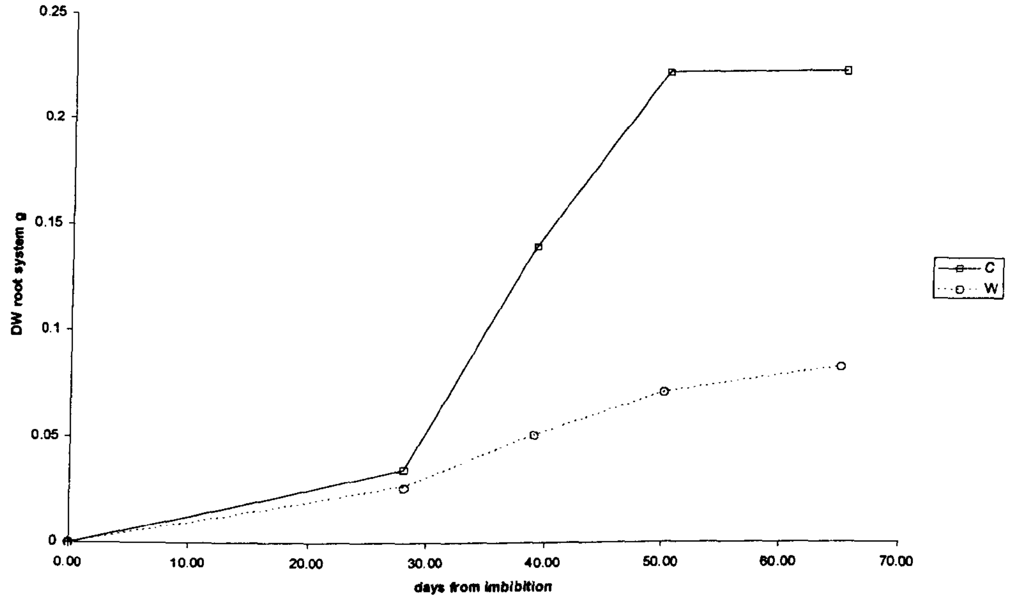

Figure 3.9. Accumulation of dry weight by the root system of wheat grown in waterlogged or drained soil, plotted against the number of days from the start of seed imbibition. Data are the means of seven varieties, for P, SED and LSD see Table 3.6.

3.3.2.4. Shoot growth and development

Waterlogging decreased the number of leaves only at the second sampling date (Table 3.7). However by the end of the experiment the lower two leaves of all waterlogged plants had senesced and all emerged leaves had some degree of chlorosis, only the youngest, still emerging leaves remained green. Therefore although the effect of waterlogging on total leaf number is equivocal, the number of green leaves and the green leaf area would be greatly decreased. The effect of variety was significant on all but the first sampling date, with Soissons and Xi-19 showing a faster rate of shoot development, expressed as the rate of production of new leaves. There was no interaction between the treatments at any sampling date. Waterlogging did not significantly affect the length of the first two leaves to emerge, as these would already have been determined before the start of waterlogging, therefore this data is not shown. The rate of expansion of all subsequent leaves was significantly decreased by waterlogging, and it appears that the final length of leaf 3 was decreased slightly, but significantly (Table 3.7). Leaves 5 and 6 were still emerging at the final harvest, but those of the waterlogged plants were significantly shorter, indicating that if the experiment had been allowed to run for longer complete leaf emergence would have been significantly delayed. Differences in leaf length between varieties were always significant, which was to be expected as varieties were specifically chosen for their differing rates of growth and development.

Table 3.7. The effect of waterlogging on the number of fully emerged leaves present on the main shoot of 7 varieties of wheat, and the length (mm) of the 3rd and 4th leaves to emerge.

Table 3.7a. Number of fully emerged leaves present.

		22/02/04	05/03/04	16/03/04	31/03/04
	C	1.91	2.95	3.57	4.36
	W	1.67	2.29	3.43	4.38
		22/02/04	05/03/04	16/03/04	31/03/04
	Claire	1.67	2.67	3.67	4.38
	Deben	1.83	2.67	3.17	4.25
	Hereward	1.83	2.50	3.17	4.00
	Hyno Esta	1.83	2.50	3.17	4.00
	Paragon	1.5	2.33	3.67	4.25
	Soissons	2.17	3.00	4.00	4.63
	Xi-19	1.67	2.67	3.67	5.00
P	treatment	0.176	<0.001	0.266	1.000
	variety	0.545	0.031	0.005	<0.001
	interaction	0.992	0.146	0.179	0.973
SED	treatment	0.172	0.095	0.126	0.120
	variety	0.321	0.178	0.257	0.225
	interaction	0.454	0.252	0.333	0.318
LSD	treatment	ns	0.1951	ns	ns
	variety	ns	0.365	0.4828	0.454
	interaction	ns	ns	ns	ns

Table 3.7b. Leaf 3 length (mm)

		22/02/04	05/03/2004	16/03/2004	31/03/2004
	C	62.9	147.2	173.5	146.5
	W	56.7	111.6	136.9	131.2
		22/02/04	05/03/2004	16/03/2004	31/03/2004
	Claire	50.0	110.5	129.0	114.6
	Deben	50.3	103.3	126.3	102.4
	Hereward	51.5	120.8	155.8	129.4
	Hyno Esta	56.2	135.7	164.0	148.4
	Paragon	53.7	142.8	196.7	170.6
	Soissons	94.0	152.2	160.0	152.2
	Xi-19	62.8	140.5	154.7	154.4
P	treatment	0.232	<.001	<.001	0.013
	variety	<.001	<.001	<.001	<001
	interaction	0.899	0.070	0.643	0.511
SED	treatment	5.09	5.32	7.08	5.95
	variety	9.52	9.96	13.24	11.13
	interaction	13.46	14.08	18.72	15.74
LSD	treatment	ns	10.9	14.49	12
	variety	19.52	20.39	27.12	22.46
	interaction	ns	ns	ns	ns

Table 3.7c. Leaf 4 length (mm)

		22/02/2004	05/03/2004	16/03/2004	31/03/2004
	C		57.2	141.5	132.4
	W		22.5	92.4	109.8
		22/02/2004	05/03/2004	16/03/2004	31/03/2004
	Claire		47.2	111.3	99.0
	Deben		32.2	82.3	103.8
	Hereward		28.0	98.2	106.2
	Hyno Esta		21.7	101.7	105.9
	Paragon		27.0	159.2	163.4
	Soissons		69.0	138.7	131.4
	Xi-19		53.8	127.3	138.1
P	treatment		<0.001	<0.001	<0.001
	variety		0.001	<0.001	<0.001
	interaction		0.657	0.675	0.244
SED	treatment		5.75	7.37	3.30
	variety		10.76	13.79	6.17
	interaction		15.22	19.50	8.72
LSD	treatment		11.78	15.09	6.65
	variety		22.04	28.24	12.45
	interaction		ns	ns	ns

3.3.2.5. Shoot dry weight

There was no significant effect of waterlogging on shoot dry weight at any sampling date.

3.3.2.6. Proportion of plant dry weight in the roots

As waterlogging decreased the root dry weight at all sampling dates but had no effect on shoot dry weight, this has resulted in a decrease in the proportion of dry matter allocated to the roots. The effect of variety was only significant at the first harvest, with Xi-19 having a proportionally larger root system. The interaction was very nearly significant at the third harvest, when Claire had the highest figure under control conditions and the lowest after waterlogging. However this should be treated with extreme caution because by the final harvest Claire had the largest root system, as a proportion of total dry weight, when waterlogged.

Table 3.8. The dry weight of the root system, as a percentage of total plant dry weight, of seven wheat varieties grown in drained or waterlogged soil. Figures in italics are the transformed values (square root) and values for P, SED and LSD refer to these.

		23/02/04		05/03/04		16/03/04		31/03/04	
	C	51.9	*7.20*	65.0	*8.01*	61.5	*7.84*	56.8	*7.53*
	W	44.4	*6.65*	40.4	*6.32*	32.5	*5.69*	31.1	*5.50*
	Claire	47.5	*6.89*	49.8	*6.97*	46.6	*6.70*	48.5	*6.70*
	Deben	42.1	*6.45*	53.9	*7.26*	49.0	*6.94*	47.0	*6.77*
	Hereward	49.6	*7.04*	56.9	*7.45*	47.7	*6.81*	42.8	*6.45*
	Hyno Esta	47.4	*6.87*	58.1	*7.58*	45.4	*6.65*	42.4	*6.42*
	Paragon	48.8	*6.98*	54.0	*7.29*	46.8	*6.77*	40.8	*6.32*
	Soissons	48.2	*6.94*	42.6	*6.35*	47.9	*6.84*	47.8	*6.83*
	Xi-19	53.5	*7.30*	53.9	*7.25*	45.7	*6.67*	38.6	*6.12*
Variety	Treatment								
Claire	C	50.4	*7.10*	64.6	*8.03*	64.1	*8.00*	58.1	*7.62*
Claire	W	44.6	*6.68*	34.9	*5.91*	29.1	*5.39*	39.0	*5.78*
Deben	C	49.0	*7.00*	68.6	*8.28*	62.1	*7.88*	61.5	*7.84*
Deben	W	35.2	*5.90*	39.2	*6.24*	36.0	*6.00*	32.6	*5.70*
Hereward	C	53.0	*7.28*	66.8	*8.17*	63.9	*7.99*	57.2	*7.56*
Hereward	W	46.2	*6.79*	46.9	*6.72*	31.6	*5.62*	28.5	*5.33*
Hyno Esta	C	49.5	*7.03*	67.6	*8.22*	59.2	*7.69*	55.8	*7.46*
Hyno Esta	W	45.3	*6.70*	48.5	*6.94*	31.6	*5.62*	29.0	*5.37*
Paragon	C	53.4	*7.31*	66.2	*8.13*	59.9	*7.73*	52.1	*7.21*
Paragon	W	44.2	*6.65*	41.7	*6.44*	33.7	*5.80*	29.4	*5.42*
Soissons	C	49.6	*7.04*	50.8	*6.85*	61.8	*7.86*	62.0	*7.87*
Soissons	W	46.8	*6.84*	34.4	*5.86*	33.9	*5.82*	33.6	*5.79*
Xi-19	C	58.5	*7.63*	70.3	*8.38*	59.9	*7.74*	51.1	*7.15*
Xi-19	W	48.6	*6.96*	37.5	*6.11*	31.5	*5.61*	26.1	*5.10*
P	treatment		<0.001		<0.001		<0.001		<0.001
	variety		0.048		0.277		0.220		0.501
	interaction		0.552		0.829		0.051		0.998
SED	treatment		0.121		0.265		0.063		0.206
	variety		0.227		0.497		0.118		0.386
	interaction		0.321		0.702		0.167		0.546
LSD	treatment		0.248		0.544		0.129		0.416
	variety		0.465		ns		ns		ns
	interaction		ns		ns		0.342		ns

3.3.2.7. Tillering

At the first sampling only two plants, one from each treatment, possessed a coleoptile tiller, both of the variety Hereward. No foliar tillers had emerged at this time so the results are not presented. Until the final harvest the data presented refer to the total number of tillers emerged, as no tiller senescence had yet occurred. For the final harvest both the total number of tillers and the number of live tillers are presented. A tiller was counted as senescent if its youngest leaf was chlorotic. Waterlogging decreased the number of tillers per plant, but this did not become significant until the third sampling. At the final harvest waterlogging decreased the total number of tillers produced, although this was not significant, and caused abortion of some existing tillers, so decreasing the number of live tillers significantly. Of the varieties tested, Hereward produced the most tillers, and the spring wheat Paragon produced the fewest. Xi-19, which includes a spring variety in its parentage, also had few tillers, and this concurs with the results of other variety experiments in the tube in 2002 and the field in 2003. There was no significant interaction between waterlogging and variety.

Table 3.9. The effect of waterlogging on the number of tillers per plant, in addition to the main shoot, of seven wheat varieties.

		05/03/2004	16/03/2004	31/03/2004 total	31/03/2004 live
	C	0.7	1.7	1.46	1.4
	W	0.4	1.2	1.25	1.0
		05/03/2004	16/03/2004	31/03/2004 total	live
	Claire	0.5	1.8	1.3	1.3
	Deben	0.7	1.8	1.8	1.8
	Hereward	0.8	2.0	2.1	2.1
	Hyno Esta	0.7	1.7	1.9	1.5
	Paragon	0.0	0.2	0.0	0.0
	Soissons	0.5	1.5	1.3	1.1
	Xi-19	0.7	1.2	1.3	0.5
P	treatment	0.192	0.048	0.300	0.009
	variety	0.296	<0.001	<0.001	<0.001
	interaction	0.475	0.744	0.617	0.128
SED	treatment	0.18	0.21	0.20	0.16
	variety	0.33	0.39	0.38	0.29
	interaction	0.47	0.55	0.54	0.42
LSD	treatment	ns	0.43	ns	0.32
	variety	ns	0.80	0.77	0.59
	interaction	ns	ns	ns	ns

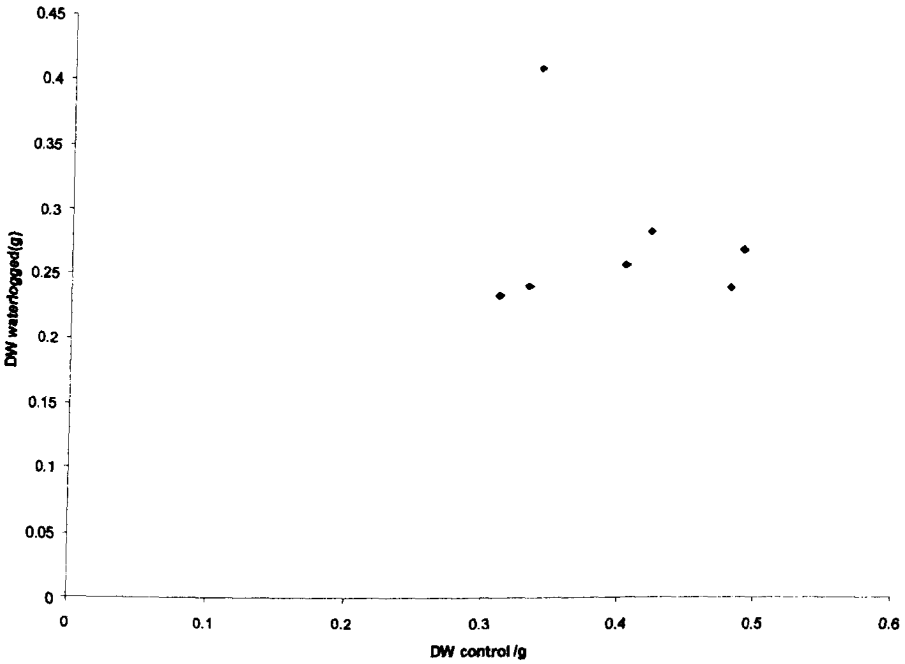

Figure 3.10. The relationship between mean plant dry weight of 7 wheat varieties grown in waterlogged soil and mean dry weight when grown in drained control conditions.

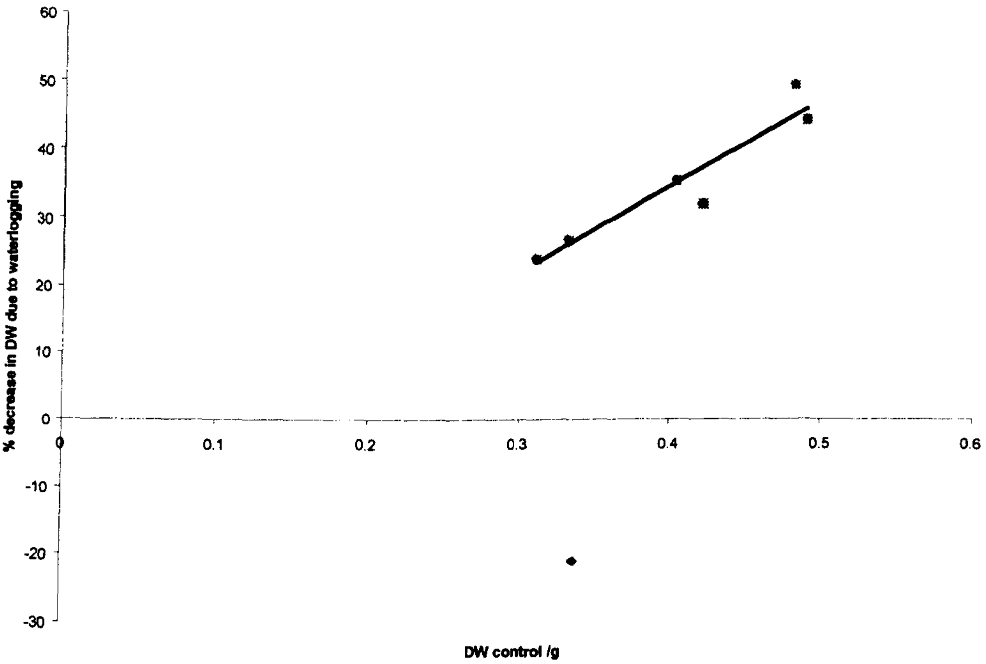

Figure 3.11. The relationship between percentage decrease in total dry weight of 7 wheat varieties and mean plant dry weight when grown in control conditions. The dry weight of the waterlogged Claire was greater than the control, so is excluded from the regression. $P < 0.001$, percentage of variation accounted for by linear regression= 88.7 %.

3.3.3. Comparison of the two experiments

In both experiments waterlogging decreased root dry weight, number of shoots per plant and the ratio of root dry weight to shoot dry weight. The waterlogged plants in both experiments had a chlorotic and unhealthy appearance by the end of the experimental period. The only major area of disagreement between the two experiments is in respect to the effect of waterlogging on shoot dry weight; in 2002 waterlogging caused a significant decrease in shoot dry weight, in 2004 the effect was not significant. The total plant dry weights (shoot + root) in the 2004 experiment were much smaller than those in 2002, so to allow comparison between the two experiments the relative dry weight of each variety was calculated as a percentage of the mean for all varieties in that experiment, with the mean being given a value of 100. It was found that when the reduction in dry weight due to waterlogging, expressed as a percentage of control dry weight, was plotted against the relative control dry weight the data from both experiments was part of the same trend. Additionally the data from the growth analysis at the end of the waterlogging period from the five varieties grown in the 2003 field trial also fitted the trend very closely, when expressed as a percentage of the mean for that experiment. Varieties with the highest dry weights under control conditions suffered the largest decreases in dry weight due to waterlogging, both in relative and absolute terms. The data for final grain dry weight from the 2003 field trial showed a similar trend, but because of the compensatory growth that occurred between waterlogging and harvest, the decreases were not as great as for the three data sets taken immediately after waterlogging.

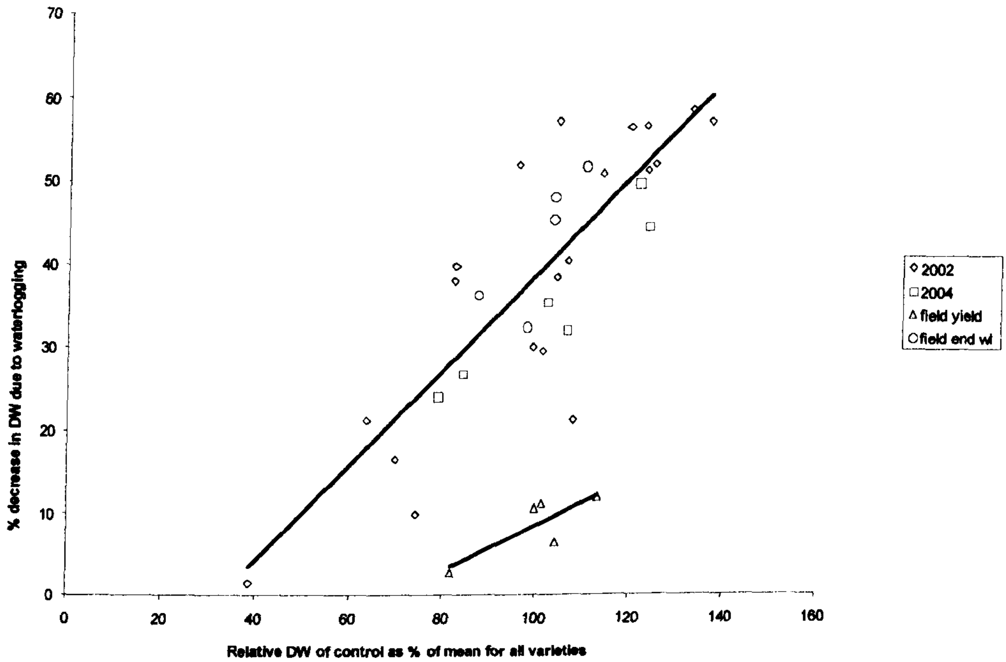

Figure 3.12. The relationship between the decrease in plant dry weight, expressed as a percentage of the dry weight of control, and the relative dry weight of control, expressed as a percentage of the mean for all varieties, of varieties of wheat grown in three experiments to compare the effects of waterlogging and variety. $P < 0.001$, percentage of variation accounted for by linear regression 65.8%.

3.4. DISCUSSION

The significant interaction between the effects of waterlogging and variety on shoot and root dry weight, tillering and proportion of dead material found in 2002 tube experiment suggested that differences in response to waterlogging existed between the wheat varieties tested. The weakness of the positive correlation between dry weight under drained and waterlogged conditions also concurred with this, implying that another factor, besides growth potential in unstressed conditions, had a role in determining growth when waterlogged. This is in contrast to the field variety experiment and the 2004 tube experiment, which found no significant interaction. The significance of the interaction in the 2002 tube experiment may be an error as a result of analysing many treatment means. However whilst the interaction in the field experiment was not significant the trend in varietal response to waterlogging was similar. The variety with the lowest grain yield, Hereward, had the smallest percentage reduction in yield due to waterlogging. In the 2002 tube experiment the general trend is for the varieties with the lowest dry weight under control conditions to suffer the smallest percentage decrease in dry weight when waterlogged.

It was observed that the differences between the best and the worst varieties were often greater under control conditions than after being waterlogged - for example root and shoot dry weights for the 2002 experiment and root length and dry weight in the 2004 experiment (see figures 3.1 and 3.2). This observation, together with the strong positive correlation between control dry weights and percentage decrease in dry weight due to waterlogging suggests that waterlogging had a levelling effect. The reason for the poor correlation between performance under control and waterlogged conditions, and the significant interaction in the 2002 experiment, was possibly not because some varieties were more tolerant of waterlogging than others, but that waterlogging cut all varieties down to a similar level. If differences between varieties were due to the superior tolerance of some varieties it would be expected that these varieties would display characteristics linked with tolerance. For example, these could include enhanced initiation of nodal roots, and aerenchyma formation, evident by the greater ability of aerenchymatous roots to penetrate below the water level. In contrast, all varieties showed a similar increase in the number of nodal root axes formed in response to waterlogging. These nodal roots were better able to penetrate the waterlogged soil than the seminal system, which was dead below the water level by the end of the 2004 experiment, thus suggesting that the nodal roots were more porous and thus more able to supply oxygen to the growing tips than the seminal roots. However there was no significant difference between varieties in the length of nodal roots by the end of the 2004 experiment.

As the effect of waterlogging on number of seminal root axes initiated was only significant on one occasion, this result must be treated with caution, in the absence of further evidence. By the end of the experiment differences between varieties in the number of seminal root axes were not significant, and the finding that there is little variation between wheat varieties in seminal root number concurs with previous work (Welbank *et al.,* 1973; Gregory *et al.,* 1978). Deben, Xi-19 and Soissons initiated seminal roots faster than the other varieties, so had significantly more seminal axes at the first and second harvests. In the case of Deben and Xi-19 this may be a result of their larger seed size, a characteristic associated with a vigorous seminal root system (MacKey, 1973). Soissons showed a faster rate of development, in respect to other characteristics such as leaf emergence. In this experiment most plants produced only five seminal roots, whilst previous work had found winter wheat usually produces six or seven (Gregory *et al.,* 1978; Wiedenroth and Erdmann, 1985). The probable reason for this difference is that this experiment was sown in spring in a glasshouse. Autumn sown winter wheat has much longer for the seminal root system to develop over winter before the nodal system takes over in the spring. Late sown winter wheat can compress development, sometimes missing out a leaf, so perhaps the last pair of seminal roots (roots numbers 6 and 7, using the numbering system of Wiedenroth and Erdmann, 1985) were missed out in these spring sown plants. All varieties increased initiation of adventitious nodal roots in response to waterlogging. Although the fastest developing varieties, Paragon and Soissons, initiated nodal roots more quickly, the other varieties had caught up by the final harvest. The fact that there was no significant interaction effect of waterlogging and variety on nodal root initiation at any stage suggests that no one variety is better able to tolerate waterlogging by producing nodal roots than any other.

The ability to maintain the ratio of root to shoot dry mass when waterlogged has been suggested as a measure of tolerance (Erdmann and Wiedenroth, 1986). In an experiment with seedlings of a range of *Triticum* species, modern bread wheat, *Triticum aestivum*, was best able to maintain its root to shoot ratio. The evidence for differences between varieties of *Triticum aestivum* found in these experiments is unclear. The first experiment in 2002 found that there was a significant interaction between waterlogging and variety, whilst the 2004 experiment found no such interaction. Additionally there were differences in the relative performances of the varieties between sampling dates in the 2004 experiment. For example in the third harvest Claire was least able to maintain root to shoot ratio, but in the final harvest it was most able.

Both these experiments raise questions concerning the validity of comparing the results of different types of experiments. Part of the problem lies with not taking the plants to yield. When biomass samples are taken during the vegetative stage the fastest developing varieties such as Xi-19 and Soissons will have the largest biomass, even though their final yield potential may be lower than other, slower developing varieties. Additionally the ability to recover from stress may be more important in determining final yield than tolerance during stress. Deben had the highest grain yield after waterlogging in the bin and field variety trials, but had large decreases in dry weight in the tube experiments. The only variety which may demonstrate some tolerance is Claire, which although did not have more or deeper nodal roots, had the highest waterlogged root dry weight in both tube experiments, had the smallest decrease in total dry weight at harvest and the second best yield. However in the variety screen in the bins Claire's grain yield after waterlogging was equal to the mean for all varieties.

These experiments also indicate that observation and measurement of seedling growth in waterlogged conditions is not predictive of effects on final yield. Therefore it is very unlikely that a reliable method could be developed to screen varieties for tolerance to waterlogging at the seedling stage. This is further discussed in the final chapter, section 7.6.

Chapter 4. LYSIMETER EXPERIMENTS TO INVESTIGATE THE INTERACTION BETWEEN WINTER WATERLOGGING AND SUMMER DROUGHT

4.1. INTRODUCTION

The variety screen in the bins established in autumn 2001 did not include drained controls, in order to maximise the amount of genetic material that could be screened for tolerance under waterlogged conditions. Therefore a second experiment was planned in concrete lysimeters in the glasshouse at the Henfaes Research Centre, to include drained controls, and allow the effects of winter waterlogging on winter wheat to be studied. The lysimeters would allow small plots of wheat to be grown inside a glasshouse, with some degree of control over soil conditions. The glasshouse conditions would also allow withholding of water for a drought treatment.

Many farmers believe that crops that have suffered winter waterlogging are more vulnerable to a subsequent summer drought, as a result of a poorly developed root system. The results of previous experiments have not validated this anecdotal evidence, and also suggested that cereals in the UK are much more likely to experience winter waterlogging than summer drought (Cannell *et al.,* 1984). However climate change models predict that as well as an increase in winter rainfall, there will be a decrease in summer rainfall, and increased threat of drought (Hulme *et al.,* 2002). To investigate the interaction between waterlogging and drought, and compare their effects on plant growth and physiology, a drought treatment was included, in a factorial design.

Waterlogging during establishment has been shown to decrease plant populations (Cannell *et al.,* 1980; Belford 1981). In a move to cut establishment costs farmers are being encouraged to cut seed rates to establish a plant population with as little as 62 plants m^{-2}, if sown in September, or 90 plants m^{-2} if sown up to mid October (HGCA, 2000). This is in contrast to normal seed rates of 300-400 seeds m^{-2} to establish a population of around 275 plants m^{-2}. Unfortunately there has been a lack of experimental work done to investigate the interaction between waterlogging and seed rate; a recent comprehensive review on waterlogging and cereals was unable to uncover any published work on the subject (Setter and Waters, 2003). Therefore the experiment planted in autumn 2001 was a split plot design, with seed rates of 264 seeds m^{-2} and 132 seeds m^{-2}. The variety chosen for the experiment was Claire, as at the time of sowing it was the most widely grown winter wheat variety in the UK. It also has a good disease resistance profile, apart from a susceptibility to powdery mildew (refer to Appendix 1).

In the second season variety was substituted for seed rate as the sub-plot factor. The varieties used were Deben, which had the highest grain yield after waterlogging in the previous variety screen in the bins, and Xi-19 which, in the same experiment, had a lower yield than what would be expected, and appeared more susceptible to damage by waterlogging than some other varieties in the 2002 tube experiment (refer to chapters 2 and 3).

4.2. MATERIALS AND METHODS

4.2.1. 2001-2002 experiment

Twenty concrete lysimeters, in a glasshouse, with a volume of approximately $1m^3$ (surface area = 1.2m x 0.9m, depth = 1m) were filled with local clay loam topsoil. The bottom of each lysimeter was filled with a 30 cm layer of coarse gravel, separated from the soil by a water-permeable membrane. This was to allow free drainage. The drainage holes of all waterlogging treated lysimeters were blocked with rubber bungs and silicon sealant. All lysimeters were treated with waterproof paint, to prevent seepage through the permeable concrete blocks. The experimental design was a split plot arranged in five randomised blocks. Blocks were used as the glasshouse only had a door at one end, and no form of ventilation at the other end, so a temperature gradient was expected. The main plot treatments applied to each whole lysimeter were: control, winter waterlogged, summer drought, winter waterlogged followed by summer drought. Each lysymeter was split in half. The split plot treatment was seed rate, either 264 plants m^{-2} or 132 plants m^{-2}. Plots were hand sown with Claire winter wheat, on 24 October 2001 using a template, to ensure even spacing of plants. Ten rows were sown in each lysimeter, 12cm apart, with 3cm between plants in the high seed rate and 6cm in the lower. Seeds were sown approximately 4cm deep, using a ‘dibber’, marked to ensure the depth was even. Two seeds were sown in each position and the plots thinned to the desired plant population when the seedlings reached the first leaf fully emerged stage (Zadoks 11)

Waterlogging was achieved by daily watering with a hose, and it proved difficult to achieve waterlogging at first due to the large volume of water needed and inadequate waterproofing of the lysimeters (the ‘waterproof paint’ proved to be porous). Thus the plots were only fully waterlogged during February. It had been planned to waterlog the lysimeters from the bottom up, however the waterproofing treatment applied was not adequate to prevent some water seeping through the porous concrete blocks, from which the lysimeters were constructed. Seepage was from the blocks below the level of the membrane at the soil-gravel interface, so there was no danger of accidentally waterlogging adjacent control lysimeters. In response to this problem, sufficient water was applied to waterlog from the top down, by applying water in excess of the rate at which it could infiltrate the soil, indicated by pooling of water on the soil surface.

Drought was applied from mid booting (Zadoks 45) on 29 April 2002. At first it was achieved by withholding water completely but the high glasshouse temperature, and resultant high transpiration rate of the plants, meant that this treatment was initially too severe. Instead droughted plots were watered twice weekly from 20 May, versa daily watering for the controls.

Weeds were removed by hand. Foliar disease was controlled by applications of Unix (0.67 g/ha) and Landmark (1 l/ha) at stem extension (Zadoks 31) and Landmark (1 l/ha) at flag leaf emerged stage (Zadoks 39). Disease levels were very low, with mildew (*Erysiphe graminis*) early in the spring being the only problem. However plants quickly grew away from this. Aphids were a problem later in the season as the plants neared maturity, but appeared too late to affect yields so no chemical treatment was required. P and K were applied to the seedbed at a rate equivalent to 40 kg/ha, and N was applied as ammonium nitrate at a total rate equivalent to 150 kg/ha, in two equal splits at Zadoks 30 and 32.

Destructive growth analyses were done at the end of waterlogging on 11 March 2002 and at ear emergence on 7 May 2002. Sample size was 15 plants from the 132 plants m^{-2} sub plots and 30 plants from the 264 plants m^{-2} subplots. Plants were cut at the stem base. At the first growth analysis the total shoot number and total plant biomass were measured. At the second growth analysis live shoots were divided into those which had formed a spike and those which had not; the latter would not be expected to survive to harvest so were counted with the dead or dying shoots. Green leaves were removed from the shoots which had formed a spike and the area measured with an area meter. One ear was chosen at random from each sample, the total spike length and the length emerged from the boot was measured, and the number of spikelets counted. All plant fractions were dried in an oven at 80 ^{0}C for 48 hours and the dry weights measured. At maturity a subsample was taken, consisting of the middle row of each sub plot. The remainder was bagged, labelled and put aside to be threshed later with the Wintersteiger machine. The subsample was divided into mature ears and dead tillers. Small green immature ears were counted as dead tillers as these would not produce grain at harvest. The mature ears were cut from the stems at the collar. A subsample of ears was taken and hand threshed, so that a grain fresh weight could be taken to allow the grain moisture content to be calculated. The remainder was dried before hand threshing to make it easier. The number of filled and empty spikelets of this second sub-sample was counted. A random sub-sample of five stems was taken to measure straw length. All plant fractions were bagged and dried in an oven at 80 ^{0}C for 48 hours. Drought and waterlogged plus drought plots were harvested on 6 June 2002; controls and waterlogged plots on 4 July 2002.

Dried grain samples were milled and the nitrogen content analysed using the Kjeldahl method. Grain crude protein was calculated by multiplying the nitrogen percentage by 5.83 (Sylvester-Bradley *et al.*, 1997).

4.2.2. 2002-2003

The same experimental design and main plot treatments were used as the previous season. However, variety was used as the split plot treatment, with each lysimeter split into half Deben and half Xi-19. Plots were sown on 29 October 2002 using the 264 seeds m^{2} template from 2001-2002. Plots were not double sown as experience last year showed that germination was almost one hundred percent and emergence very quick because of the warm soil in the glasshouse. Thinning may also cause unnecessary damage to the remaining seedlings.

Waterlogging treatment was applied using an irrigation system, similar to that used in the field in 2002-2003. This allowed waterlogging to be imposed through January and February. Waterlogging was from the top down, as in the field, and plots were considered waterlogged when water pooled on the soil surface. Drought stress was applied by reducing watering of selected plots to twice a week from anthesis (Zadoks 61) on 12 May 2003 to harvest. Crop management followed the exact protocol of the previous year, in timings at rates of inputs.

No destructive sampling or growth analysis was done to allow plots to recover from mouse damage in January. Also the field experiment run during this season provided a larger area to allow destructive sampling and still give well replicated harvest results. However none destructive counts of the tiller number of random samples of five plants were carried out *in situ*. The same protocol was used for the harvest at maturity as the previous experiment in 2002. Drought and waterlogged plus drought plots were harvested on 3 July 2003: controls and waterlogged plots on 8 July 2003.

4.2.3. Statistical Analysis

Data was analysed as a split plot design using a general ANOVA, with treatment structure = drought*waterlogging*seed rate, and block structure = blocks/ lysimeter/ split plot, using Genstat 7 (for 2002-2003 read 'variety' for 'seed rate'). There were 12 residual degrees of freedom in the main plot stratum, and 16 in the subplot stratum. (In 2002-2003, crows damaged the last two plots in block 5 at emergence, so the drought treatment in this block was discarded; therefore there were 10 main plot residual degrees of freedom, and 14 in the subplot stratum). The SED and LSD values quoted for the interactions are those that should be used when comparing means with the same main plot treatment. Means presented are restricted to waterlogging, drought, waterlogging x drought, and seed rate. The interactions; waterlogging x seed rate, drought x seed rate, and waterlogging x drought x seed rate were not significant at any time so are not presented, with one exception – grain yield in 2001-2002, see Table 4.5a .

4.3. RESULTS

4.3.1. Growth measurements

4.3.1.1. 2001-2002 experiments

At the end of the waterlogging period the decrease in shoot number due to waterlogging was not significant (Table 4.1). Although the interaction between waterlogging and plant density was not significant, waterlogging appeared to substantially decrease the number of shoots in the higher plant density, but actually increased shoot number slightly in the lower density. Waterlogging did significantly decrease the total above ground biomass of the plants. The lower density plots had a significantly smaller dry weight per area, but the total was greater than half that of the higher seed rate (which had twice as many plants per area), indicating that these plants had compensated to some extent. There was no significant interaction between the waterlogging and seed rate. There was no loss of plants due to waterlogging. Drought had not yet been applied at this time.

Table 4.1. Shoots m^{-2} and total shoot system dry weight m^{-2} of Claire winter wheat at the end of the waterlogging period

Treatment	Level	Shoots m^{-2}	Biomass (DW g m^{-2})
Waterlogging	Control Waterlogged	437 415	119.8 94.9
Sowing density (plants m^{-2})	264 132	507 345	132.8 81.9
P	Treatment Sowing density Interaction	0.657 0.001 0.243	0.024 0.002 0.295
SED	Treatment Sowing density Interaction	45.7 33.2 47.0	7.03 11.49 16.21
LSD	Treatment Sowing density Interaction	ns 76.6 ns	19.52 26.42 ns

At ear emergence both waterlogging and drought decreased the number of ears per unit area and the total number of shoots, with and without ears, significantly (Table 4.2). This is in contrast to the growth analysis at the end of the waterlogging period, where the decrease in shoot number per unit area was not significant. This indicates that waterlogging has a residual effect on tiller production. Drought would be expected to decrease ear number but not the total number of tillers present. However the total number of shoots was decreased, probably as a result of small tillers being aborted due to the drought, sloughing away from the main shoot and being lost. Waterlogging and drought significantly decreased shoot dry weight and green area. Decreasing seed rate significantly decreased shoot and ear number, shoot dry weight and green area. Waterlogging had no effect on the number of spikelets per ear, but both waterlogging and drought decreased the total length of the spike (Table 4.3). Waterlogging also decreased the percentage of the total spike length that had emerged from the boot, indicating a suppressive effect on development, but drought had no effect. The low seed rate plants had slightly more spikelets per ear, although not quite significantly so ($P = 0.08$), and a significantly longer spike. This is evidence of a compensation mechanism, in response to the sparser canopy. There were no interactions between seed rate and waterlogging treatment for any of the variables recorded at ear emergence.

Table 4.2. Shoot and ear number per unit area, total shoot dry weight and green area from a growth analysis at ear emergence 7/5/02

Treatment	Level	Shoots m^{-2}	Ears m^{-2}	Shoot dry weight (g/m^2)	Green Area Index
Waterlogging	Control (C)	649	512	1584	8.3
	Waterlogged (W)	458	359	1009	6.2
Drought	Control (C)	633	507	1586	9.8
	Drought (D)	474	365	1007	4.7
Interaction (Waterlogging x Drought)	C x C	757	590	1949	11.0
	W x C	508	423	1222	8.6
	C x D	541	434	1259	5.5
	W x D	407	295	796	3.8
Seed Rate	132	448	350	1083	6.2
	264	658	522	1511	8.3
P	Waterlogging	<0.001	<0.001	<0.001	<0.001
	Drought	<0.001	<0.001	<0.001	<0.001
	Interaction	0.014	0.524	0.024	0.203
	Seed Rate	<0.001	<0.001	0.023	0.016
SED	Waterlogging	20.0	20.8	59.0	0.29
	Drought	20.0	20.8	59.0	0.29
	Interaction	28.3	29.4	83.5	0.41
	Seed Rate	52.3	42.0	169.5	0.79
LSD	Waterlogging	43.6	45.3	128.6	0.63
	Drought	43.6	45.3	128.6	0.63
	Interaction	61.6	ns	181.9	ns
	Seed Rate	110.8	89.0	359.3	1.67

Table 4.3. Number of spikelets per spike, total spike length, and percentage of total spike length emerged at time of growth analysis on 7/5/02.

Treatment	Level	Number of spikelets per ear (spike)	Total spike length (mm)	% of spike emerged from boot
Waterlogging	Control (C)	27.9	137.8	86.3
	Waterlogged (W)	27.7	123.6	35.5
Drought	Control (C)	28.2	138.4	60.3
	Drought (D)	27.4	123.0	61.5
Interaction (Waterlogging x Drought)	C x C	28.4	143.0	81.9
	W x C	27.9	133.8	38.8
	C x D	27.4	132.6	90.8
	W x D	27.4	113.4	32.1
Seed Rate	132	28.3	134.7	59.4
	264	27.3	126.7	62.4
P	Waterlogging	0.616	<0.001	<0.001
	Drought	0.148	<0.001	0.885
	Interaction	0.616	0.098	0.327
	Seed Rate	0.080	0.008	0.474
SED	Waterlogging	0.49	2.79	7.63
	Drought	0.49	2.79	7.63
	Interaction	0.69	3.94	10.79
	Seed Rate	0.51	2.62	4.06
LSD	Waterlogging	ns	6.08	16.62
	Drought	ns	6.08	ns
	Interaction	ns	ns	ns
	Seed Rate	ns	5.56	ns

4.3.1.2. 2002-2003 experiment

Waterlogging significantly decreased the number of tillers on both counting dates (Table 4.5). Deben showed greater tiller production than Xi-19, both under control and waterlogged conditions, but Xi-19 had begun to catch up by the second date. The data in table 4.5 suggest that the reduction in ear number at harvest (discussed later) due to waterlogging is caused by inhibition of tiller initiation, or abortion at a very early stage, before emergence from the leaf sheath. The number of tillers of waterlogged plants did not increase between the two counting dates, whilst that of the controls of both varieties did. Drought had yet to be applied. The measurements of leaf length and length of the pseudostem illustrate the restriction of shoot growth in response to waterlogging stress. Xi-19 also demonstrates its higher early season growth seen in the bin, tube and field experiments. This increased demand from the shoot system may cause this variety to show stress symptoms more readily when the nitrogen uptake of the roots is restricted by waterlogging.

Table 4.4. The total number of shoots on five plants during and at the end of the waterlogging period, and the length of the youngest fully emerged leaf and pseudostem at the end of waterlogging.

	No. shoots /plant 21/1/03	No. shoots /plant 10/3/03	Length of youngest leaf (mm)	Length of pseudo-stem (mm)
Treatment				
Control	1.8	2.5	325	14.7
Waterlogged	1.4	1.3	266	8.0
Variety				
Deben	2.1	2.2	286	11.0
Xi-19	1.1	1.6	305	11.7
Interaction				
Control x Deben	2.4	2.7	318	14.6
Control x Xi-19	1.1	2.2	333	14.8
Waterlogged x Deben	1.7	1.6	254	7.4
Waterlogged x Xi-19	1.0	1.0	278	8.6
P				
Treatment	0.007	0.003	<0.001	<0.001
Variety	<0.001	0.003	0.010	0.036
Interaction	0.050	0.939	0.498	0.154
SED				
Treatment	0.08	0.17	3.52	0.46
Variety	0.11	0.13	5.85	0.30
Interaction	0.16	0.18	8.26	0.42
LSD				
Treatment	0.22	0.48	9.77	1.28
Variety	0.26	0.29	13.50	0.68
Interaction	0.30	ns	19.9	ns

4.3.2. Harvest Measurements

In both years, both winter waterlogging and summer drought decreased grain yield (Tables 4.5 and 4.6). In the both years, of the yield components, only the number of ears per unit area was decreased significantly by waterlogging. In 2001-2002 drought decreased ear number, TGW and the number of grains per ear significantly, indicative of poor grain-fill, and also significantly decreased harvest index in both years. Waterlogged plants had more grains per ear and slightly higher harvest indices, although the differences between them and the controls were smaller than the LSD, and so not significant. However the trend suggests that this is a compensation measure. In the 2001-2002 experiment the low seed rate plots had a significantly lower yield, but there was no significant effect of seed rate on yield components. There was a significant interaction between the effects of waterlogging, drought and seed rate on grain yields. The difference in grain yield between the two seed rates was much greater where no stress – neither waterlogging nor drought – was applied (Table 4.5a). In the second year drought had no effect on ear number, as treatment was applied later than in the first season. Drought significantly decreased TGW, but waterlogging had no effect (Table 4.6). All harvest indices were abnormally low due to the very hot glasshouse conditions during grain filling. There were no significant differences due to waterlogging or drought, but the harvest index of Xi-19 was slightly higher than Deben, indicating that this variety coped better with the atypical conditions.

Figure 4.1 illustrates that, as in the field experiment (chapter 2) there was a positive linear relationship between green area at the point of maximum canopy size (ear emergence in the lysimeters, anthesis in the field) and grain yield. Waterlogged plants tended to have a smaller green area and lower yield. Drought had a more severe effect on both green area and yield than waterlogging at harvest 2002. If the drought plots are considered on their own there appears to be a much weaker correlation between green area and yield, due to poor grain fill, evidence of which are the lower TGWs and fewer grains per ear.

Table 4.5 The effect of waterlogging, drought and seed rate on grain yield (tha^{-1}) at 14% moisture, and yield components of Claire winter wheat in 2001-2002.

Treatment	Level	Yield (t/ha)	Ears m^{-2}	TGW (g)	Grains ear^{-1}	Harvest Index
Waterlogging	Control (C)	10.51	374	47.4	55.2	47.0
	Waterlogged (W)	8.46	347	46.8	56.5	48.9
Drought	Control (C)	12.90	417	52.1	63.6	52.6
	Drought (D)	6.07	304	42.1	48.0	43.3
Interaction (Waterlogging x Drought)	C x C	14.97	445	52.3	62.5	51.8
	W x C	10.83	390	52.0	64.7	53.4
	C x D	6.05	304	42.6	47.8	42.2
	W x D	6.08	305	41.6	48.3	44.4
Seed Rate	132	8.90	347	46.9	56.6	48.5
	264	10.06	374	47.3	55.1	47.4
P	Waterlogging	<0.001	0.022	0.703	0.387	0.029
	Drought	<0.001	<0.001	<0.001	<0.001	<0.001
	Interaction	<0.001	0.019	0.805	0.576	0.738
	Seed Rate	0.003	0.121	0.621	0.461	0.251
SED	Waterlogging	0.310	9.9	1.53	1.50	0.77
	Drought	0.310	9.9	1.53	1.50	0.77
	Interaction	0.439	14.0	2.16	2.12	1.08
	Seed Rate	0.309	16.2	0.77	2.03	0.89
LSD	Waterlogging	0.715	22.1	ns	ns	ns
	Drought	0.715	22.1	3.33	3.30	1.67
	Interaction	1.011	31.3	ns	ns	ns
	Seed Rate	0.674	ns	ns	ns	ns

Table 4.5a. The interaction between waterlogging, drought and seed rate on yield.

Waterlogging	C	C	W	W	
Drought	C	D	C	D	P = 0.007
Seed rate 132	13.09	6.00	10.72	5.69	SED = 0.438
264	16.73	6.10	10.95	6.48	LSD = 1.348

Table 4.6 The effect of waterlogging and drought on grain yield (tha^{-1}) at 14% moisture, and yield components of Deben and Xi-19 winter wheat in the 2002-2003 experiment.

Treatment	Level	Yield (t/ha)	Ears m^{-2}	TGW (g)	Grains ear^{-1}	Harvest Index
Waterlogging	Control (C)	9.99	408	43.3	53.5	22.9
	Waterlogged (W)	7.62	334	40.8	49.6	23.8
Drought	Control (C)	9.53	361	45.7	53.0	24.1
	Drought (D)	7.89	384	37.5	49.8	22.1
Interaction (Waterlogging x Drought)	C x C	10.84	393	46.6	57.4	24.0
	W x C	8.23	328	44.9	48.5	24.8
	C x D	8.93	426	39.3	48.5	21.6
	W x D	6.85	342	35.7	51.0	22.6
Variety	Deben	8.26	392	39.3	48.8	22.0
	Xi-19	9.35	350	44.9	54.3	24.8
P	Waterlogging	<0.001	0.002	0.280	0.135	0.347
	Drought	0.014	0.232	0.006	0.236	0.039
	Interaction	0.620	0.620	0.667	0.037	0.897
	Variety	0.051	0.032	0.006	0.103	<0.001
SED	Waterlogging	0.517	17.2	2.20	2.37	0.91
	Drought	0.549	18.3	2.34	2.52	0.97
	Interaction	0.756	17.8	3.22	3.47	1.33
	Variety	0.510	25.2	1.71	3.15	0.59
LSD	Waterlogging	1.153	38.40	ns	ns	ns
	Drought	1.222	ns	5.20	ns	2.15
	Interaction	1.640	ns	ns	7.73	ns
	Variety	1.102	56.14	3.69	ns	1.27

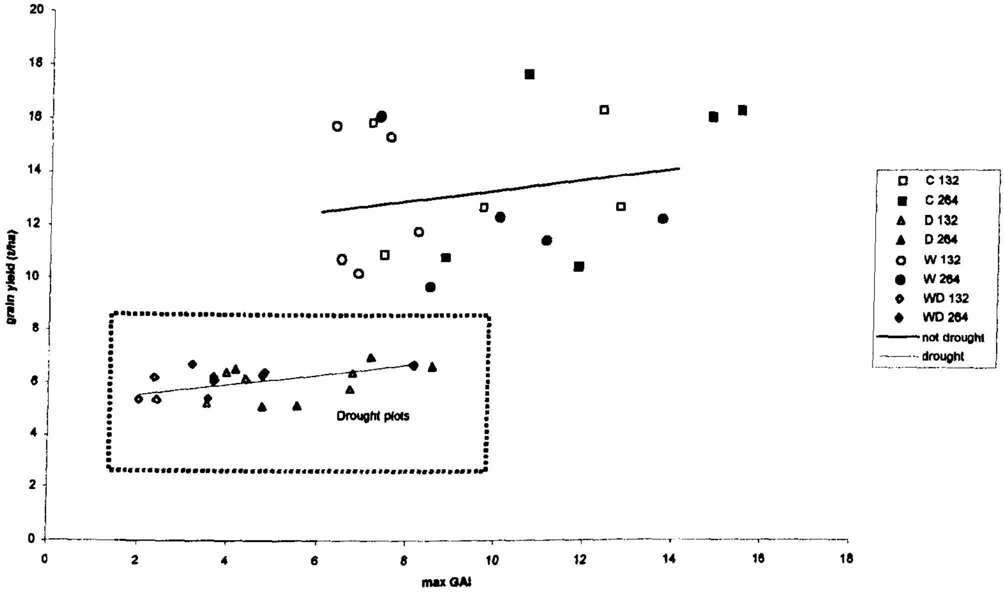

Figure 4.1. The relationship between green area at ear emergence and grain yield (dry weight g/m^2) in the 2001-2 lysimeter experiment. $P < 0.001$, percentage of variation accounted for = 52.8, addition of drought, $P < 0.001$, percentage of variation accounted for by the model = 80.2%.

Waterlogging significantly decreased grain protein percentage and the total amount of nitrogen taken up and partitioned into the grain (Table 4.7). Drought significantly increased grain protein content, by curtailing carbohydrate deposition during grain fill, evidence of which is the depression of TGW by the drought treatment. However total nitrogen content of the grain per unit area was decreased by drought. Unlike the variety screen (Chapter 2, Figure 2.12) there was not a strong negative relationship between grain yield and protein percentage content (Figure 4.2).

Table 4.7. Grain protein concentration of grain dry weight and the total nitrogen content of grain per unit area.

Treatment	Level	Grain protein concentration	Uptake in grain (g/m^2)
Waterlogging	Control (C)	11.34	95.7
	Waterlogged (W)	10.12	80.7
Drought	Control (C)	9.76	114.2
	Drought (D)	11.70	62.2
Interaction (Waterlogging x Drought)	C x C	10.19	125.2
	W x C	9.33	103.1
	C x D	12.49	66.1
	W x D	10.92	58.3
Seed Rate	132	10.68	86.9
	264	10.78	89.5
P	Waterlogging	0.001	0.030
	Drought	<0.001	<0.001
	Interaction	0.243	0.261
	Seed Rate	0.649	0.644
SED	Waterlogging	0.287	6.09
	Drought	0.287	6.09
	Interaction	0.406	8.61
	Seed Rate	0.228	5.51
LSD	Waterlogging	0.625	13.27
	Drought	0.625	13.27
	Interaction	ns	ns
	Seed Rate	ns	ns

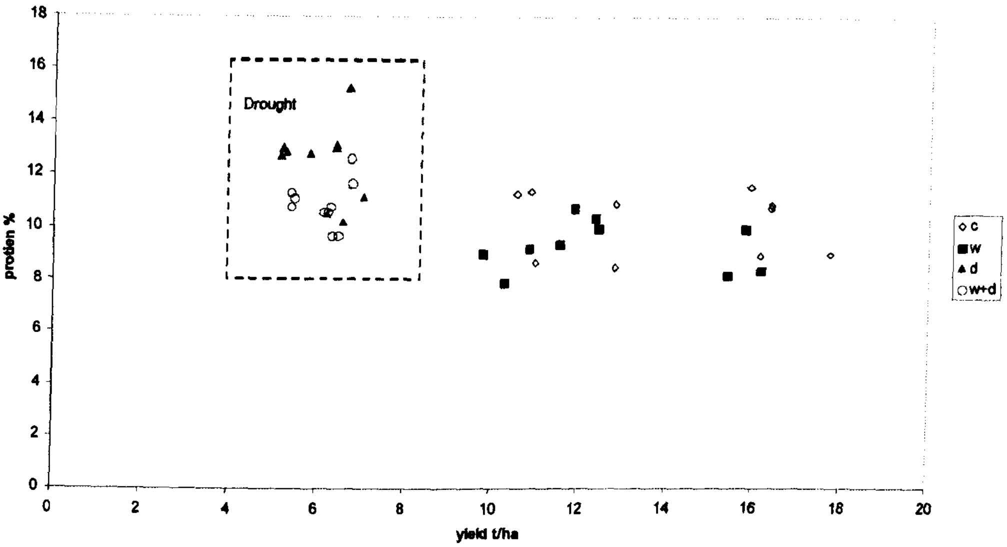

Figure 4.2. The relationship between grain yield and grain protein content of Claire winter wheat subjected to waterlogging and drought.

4.3.3. Effects of waterlogging on soil structure

After harvest in 2002 it was noticed that the soil in the waterlogged lysimeters had slumped considerably. As the total volume of the lysimeters was known, the volume of soil could be calculated by measuring the distance between the top of the lysimeter and the soil surface (Table 4.8). Waterlogging caused a decrease in soil volume of 9.7%, which must have been due to a decrease in air pore volume, as no soil particles could have leached from the lysimeters through the membrane. This concurs with farmers' observations that waterlogged soils slump and become 'sad'. When the lysimeters were dug out at the end of these experiments to prepare them for a new experiment, lumps of grey 'gley soil' were found in the waterlogged plots, a symptom of anaerobic conditions.

Table 4.8. The effect of waterlogging and drought on the volume of soil in the lysimeters at harvest 2002.

Treatment	Level	Soil volume (m^3)
Waterlogging	Control	0.72
	Waterlogged	0.65
Drought	Control	0.69
	Drought	0.68
Interaction	Control	0.72
	Waterlogged	0.66
	Drought	0.72
	Waterlogged + Drought	0.65
P	Waterlogging	<0.001
	Drought	0.533
	Interaction	0.775
SED	Waterlogging	0.008
	Drought	0.008
	Interaction	0.011
LSD	Waterlogging	0.017
	Drought	ns
	Interaction	ns

4.4. DISCUSSION

4.4.1. The effects of waterlogging

In both years waterlogging decreased grain yield at harvest. The yields for harvest 2003 were lower due to two periods of unusually hot weather. The first was a period of sunny weather in March and April, causing glasshouse temperatures to reach 30^0C. This caused early and excessive stem extension in both varieties, both naturally long strawed, leading to wasteful early vegetative growth and very poor harvest indices.

Secondly very hot weather in June and July (up to 40 ^{0}C in the glasshouse) shortened grain-fill.

The effect of waterlogging was more severe in the second year, 25.3% yield loss in 2002-2003 verses 10.2% in 2001-2002. These losses are in the range of those found in the experiments at Letcombe using lysimeters (Cannell *et al.*, 1980; Belford 1981; Cannell *et al.*, 1984; Belford *et al.*, 1985). However the differences in severity of waterlogging yield losses between the two seasons does not agree with the trend found by Cannell *et al.* (1980), where losses were largest in high yield years. The higher losses in the 2002-2003 season when control yields were lower were possibly due to the improved irrigation system and cumulative damage to the soil structure as plots received the same treatment level in both years.

The results suggested that any reduction in grain yield due to waterlogging at harvest was due to a reduction in tillering rather than reduction in spikelet number, in agreement with previous workers (Belford *et al.* 1985). In both years waterlogging significantly reduced the total number of tillers (with a spike and dead tillerts) at harvest. The results agree with shoot counts done during the growing season and show that the reduction of ear number at harvest was due to the inhibition of tiller initiation rather than an increased rate of tiller abortion. In both years waterlogging significantly decreased ear number at harvest, and this was the main mechanism by which yield was reduced. In the first year's experiment drought also decreased ear number, but not in the second. This was because in the 2002-2003 experiment drought was applied later, during grain fill only, so did not cause tiller abortion.

In 2001-2002 waterlogging increased the harvest index slightly, due to shorter straw, fewer aborted tillers and more grains per ear. This agrees with the work of Belford *et al.* (1984), who found a greater decrease in the weight of straw than grain. This reduced vegetative growth was a result of waterlogging restricting the supply of nitrogen to the shoot in early spring (observed in the field experiment and by Trought and Drew, 1980). Interestingly delaying application of nitrogen and avoiding early spring applications is advocated by Blackman in the Cambridge Agronomy Model as a method of manipulating resource partitioning in favour of grain rather than straw production (CPB Twyford, 2000).

Drought reduced the harvest index by restricting grain fill. The harvest indices in 2002-2003 results were very low due to excessive straw growth and shortened grain fill, caused by an unusually warm, sunny spring and very hot temperatures in July respectively. The effect of the treatments was not quite significant, and there was no difference between control and waterlogged plots. However the results do suggest that, like the previous season, drought has reduced the harvest index. There was a significant difference between varieties. Deben produced a lot of equally sized tillers which competed with each other and failed to fill. Xi-19 also produced many very small secondary tillers but the main tillers, which were large and well filled, increased the mean ear size.

The effect of waterlogging on shoot development was still apparent at the second sampling in 2002, two months after the end of the waterlogging period. Belford (1981) found that 120 days waterlogging in mid winter delayed ear emergence by two days compared to drained controls.

4.4.2. The effects of drought and the interaction with waterlogging

In the first year the drought treatment was too severe, masking the effect of waterlogging, so that there was no difference between the drought and waterlogged followed by drought plots. This resulted in a significant interaction between waterlogging and drought. The less severe drought treatment in the second year allowed the cumulative effect of waterlogging and drought. The results do suggest that the effects of the stresses on grain yield are additive, with waterlogging or drought each causing around 2 tha^{-1} yield loss as a single treatment or 4tha^{-1} in combination. Therefore there was no interaction between waterlogging and drought, of the type that had been suggested using anecdotal evidence that the restricted roots systems of waterlogged plants were unable to follow a falling water table. Cannell *et al.* (1980) also found no evidence that winter waterlogging increased susceptibility of autumn sown winter wheat to subsequent summer drought.

4.4.3. The effects of seed rate and the interaction with waterlogging

By the time of harvest the plants in the low seed rate plots had been able to partially compensate by producing a larger weight of grain per plant. However the decrease in grain dry weight due to waterlogging of the low seed rate plots was only half of that of the high seed rate plots, when compared to drained controls at the equivalent seed rate. This resulted in a statistically significant interaction between waterlogging, drought and seed rate (Table 4.5a). This finding also fits the general trend observed in this series of experiments, where the effects of waterlogging are partially ameliorated by environments with a lower level of interplant competition. For example, in the field, less competitive varieties with erect leaves such as Xi-19 were able to maintain a higher plant population during waterlogging than more competitive varieties such as Deben. No plant death was observed in the lysimeters, as the plants had a more erect growth habit, and were evenly spaced, so competition was less than in the field.

The lower seed rate plots had a significantly smaller maximum GAI (25% less than the high seed rate) and whilst there was a strong positive relationship between GAI and grain yield, by harvest the difference in grain yield between the seed rates was only 11%. This implies that the low density plants were more efficient in converting green area into grain yield. This can be seen in figure 4.2, which shows the relationship between yield and GAI, and where the low density plots are generally found above the line of best fit, indicating a greater weight of grain per unit of green area. This illustrates the principle that in dense canopies there is less PAR available to individual leaves, due to mutual shading, so these canopies are less efficient.

This experiment set out to investigate the interaction between waterlogging and seed rate, and to find if it would be safe to use a lower seed rate in situations where waterlogging may occur. As mentioned previously, as a result of different conditions and differences in plant growth habit between the two environments, plant death occurred in the field but not in the lysimeter experiment. Therefore it is not possible to safely say that waterlogging will not cause sufficient death of plants in low seed rate situations in a field environment, to decrease the plant population to a level below which compensatory tillering is unable to maintain grain yield. However, the evidence suggests that decreasing sowing density relieves interplant competition, so at low plant populations waterlogging may not cause further loss of plants. Unfortunately the critical plant density for waterlogging to no longer have an effect may well be below that needed to achieve an economic yield. For the moment the safest advice for farmers is to sow at a conventional seed rate when waterlogging may occur. To clarify the situation a series of experiments using a range of seed rates and varieties (low/high tillering, erect/prostrate leaves) is needed in field conditions.

4.4.4. The effects of variety and the interaction with waterlogging

There was a significant difference in grain yield between the two varieties tested, with Xi-19 having a greater yield than Deben, this being the reverse of the situation in the field and in the bin variety screen (see chapter 2). There was no interaction between waterlogging and variety. The very hot conditions in the glasshouse favoured Xi-19, which has more stem soluble carbohydrate (NIAB, 2002) and a faster winter growth rate, allowing it to accumulate resources in the early spring before temperatures became restrictively hot. Additionally the growth habit of the varieties was not as would be expected in the field; both had erect leaves, whilst in the field Deben showed a prostrate growth habit. The field, therefore, is the fairest environment in which to compare the responses of different varieties, as in the case of seed rate.

Deben produced more tillers than Xi-19 during the waterlogging period, and had more ears per unit area at harvest. Deben also suffered the largest decrease in tiller number, due to waterlogging, although the interaction was not significant. This observation fits the general trend of the experiments where prolifically tillering varieties suffer the largest decrease in tiller number; the varieties with the largest seedling biomass, the largest decrease in dry weight; those with the highest yield potential, the greatest decrease in grain yield.

Chapter 5. EXPERIMENT TO INVESTIGATE THE INTERACTION BETWEEN SOWING DATE AND TIMING OF WATERLOGGING

5.1. INTRODUCTION

The experiment was performed to test the hypothesis that the effects of waterlogging at different times would be dependent on the sowing date of the crop. As discussed in the literature review, the stage of plant development (Boa, 1997) and the temperature at which waterlogging occurs (Luxmore *et al.*, 1973) may affect the severity of the effects of waterlogging. Therefore three timings of waterlogging, determined by calendar date, plus a continuously drained control, were used to provide a range of temperatures and, in an interaction with sowing date, a range of development stages at which waterlogging occurred. Experiments in the previous season suggested that waterlogged plants shared some characteristics with late sown crops. The waterlogging and drought experiment in the lysimeters (Chapter 4) found that waterlogged plants had fewer tillers, lower yield of grain and shorter straw. Additionally development was slightly delayed, the ears in the waterlogged treatments emerging about two to three days later than in the controls. However, harvest was not delayed, and there was no difference in percentage moisture of the grain so later development stages were compressed. This is similar to late sown plants which have fewer tillers, lower yield and shorter straw and compress their later development; for example a two month delay in sowing will only delay harvest by a week or two. This experiment was designed to further investigate the similarities in the effects of late sowing and waterlogging. Three sowing dates (September, October and November) and four waterlogging treatments (Autumn, Winter, Spring and Drained Control) were tested in a factorial experiment.

5.2. MATERIALS AND METHODS

5.2.1. Experimental layout and design

Each plot was sown in a 70 litre plastic dustbin filled with local topsoil, from the same source as the earlier variety experiment in the bins and the drought experiment in the lysimeters (for a full description see Chapter 2). The bins were also the same as those used previously in the variety trial, with a surface diameter of 42 cm and depth of 64 cm. The bins were arranged in five blocks, inside the netted area, to protect the plants from birds. Treatments were randomised within each block. A template was used to ensure even spacing, with two seeds sown in each position. Plants were sown in three rows, 12cm apart, with 3cm spacing between the plants within each row. The variety used was Xi-19, which the results of the variety screens in the bin and tube experiments had suggested to be sensitive to waterlogging, so would give a greater response to the waterlogging treatments. Seed was treated with Sibutol Secur seed dressing, which contains bitertanol, fuberidazole and imidacloprid. Plants were thinned to 36 per plot at first leaf fully emerged stage (Zadoks 11), a density of 260 plants m^{-2}, the same as used in the previous variety screen in the bins. Three sowing dates were used; 23 September, 16 October and 18 November 2002. These are referred to as early, mid and late sown respectively. The mid sowing date was chosen to be close to the date of sowing for the first variety experiment in the bins on 18 October 2001.

5.2.2. Waterlogging treatments

Four watering treatments were applied to each sowing date: drained control, autumn waterlogging (November 5 to December 17), winter waterlogging (December 17 to March 4) and spring waterlogging (March 4 to April 7). Waterlogging was achieved by blocking all drain holes except those at the soil surface and daily watering until water flowed freely from these holes. Waterlogging of autumn waterlogged, late sown plots began immediately after sowing as the autumn waterlogging period had already begun. At the end of each treatment period the drainage holes at the base were reopened.

5.2.3. Crop management

All plots received the same fertilizer regime, 40 kg/ha P and K at emergence as P_2O_5 and K_2O, and 175 kg/ha N in two splits at GS 30 and GS 32 as ammonium nitrate (34.5 % N). Landmark (kresoxim-methyl + epoxiconazole) fungicide was applied at a rate of 1L/ha at the T1 and T2 timings on 8 May and 23 May respectively. Foliar disease levels were very low, but some mildew (*Erysiphe graminis*) was found on the

September sown plots during the mild spell in January, as these plants were too lush for the time of year and had produced 'soft growth'. This infection was killed off by subsequent cold and, as spring 2003 was unusually dry, did not cause problems later in the season. Aphids were spotted in the plots in the north -west corner of the trial on 4 April and these were sprayed with Sybol Extra using a hand sprayer. However virus symptoms of yellow streaking on the leaves were observed in these plots on 6 May. By harvest infected plants were noticeably stunted with poor grain fill. Many of the ears of these plants remained upright at harvest, instead of the characteristic drooping of ripe ears. No PGR was used to avoid masking treatment effects. This was because sowing date and waterlogging may affect development rates and the development stage at which PGR is applied determines its effectiveness. There was some lodging, almost entirely of the mid sown plots, on 30 June following a storm, as these plots had tall weak straw and this is discussed in the results section.

5.2.4. Measurements

The number of plants that had emerged was counted at the first leaf stage (Zadoks 11). Percentage establishment was calculated as the proportion of seeds sown that produced a plant with at least one leaf unrolled by the time of counting. After counting all bins were thinned to thirty-six plants to prevent lower plant populations affecting tillering. Shoots of five plants were counted *in situ* during and at the end of each waterlogging treatment period. Due to the small size of the plots no destructive sampling was done until final harvest. September sown plots were harvested on 18 July 2003, October sown plots on 21 July 2003 and November sown plots on 28 July 2003. The November sown, spring waterlogged, plants were less ripe (some green left in the straw) than the other treatments, but delaying harvest of just these five plots would have left them vulnerable to pests. The method for sampling and processing at harvest was the same as that used for the variety screen in the bins described in chapter 2.

The soil temperature at 10cm depth was measured using two angle thermometers, one in block II and one in block IV. These were read at 9:00 GMT and the mean calculated.

Statistical analysis of all results was done by a two factor ANOVA in randomised blocks using Genstat 6, with 35 residual degrees of freedom (9 missing values).

5.3. RESULTS

5.3.1. Emergence

Early, mid and late sown plots took 8, 11 and 15 days respectively from sowing to the beginning of emergence. The only plants to be waterlogged before emergence were the November sown, autumn waterlogged treatment combination, and there was no observed effect of delayed emergence due to waterlogging. Mean soil temperatures during emergence were 12 ^{0}C for the September sowing, 7 ^{0}C for the October sowing and 8 ^{0}C for the November sowing.

Table 5.1. The effect of sowing date and autumn waterlogging on establishment. All means are expressed to 3sf. An ANOVA was performed on transformed values (square root), which are given in parenthesis and the values for P, SED and LSD refer to these transformed values.

	Control	Autumn	Winter	Spring	Mean
Early	95.8(9.79)	96.1(9.80)	95.8(9.79)	94.4(9.71)	95.6(9.77)
Mid	98.1(9.90)	96.4(9.82)	98.1(9.82)	95.6(9.77)	96.6(9.83)
Late	91.7(9.57)	75.0(8.63)	93.9(9.69)	92.5(9.62)	88.3(9.38)
Mean	95.2(9.75)	89.2(9.42)	95.4(9.76)	94.2(9.70)	

	Sowing Date	Waterlogging Treatment	Sowing Date x Waterlogging
P	<0.001	0.007	<0.001
SED	0.094	0.108	0.187
LSD	0.189	0.217	0.377

Late sowing (November) slightly reduced percentage establishment, measured by a plant count at first leaf fully emerged stage (Zadoks 11). The only treatment that was waterlogged during establishment, late sown and autumn waterlogged, showed a 17%

decrease in establishment, which accounts for the significant interaction between sowing date and waterlogging (Table 5.1).

5.3.2. Post emergence plant survival

Waterlogging decreased the plant population, when it occurred when the plants were small, with few tillers. This was autumn waterlogging in the September sown plants, and all waterlogging treatments in the November sown plants. Although autumn and winter waterlogging decreased the plant population of October sown plants slightly, this was smaller than the LSD, and so not significant.

Table 5.2. Plant number per square metre counted at harvest. All plots had a plant density of 260 plants per square metre after thinning, at GS 11.

	Control	Autumn	Winter	Spring	Mean
Early	248	234	241	259	246
Mid	244	240	238	247	242
Late	253	230	230	221	233
Mean	248	234	236	242	

	Sowing Date	Waterlogging Treatment	Sowing Date x Waterlogging
P	0.008	0.014	0.010
SED	3.87	4.47	7.75
LSD	7.81	9.02	15.6

5.3.3. Soil Temperature

The grand means for the three waterlogging periods were 6.8, 4.9 and 7.0 °C, for autumn, winter and spring respectively. The general trend was for soil temperatures to fall during the autumn and rise during spring. There was a mild period during the third and fourth weeks of January, and this allowed the outbreak of mildew (*Erysiphe* *graminis*) on some of the lush September sown plots, but this was stopped by the colder spells at the end of January and in mid February.

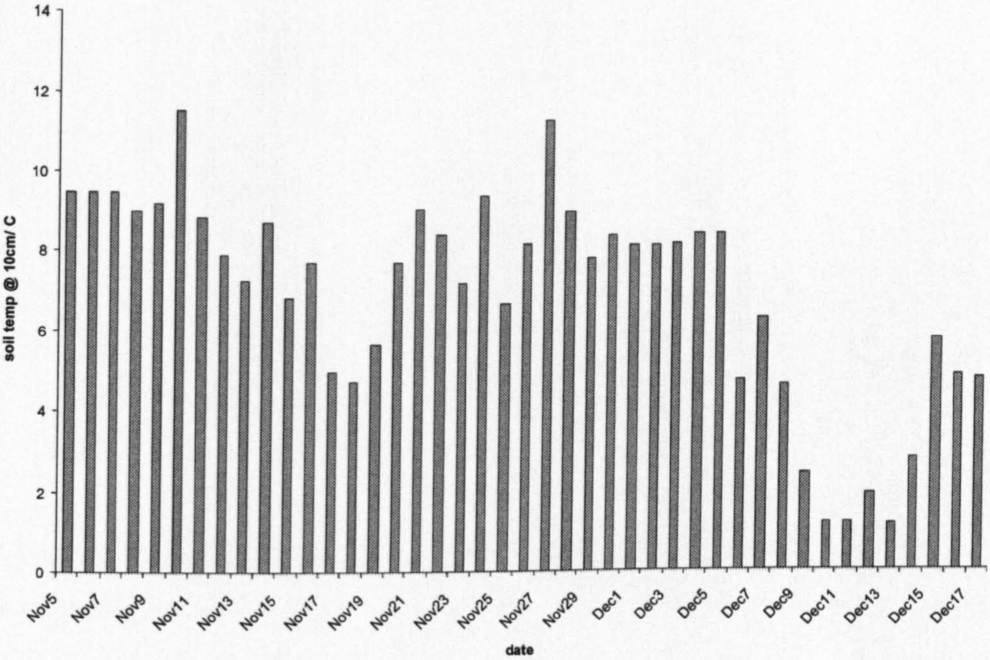

Figure 5.1. Mean soil temperature at 10 cm depth at 09:00 GMT during the autumn waterlogging period.

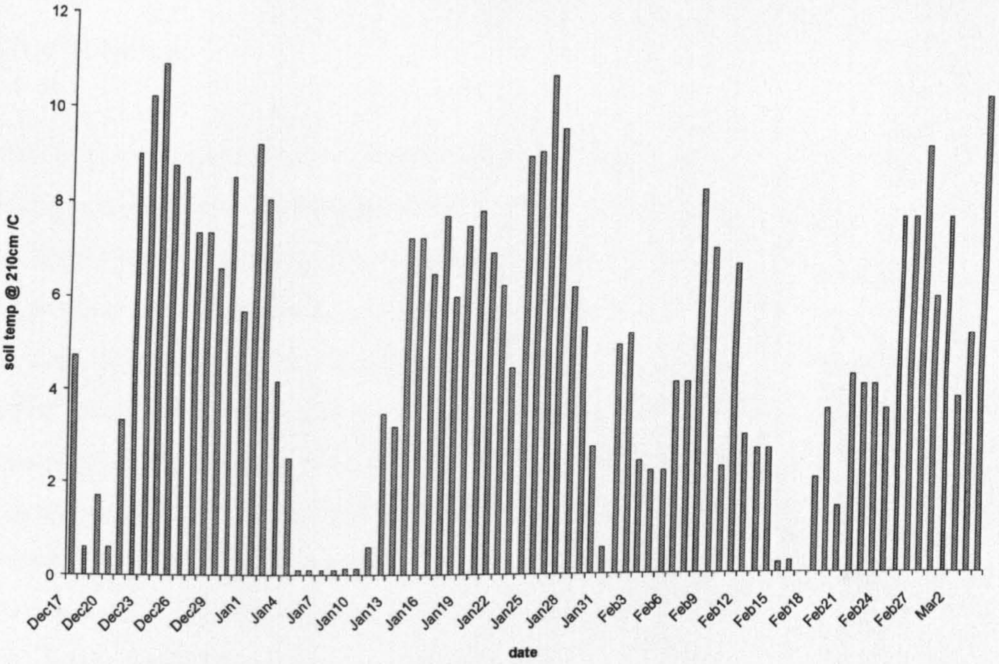

Figure 5.2. Mean soil temperature at 10 cm depth at 09:00 GMT during the winter waterlogging period.

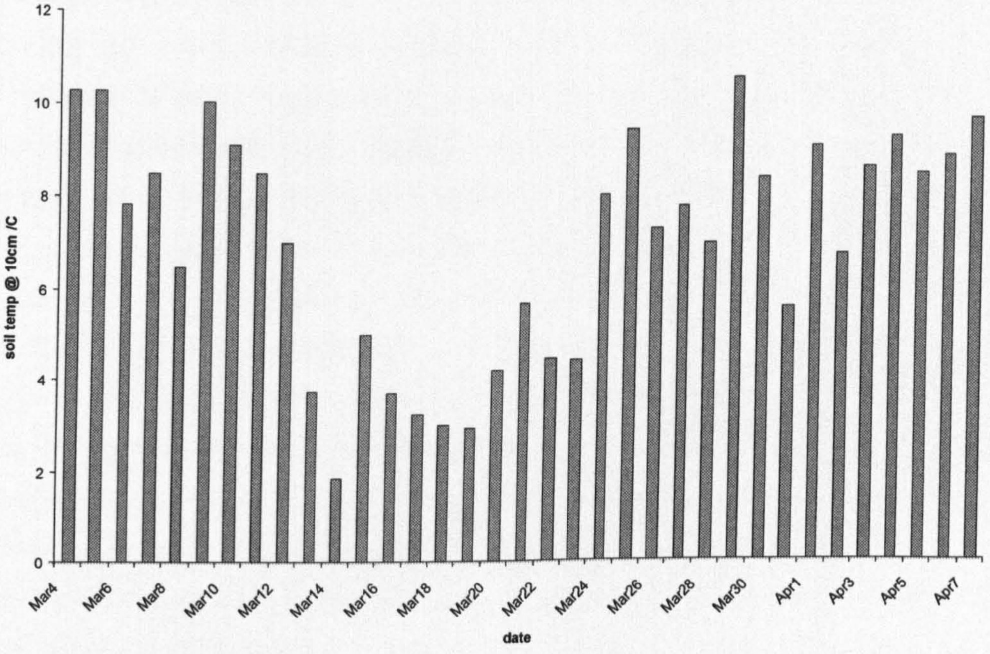

Figure 5.3. Mean soil temperature at 10 cm depth at 09:00 GMT during the spring waterlogging period.

5.3.4. Tillering

Neither the mid nor late sown plants tillered in the autumn as colder weather slowed development. Early sown plants tillered profusely in the autumn and then there was no further increase in the spring (except for the autumn waterlogged plants, which had fewer tillers and so needed to compensate), as these plants were already very lush, and infected with mildew. The combination of mildew and the cold periods mentioned earlier (section 5.3.3) actually decreased the number of tillers of the September sown plant slightly during early spring. The pattern of autumn tillering in early sown crops and spring tillering of late sown crops, is well documented (refer to *The Wheat Growth Guide*, p14, HGCA, 1997). Waterlogging usually decreased the numbers of tillers per plant. For the September sown plants this decrease was by inhibition of the rate of tiller production when waterlogging occurred in the autumn and by increased death of existing tillers when waterlogging occurred in the winter and spring. This is shown on figure 5.5, which also shows that the autumn waterlogged plants behaved in a similar way to those sown later, which tillered in the spring to compensate for missing the autumn tillering window. Of the September sown plants those waterlogged in spring had the lowest number of tillers at harvest, as by the end of this waterlogging period the spring tillering window had passed and there was no time for compensatory tillering. In fact tiller number continued to decrease. In contrast to the autumn waterlogged plants which increased their number of tillers in the spring, and those that were spring waterlogged which lost tillers, the winter waterlogged plants maintained a constant number of tillers from the ends of waterlogging to harvest. Autumn waterlogging had no effect on the tillering of the October or November sown plants, but winter and spring waterlogging slowed the rate of tillering in the spring. It should also be noted that a larger proportion of the shoots found on the early sown plants at the maximum period in the spring survived to maturity. The most likely explanation is that these tillers were autumn produced, and thus larger, having had time to produce their own root systems and stores of carbohydrates and amino acids.

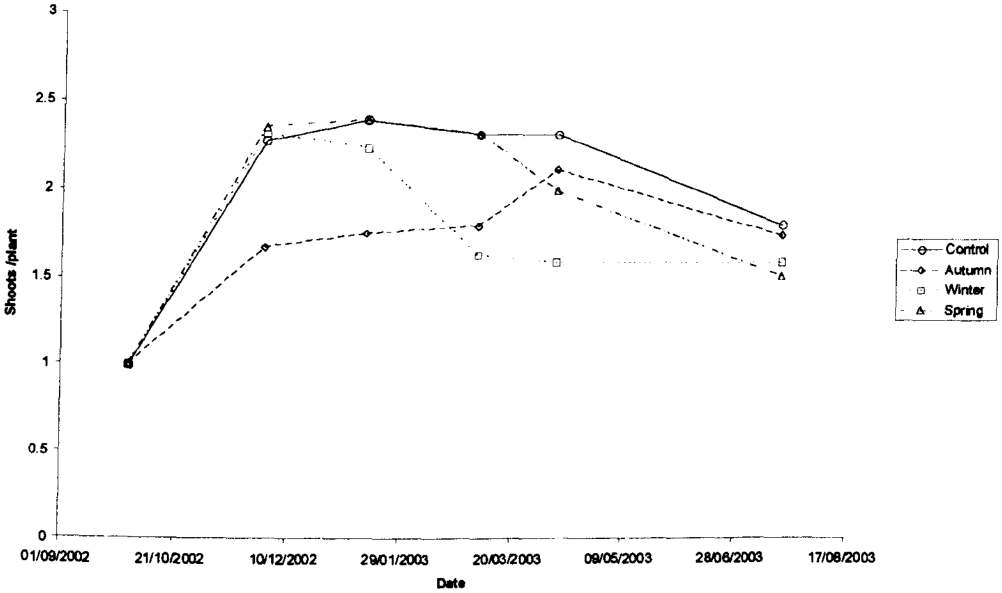

Figure 5.4. Shoots per plant of Xi-19 winter wheat sown on September 23 and subjected to four different waterlogging treatments. The last set of values refers to the number of fertile ears per plant at harvest.

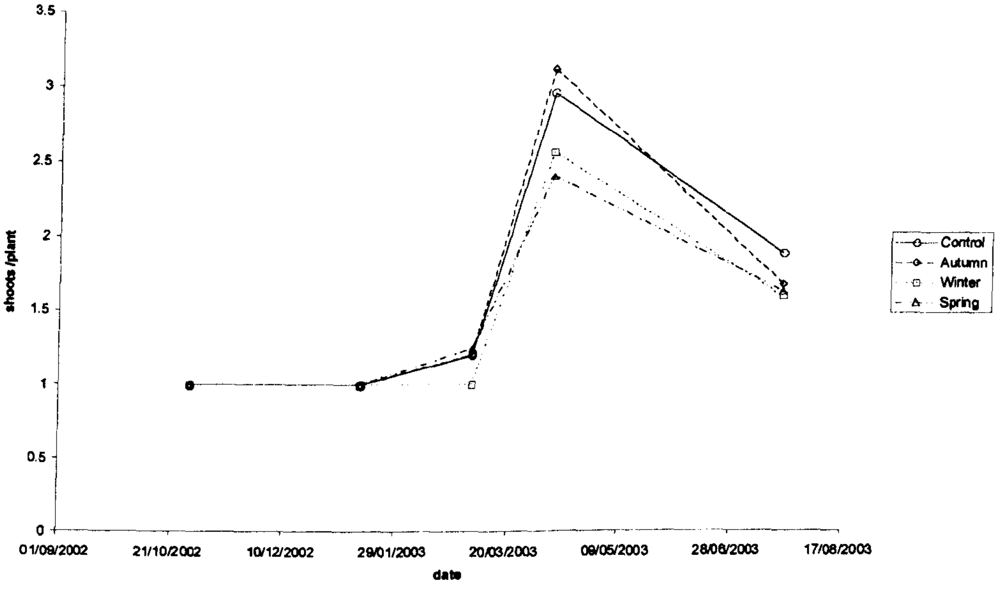

Figure 5.5. Shoots per plant of Xi-19 winter wheat sown on October 16 and subjected to four different waterlogging treatments. The last set of values refers to the number of fertile ears per plant at harvest.

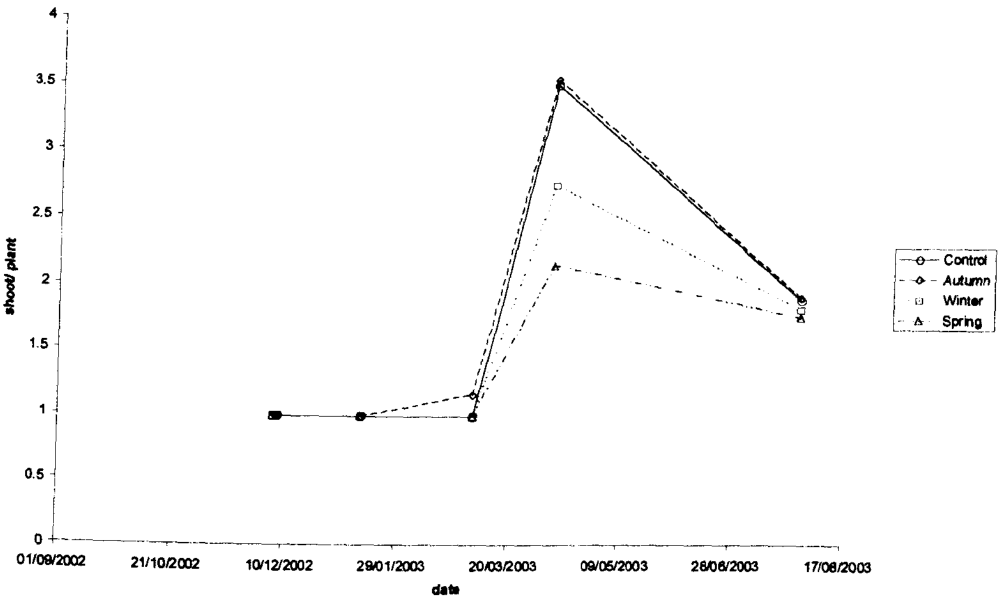

Figure 5.6. Shoots per plant of Xi-19 winter wheat sown on November 18 and subjected to four different waterlogging treatments. The last set of values refers to the number of fertile ears per plant at harvest.

5.3.5. Date of anthesis

Later sowing delayed anthesis, especially for the November sowing date (Table 5.3). Spring waterlogging had the greatest effect of the waterlogging treatments on the October and November sown plants, but no effect on those sown in September.

Table 5.3. Date of the start of anthesis relative to that of the September sown, drained controls, which began anthesis on May 27, 2003. The values refer to the number of days later than the early-control treatment that anthesis occurred.

	Control	Autumn	Winter	Spring
Early	0	+2	+2	0
Mid	+3	+4	+5	+7
Late	+16	+16	+16	+18

5.3.6. Harvest measurements

Aphid transmitted BYDV caused leaf chlorosis, stunted internode elongation and caused very poor grain fill, leading to shrivelled grains with low dry weights in some pots. This occurred in the north west corner of the experiment. As infection was after tillering there was no effect on ear or tiller number, plant number or spikelet production. The results for grain yield, TGW, straw length, straw DW, straw density, total biomass and harvest index are presented below after an analysis excluding affected plots [plot 2 (due to damage by mice) and plots 9, 10, 11, 15, 16, 19, 21 and 22 (affected by BYDV)]. The full results, with no correction for BYDV, are presented in Appendix 2.

5.3.6.1. Grain yield

Delayed sowing significantly decreased grain yield, the mean grain dry weight of the September sown plots was greater than that of October sown plots, which was greater than that of those sown in November. The means of drained controls and the autumn waterlogged plots were significantly greater than the means of the winter and spring waterlogged plots. Autumn waterlogging decreased grain yield compared to the controls and spring waterlogging caused a greater decrease than winter waterlogging but these differences were smaller than the LSD. There was a significant interaction between sowing date and waterlogging. Spring waterlogging did not affect those plants sown in September, but significantly decreased the yields of the two later sowings, especially the November sowing. Autumn and winter waterlogging significantly decreased the yield of plants sown in October, but had no significant effect on the others.

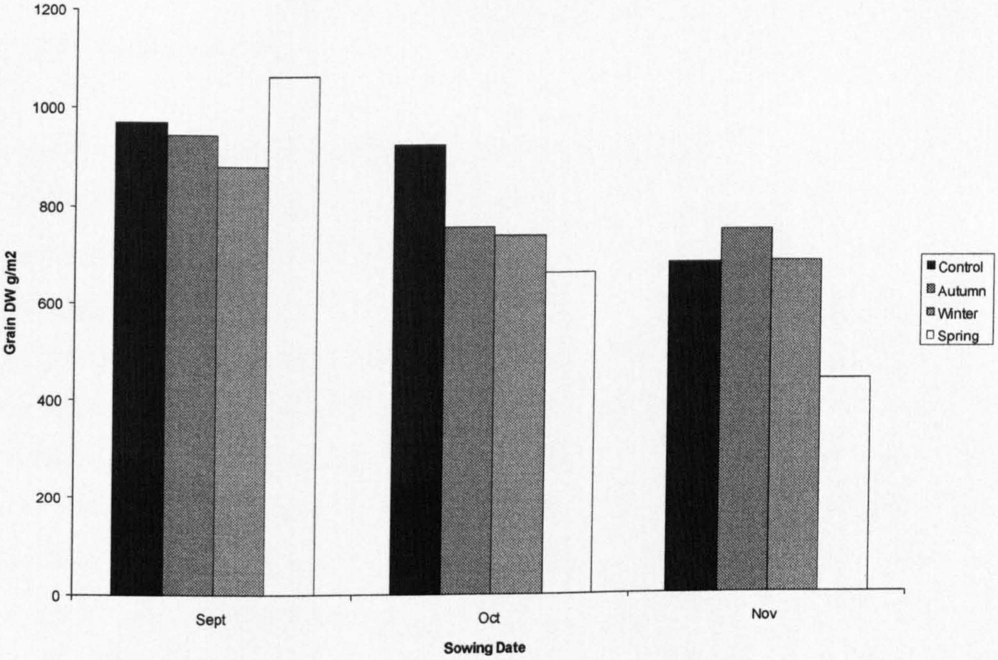

Figure 5.7: The effects of sowing date and waterlogging period on grain yield of Xi-19 winter wheat. The sowing dates were September 23, October 16 and November 18. Waterlogging treatments were control (freely drained), autumn (November 5 to December 17), winter (December 17 to March 4) or spring (March 4 to April 7).

Table 5.4. The effects of sowing date and waterlogging period on grain yield (g m^{-2}) of Xi-19 winter wheat.

	Control	Autumn	Winter	Spring	Mean
Early	974	947	884	1066	968
Mid	925	759	741	665	773
Late	685	751	689	441	642
Mean	861	819	771	724	

	Sowing Date	Waterlogging Treatment	Sowing Date x Waterlogging
P	<0.001	0.028	0.003
SED	39.4	45.5	78.8
LSD	80.0	92.4	160.0

5.3.6.2. Yield components

Delayed sowing generally increased the number of fertile ears at harvest, but only the difference between September and November sowing was significant. All waterlogging treatments reduced the number of fertile ears, but there were no significant differences between the three timings of waterlogging. Although the interaction was not significant the effects of waterlogging on ear number appeared to be greatest on the mid and late sowing. Delaying sowing resulted in fewer grains per ear, and differences between all three of the means were greater than the LSD (Table 5.6). Although there was no significant effect of waterlogging or interaction, spring waterlogging appears to have resulted in a marked decrease in the number of grains per ear in the November sowing. Delayed sowing decreased the thousand grain weight (Table 5.6). Although waterlogging had no significant effect on TGW the interaction was almost significant $P=0.072$ and the grains of the November sown, spring waterlogged plants were markedly lighter. Both delayed sowing and waterlogging decreased grain yields of Xi-19 winter wheat. Later sown plants had smaller ears with fewer grains per ear and a lower TGW, but a slightly higher ear population. A varietal characteristic of Xi-19 is the production of secondary tillers, bearing much smaller ears than the main stems (see Chapter 2). These smaller ears have around 16 spikelets, in contrast to the larger ears which typically have up to 28 spikelets. The abortion of these smaller tillers, due to the effects of mildew and frost on the lush September sown plants in January and February, appears to have increased the mean number of grains per ear and the TGW of these plants, as only the main stems and strongest of the primary tillers survived to produce ears. Where waterlogging decreased grain yield this occurred as a result of fewer ears per plant (see figures 5.4, 5.5 and 5.6) and fewer plants (table 5.2). Waterlogging had no significant effect on number of grains per ear or TGW. There was a significant interaction between the effects of delayed sowing and waterlogging on yield. The November sown, spring waterlogged plants, had the smallest fertile ear population (of the late sown plants), fewest grains per ear, and the lowest TGW, resulting in the lowest yield of any of the treatment combinations.

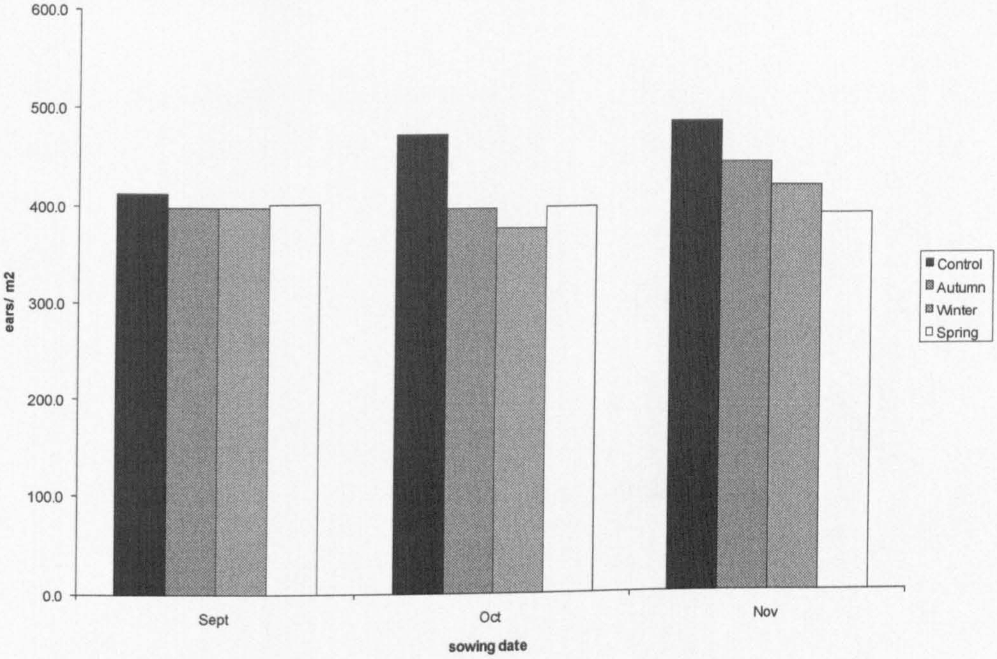

Figure 5.8: The effects of sowing date and waterlogging period on the number of fertile ears m^{-2} of Xi-19 winter wheat. The sowing dates were September 23, October 16 and November 18. Waterlogging treatments were control (freely drained), autumn (November 5 to December 17), winter (December 17 to March 4) or spring (March 4 to April 7).

Table 5.5. The effects of sowing date and waterlogging on the number of fertile ears m^{-2} of Xi-19 winter wheat.

	Control	Autumn	Winter	Spring	Mean
Early	414	400	400	403	404
Mid	473	398	378	399	412
Late	484	443	420	391	435
Mean	457	413	399	398	

	Sowing Date	Waterlogging Treatment	Sowing Date x Waterlogging
P	0.044	<0.001	0.141
SED	12.1	14.0	24.2
LSD	24.6	28.4	ns

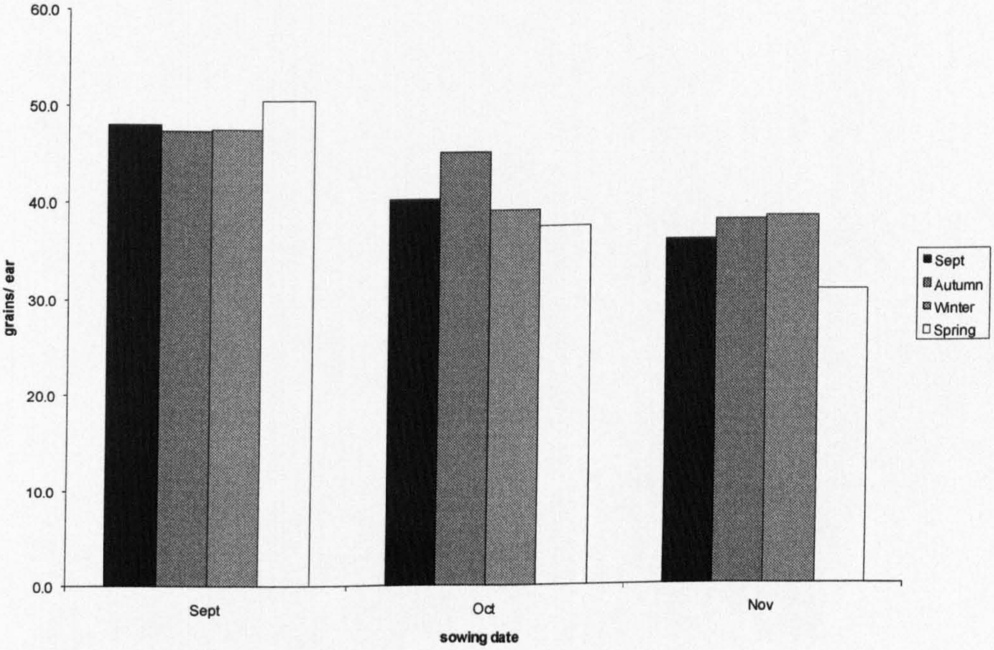

Figure 5.9: The effects of sowing date and waterlogging period on the number of grains per fertile ear of Xi-19 winter wheat. The sowing dates were September 23, October 16 and November 18. Waterlogging treatments were control (freely drained),

autumn (November 5 to December 17), winter (December 17 to March 4) or spring (March 4 to April 7).

Table 5.6. The effect of sowing date and waterlogging on the number of grains per fertile ear of Xi-19 winter wheat.

	Control	Autumn	Winter	Spring	Mean
Early	48.1	47.5	47.7	50.6	48.5
Mid	40.3	45.1	39.1	37.5	40.5
Late	35.9	38.0	38.6	30.7	35.8
Mean	41.5	43.5	41.8	39.6	

	Sowing Date	Waterlogging Treatment	Sowing Date x Waterlogging
P	<0.001	0.188	0.110
SED	1.54	1.78	3.08
LSD	3.12	ns	ns

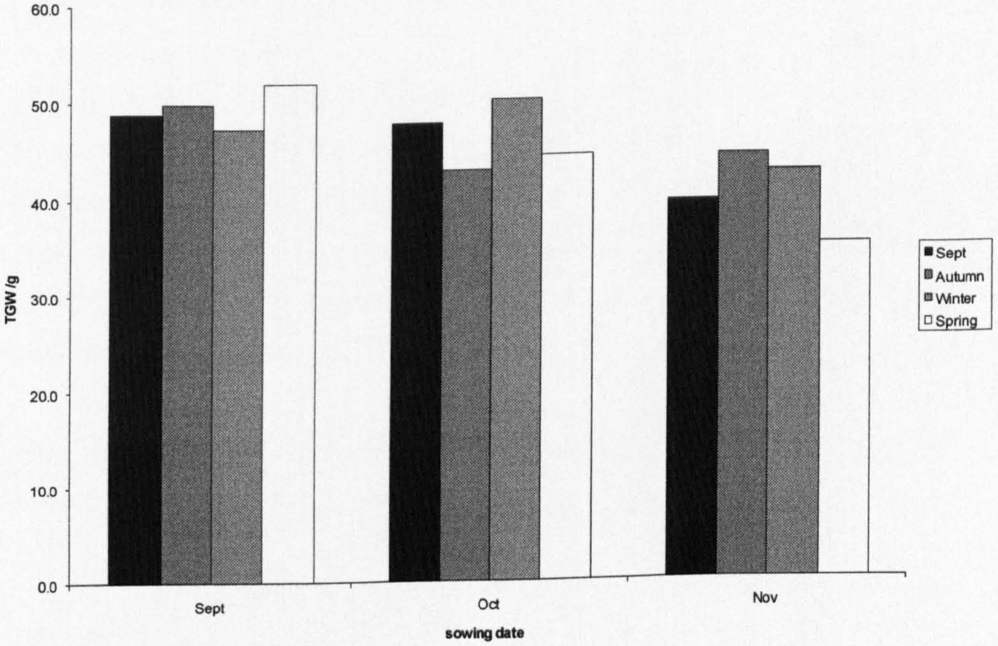

Figure 5.10: The effects of sowing date and waterlogging period on the thousand grain weight TGW (g) of Xi-19 winter wheat. The sowing dates were September 23, October 16 and November 18. Waterlogging treatments were control (freely drained),

autumn (November 5 to December 17), winter (December 17 to March 4) or spring (March 4 to April 7).

Table 5.7. The effects of sowing date and waterlogging on the TGW (g) of Xi-19 winter wheat.

	Control	Autumn	Winter	Spring	Mean
Early	49.0	50.0	47.5	52.2	49.7
Mid	48.0	43.2	50.3	44.5	46.5
Late	39.2	44.3	42.6	35.1	40.4
Mean	45.6	45.8	46.8	43.9	

	Sowing Date	Waterlogging Treatment	Sowing Date x Waterlogging
P	<0.001	0.577	0.072
SED	1.76	2.03	3.51
LSD	3.57	ns	ns

5.3.6.3. Other harvest measurements

Delaying sowing to November significantly decreased straw length, compared to the September or October sowing. Both the effect of waterlogging and the interaction were significant, although there was no clear trend. Winter waterlogging of the September sowing and spring waterlogging of the spring sowing decreased straw length significantly and autumn waterlogging of the October sowing caused a significant increase.

Table 5.8. The effects of sowing date and waterlogging on straw length (cm) at harvest, from basal node to collar, of Xi-19 winter wheat.

	Control	Autumn	Winter	Spring	Mean
Early	78.1	79.8	73.8	77.6	77.3
Mid	71.6	80.1	76.1	75.2	75.8
Late	72.0	70.1	70.8	67.1	70.0
Mean	73.9	76.6	73.6	73.3	

	Sowing Date	Waterlogging Treatment	Sowing Date x Waterlogging
P	<0.001	0.047	0.014
SED	1.10	1.27	2.19
LSD	2.24	2.59	4.48

Only the effect of sowing date on straw dry weight was significant; delaying sowing decreased the mass of straw per unit area (Table 5.9). Whilst not significant, there is a marked decrease caused by spring waterlogging of the November sowing.

Table 5.9. The effects of sowing date and waterlogging on straw dry weight (gm^{-2}) of Xi-19 winter wheat.

	Control	Autumn	Winter	Spring	Mean
Early	718	782	777	777	764
Mid	665	631	590	633	630
Late	594	623	602	490	577
Mean	659	679	656	633	

	Sowing Date	Waterlogging Treatment	Sowing Date x Waterlogging
P	<0.001	0.449	0.113
SED	23.9	27.6	47.8
LSD	48.9	ns	ns

Table 5.10. The effects of sowing date and waterlogging on straw density (mg cm^{-1}) of Xi-19 winter wheat.

	Control	Autumn	Winter	Spring	Mean
Early	20.7	24.7	26.9	25.0	24.3
Mid	19.9	19.8	20.7	20.7	20.3
Late	17.4	20.2	20.2	19.2	19.3
Mean	19.3	21.6	22.6	21.6	

	Sowing Date	Waterlogging Treatment	Sowing Date x Waterlogging
P	<0.001	0.017	0.415
SED	0.849	0.981	1.698
LSD	1.737	2.006	ns

5.3.6.4. Grain protein content and N uptake

The November sown plants had higher grain protein content than the other sowing dates, because their lower grain yield meant there was less dilution of nitrogen with carbohydrate (Table 5.11). There was no significant effect of waterlogging or interaction. Total nitrogen content of the grain is the product of nitrogen percentage and grain yield. The September sown plants had a higher total uptake of nitrogen that the other sowing dates because of the longer growing season and greater autumn root growth. Waterlogging decreased nitrogen uptake as a result of lower yields, not by lowering grain nitrogen concentration. The significant interaction was due to the very low nitrogen uptake of the spring waterlogged October and November sown plants. The first application of nitrogen was made during the spring waterlogging period, so uptake was restricted by the smaller root system. September sown plants were unaffected, as they must have already had a well developed root system from the vigorous autumn growth.

Table 5.11. The effects of sowing date and waterlogging on grain crude protein concentration of Xi-19 winter wheat.

	Control	Autumn	Winter	Spring	Mean
Early	7.99	8.70	8.75	8.59	8.51
Mid	9.02	8.85	8.83	8.33	8.75
Late	9.64	8.82	10.03	9.81	9.57
Mean	8.88	8.79	9.20	8.91	

	Sowing Date	Waterlogging Treatment	Sowing Date x Waterlogging
P	0.008	0.741	0.522
SED	0.337	0.389	0.673
LSD	0.683	ns	ns

Table 5.12. The effects of sowing date and waterlogging on total nitrogen content of grain at harvest (gm^{-2}) of Xi-19 winter wheat.

	Control	Autumn	Winter	Spring	Mean
Early	13.2	14.2	13.1	15.5	14.0
Mid	14.3	11.5	11.2	9.4	11.6
Late	13.2	11.1	11.7	7.0	10.3
Mean	12.9	12.3	12.0	10.6	

	Sowing Date	Waterlogging Treatment	Sowing Date x Waterlogging
P	<0.001	0.016	<0.001
SED	0.597	0.689	1.19
LSD	1.21	1.40	2.42

5.4. DISCUSSION

There was a much smaller loss of plants due to pre emergence waterlogging of the November sown, autumn waterlogged treatment than expected. Cannell *et al.* (1980) found that six days of waterlogging at this time reduced plant populations to 12% and

38% of drained controls on clay and sandy soils respectively. Belford *et al.* (1985) reported a reduction in established plant population from 338 plants m^{-2} to 35 plants m^{-2}. The probable reason for the lower rates of seedling death observed in this study is that the plants emerged before soil oxygen levels dropped to dangerous levels. Once emerged the shoot system can provide oxygen to the root system allowing it to survive in hypoxic conditions.

In the case of the early and mid sowing dates the autumn and winter waterlogging treatments did cause some plant death, whilst the spring waterlogging had no effect on plant population, presumably because the plants were much larger and stronger by this stage. In contrast all three waterlogging treatments reduced plant population of the late sown plots. As can be seen by looking at the data in figure 4.3, these plants did not start to tiller until April so were still small and vulnerable during the spring waterlogging period. As plots were double sown and thinned at GS 11 all differences in plant population must be due to post establishment stress.

These results contrast with those of the lysimeter experiments in the glasshouse and the work at Letcombe (Cannell *et al.* 1980; Belford 1981; Cannell *et al.* 1984; Belford *et al.* 1985), where waterlogging after establishment did not cause plant death. However the growth analysis of the field experiment after waterlogging did find significant reductions in plant population (see Chapter 2). The glasshouse and Letcombe experiments were hand sown. It is possible that the even plant spacing attained in the hand sown plots would prevent the competition between plants found in the field which was sown using a plot drill. This may explain the observed differences in the effects of waterlogging between the lysimeters and field. Differences between the lysimeters and bins can be explained by the more favourable conditions in the glasshouse. The bins though, would be expected to give similar results to the Letcombe lysimeters as both experiments were hand sown and outdoors. However some of the Letcombe experiments received nitrogen fertilizer as a seed bed application at the time of sowing. Hence these plants would be expected to make more vigorous autumn growth. In line with current scientific thinking and commercial practice all the Henfaes experiments received no autumn N fertilizer. Additionally some of the Letcombe experiments followed peas, so soil nitrogen levels would likely to have been high during autumn.

There were significant differences in grain yield between sowing dates and waterlogging treatments and a significant interaction between the two treatments. The differences between the three waterlogging periods were smaller than the least significant difference but all had significantly lower grain yield than the drained control. Spring waterlogging prevented the November sown plants from compensating for being late sown by spring tillering. These plants also started grain filling later due to delayed development but high summer temperatures evened up ripening dates, so that the date of maturity was unaffected and the shorter grain fill period decreased the TGW and number of grains per ear.

The waterlogging treatments reduced harvest ear number m^{-2} both by reducing the plant population and the number of ears per plant. The larger the reduction in the plant population, such as in the case of autumn waterlogging, the smaller the reduction in ear number per plant, presumably as the thinner crop encouraged compensatory tillering.

The spring waterlogging treatment had a much more severe effect on grain yield, tillering and nitrogen uptake, of the October and November sown plants than those sown in September. Certainly spring waterlogging did coincide with the later sown plants' tillering period, whilst the September sown plants already had sufficient tillers from the autumn tillering period. September sown plants are likely to have had more nodal roots by the spring, as production of these is associated with tillering (Klepper *et al.,* 1984) and these plants were more developed, with more tillers. Nodal roots have a constitutively higher porosity, and greater ability to produce lysogenous aerenchyma, so possessing more of these would be an advantage that the early sown plants had over those sown later, in coping with spring waterlogging.

The October sown plants had the greatest amount of lodging due to their tall weak straw. The November sown plants had weak straw with a low density, in terms of dry weight per cm length, but were much shorter. The September sown plants were tall and would be expected to lodge due to a higher stem leverage moment but the straw was thicker and stronger than the other two sowing dates. There were significant effects of waterlogging on straw length and a significant interaction between waterlogging and sowing date, but unlike the lysimeter and field experiments, waterlogging did not always decrease straw length. The closest sowing date to that in the field experiment was September sown (bins sown on September 23, field on September 30) and here winter waterlogging (the waterlogging treatment used in the field) decreased straw length compared to the control, so the results concur. However for September sowing the autumn waterlogging treatment increased straw length compared to the control as did all waterlogging treatments for the October sowing. For the November sowing all waterlogging treatments decreased straw length, although only the decrease due to spring waterlogging was significant. Again in concurrence with the field variety experiment all waterlogging treatments (except autumn waterlogging on October sown) increased the dry weight of straw per unit length, appearing to have a PGR effect.

Waterlogging did have a similar effect on crop growth and development as late sowing, in several respects. Grain and straw yields were decreased, both by waterlogging and late sowing, as was straw length, though not by all waterlogging treatments. Late sown and waterlogged plants would be expected to have a lower tillering potential, although profuse spring tillering meant that there was no decrease in ear number per unit area at harvest due to late sowing, despite the very different patterns of tiller production of the three sowing dates (see Figures 5.4, 5.5 and 5.6). Although both late sowing and waterlogging decreased grain yields, the mechanisms involved were different; waterlogging decreased the number of ears per unit area and had no effect on the number of grains per ear or TGW; in contrast late sowing had no effect on ear number but decreased the number of grains per ear and TGW. Waterlogging did delay development slightly, evidence of which was the delay in the start of anthesis (Table 5.3), but compression of later growth stages allowed the waterlogged plants to mature at the same date as the equivalent controls. Later sowing did delay maturity by a few days, but the plants still showed signs that they had been able to compress later growth stages in order to catch up, for example delaying sowing by two months from September to November only delayed maturity by ten days. Therefore it may be concluded that an altered pattern of development, to compensate for lost time (late sowing or a dormant period during waterlogging) is a feature common to late sown and waterlogged plants. In conclusion waterlogging and late sowing have deleterious, and in some ways similar, effects on crop growth and yield and it is recommended that winter wheat be sown early, if possible, on land likely to be affected by winter waterlogging. Unfortunately it must be accepted that often the reason for delayed sowing, such as wet weather (e.g. autumn 2000) or harvesting of a root crop (and the resultant damage to soil structure), will make problems with waterlogging more likely. In such cases where it is unavoidable that both waterlogging and late sowing will combine over winter, it may be best to reconsider cropping options in favour of a spring sown break crop.

Chapter 6. RHIZOTRON EXPERIMENTS TO INVESTIGATE THE EFFECT OF WATERLOGGING ON ROOT GROWTH

6.1. INTRODUCTION

The study of the growth of root systems in the field is extremely labour intensive, and destructive of the subject being studied, as discussed in the literature review in chapter 1, and for this reason root systems have been neglected by crop scientists. In stony soils, such as those found at the Henfaes site, extracting soil cores or digging soil pits is practically impossible. Therefore a method was needed of studying the effects of waterlogging on growth of wheat root systems over time, which was simple and non destructive. Rhizotrons are artificial root growth chambers, which allow the growth of root systems to be studied in control conditions. The glass sides of the chambers allow rates of root growth to be measured *in situ,* and non-destructively. These results only refer to the part of the root system adjacent to the glass, but destructive harvests at maturity can be used for calibration. The major disadvantage of the rhizotron system is that only single plants can be studied, therefore these experiments were run in conjunction with lysimeter and field plot experiments that allowed the effects of waterlogging on plant communities to be studied, to provide a comparison and help overcome this shortcoming.

Experiments were run over two seasons; the first was a simple experiment, with one variety of winter wheat (Claire), to compare root growth in waterlogged and drained conditions and to test the viability of the technique in investigating waterlogging. In the second season a larger factorial experiment was planned, to compare the root growth of two varieties (Deben and Xi-19), under waterlogged and drained conditions. Lessons learned in the first season were incorporated into the second experiment.

6.2. MATERIALS AND METHODS

6.2.1. 2001-2002 experiment

Rhizotron root chambers were constructed using a method based on that described by Riedacker (1974). Each chamber consisted of two plates of glass, 120cm long and 30cm wide, with 2cm of soil between the plates. Even spacing between the plates was achieved using two 20mm square sections of soft wood as spacers. The plates were secured together with four layers of waterproof "Duck Tape", with the spacer in place, and filled with oven dried, sieved soil. The spacers were then removed gradually as the chambers were filled. A piece of the same 20mm wood as used for the spacers was put in the end of the chamber to serve as a base and prevent soil leaking. The wooden bases of chambers that would be controls were drilled to allow free drainage, whilst those to be waterlogged were sealed with Duck Tape. Twelve rhizotrons were constructed, six to be drained controls and six waterlogged.

Seeds of Claire winter wheat, the same cultivar used in the 2001-2002 lysimeter experiment, were sown on 6 December 2001 and watered in. Each chamber was wrapped in black polythene, held in place with parcel tape to exclude light. The rhizotrons were arranged on a frame so they were inclined 30^0 from the vertical. The positive geotropism of the roots would than cause them to grow along the ventral pane of glass, allowing growth to be traced onto acetate sheets. The length of root growth was then measured using a map measuring pen.

Waterlogging began on 18 January 2002 and was achieved by watering each morning until the water table was at the soil surface. The treatment continued until 19 February when it became clear that excessive watering was damaging the adhesion of the tape. One replicate of each treatment was harvested at this time and root dry weight in each 20cm soil horizon measured. Further harvests were done on 21 March and 13 May to monitor recovery of the plants after waterlogging. The remaining three chambers of each treatment were harvested 16 July. These were photographed using a photocopier, in photo mode, to record the structure of the root system before cutting up to measure dry weight in each soil horizon as before.

6.2.2. 2002-2003 experiment

The rhizotrons were built using a similar method to that described previously. However, this time the wooden spacers were left in and sealed with silicon glass sealant. This was to provide extra support to the glass and prevent water seeping from the seams, as it was found that waterlogging caused the tape to lose adhesion. A factorial treatment structure was used, combining waterlogging and variety. The varieties chosen were Deben and Xi- 19, which the variety screen last year suggested had different tolerances to waterlogging. There were four replicates of each treatment combination. Each chamber was held in a cradle, made from MDF, to provide support and exclude light from the ventral glass pane. Only the dorsal pane was covered with black polythene, so the root growth could be traced by removing the rhizotron from its cradle. This was quicker than unwrapping and rewrapping before and after tracing. The waterlogging period was from 27 January until 26 February 2003.

Mouse damage in early January, when shoots were bitten off at the base, reduced the number of replicates of Deben controls to three and Deben waterlogged to two. Replacements were sown immediately, but these failed to catch up with the earlier sown plants, and were discarded.

Root growth was traced before, during and after the waterlogging period as previously but no destructive samples were taken. All chambers were harvested at anthesis as previous work suggests that the roots would be expected to have reached their maximum dry weight at this time (Gregory *et al.* 1978, Welbeck *et al.* 1974). Again all root systems were photocopied and weighed.

6.3. RESULTS

6.3.1. 2001-2002 experiment

Daily growth of the root systems of the waterlogged plants immediately decreased at the start of waterlogging, and continued to decline throughout the treatment period (Figure 6.1). Approximately one month after the end of waterlogging, growth rate began to increase, following an exponential curve similar to the control. The growth rate of the waterlogged plants did not recover to that of the controls during the period when measurements were taken (Figure 6.2). The total length of the control root system increased linearly until late February, when growth became exponential. The waterlogged roots followed a similar pattern, but growth virtually ceased during the waterlogging period, and the exponential growth phase began a month later.

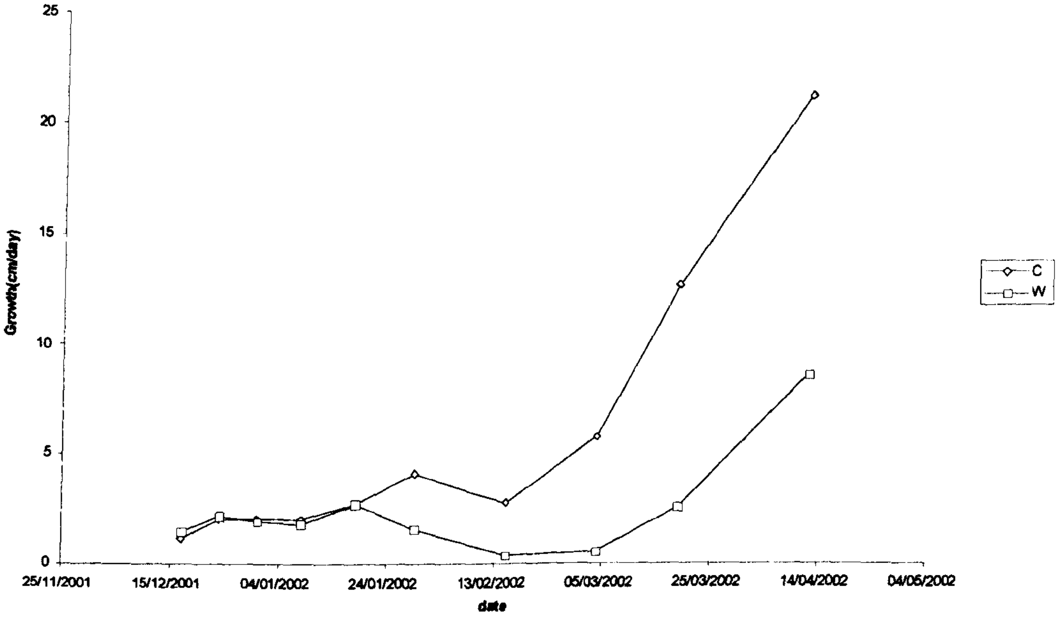

Figure 6.1. Growth rate in centimetres per calendar day of the root system of Claire winter wheat grown in rhizotrons containing drained or waterlogged soil. The waterlogging period was from 18 January 2002 to 19 February 2002.

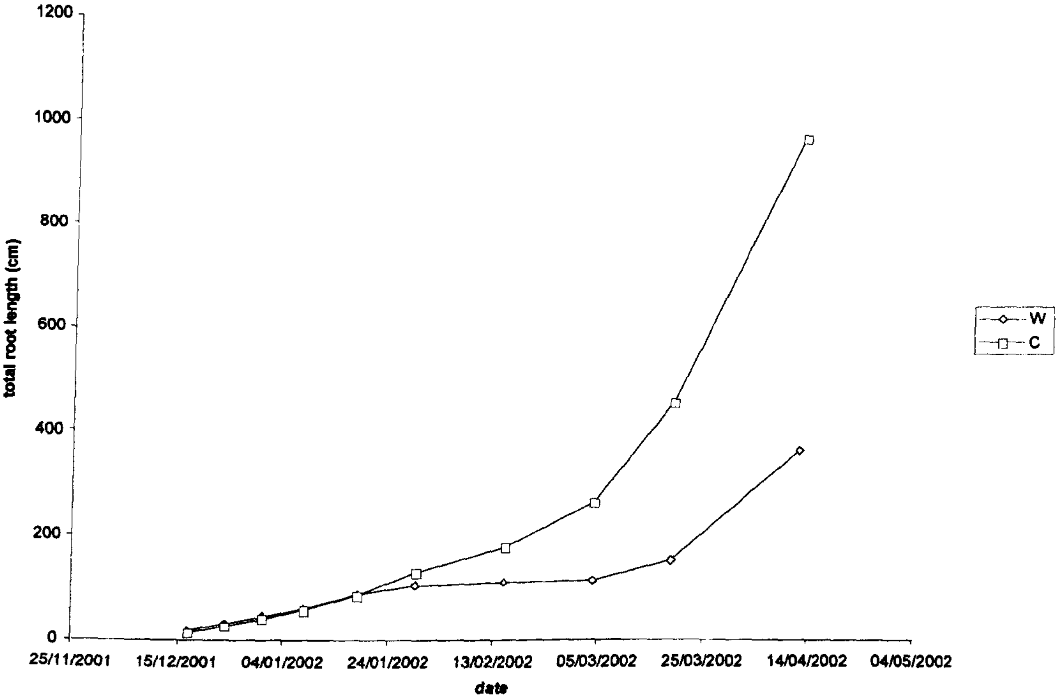

Figure 6.2. Total length of the root system of Claire winter wheat grown in rhizotrons containing drained or waterlogged soil. The waterlogging period was from 18 January 2002 to 19 February 2002.

As Figures 6.3, 6.4 and 6.5 were based on single replicates no statistical analysis could be done, although the graphs show a clear trend that waterlogging decreased root dry weight, especially in the lower soil layers. At harvest waterlogged plants had a greater, but not significantly so, dry weight of roots in the upper 20cm (Figure 6.6). This is indicative of increased nodal root production. Control plants had significantly greater root weights in the lower soil layers.

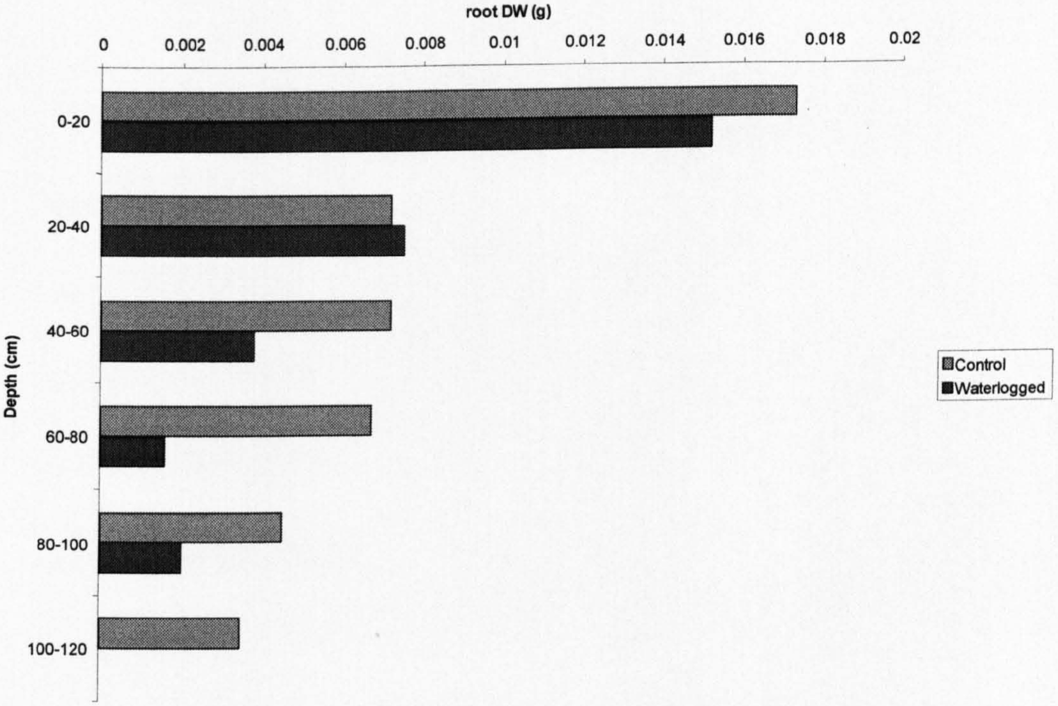

Figure 6.3. Dry weight of roots contained in each 20cm soil horizon of Claire winter wheat at the end of the waterlogging period. The data refers to a single replicate only.

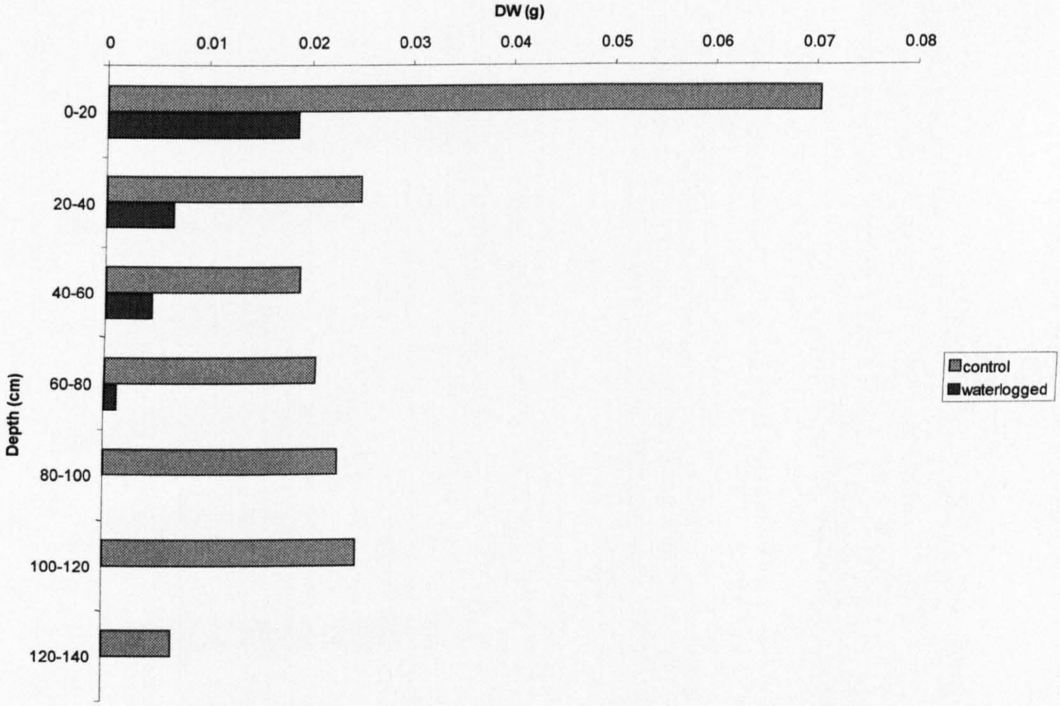

Figure 6.4. Dry weight of roots contained in each 20cm soil horizon of Claire winter wheat, one month after the end of the waterlogging period. The data refers to a single replicate only.

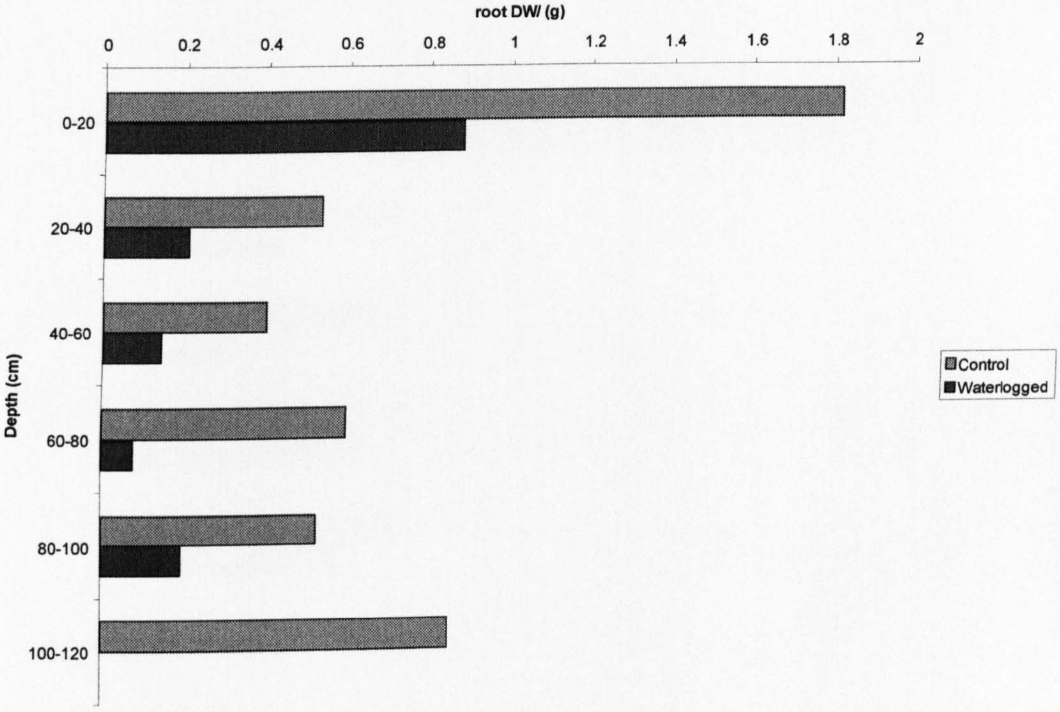

Figure 6.5. Dry weight of roots contained in each 20cm soil horizon of Claire winter wheat, at anthesis. The figure refers to a single replicate only.

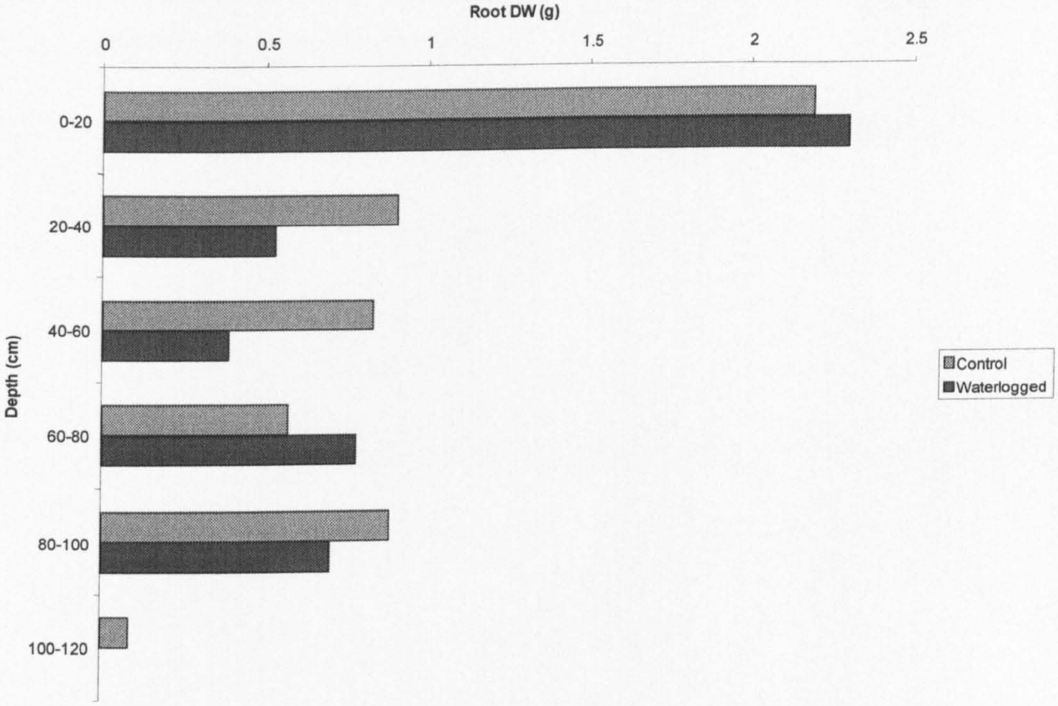

Figure 6.6. Root dry weight of Claire winter wheat at harvest grown in rhizotrons in drained and waterlogged conditions. Differences between treatments were significant only in the 20-40 cm (P = 0.04, LSD = 0.35) and 40-60 cm (P = 0.03, LSD = 0.38) soil layers.

6.3.2. 2002-2003 experiment

Waterlogging immediately decreased daily growth rate of the root systems (Figure 6.7). Unlike the previous experiment growth rates did not decline further, during the treatment period. The decrease in growth rate of the controls at the end of January was due to very low temperatures at this time. After the initial sharp decrease the growth rate of the waterlogged Deben roots began to increase, and unlike the previous experiment, this increase began during the waterlogging period. Xi-19 suffered a similar decrease in growth rate but showed a much weaker recovery. The growth rate of Deben, both control and waterlogged, decreased on March 7, then recovered before the final measurement. The weather during this time is described in the trials diary as 'foul', so cold and lack of sunshine must have slowed growth.

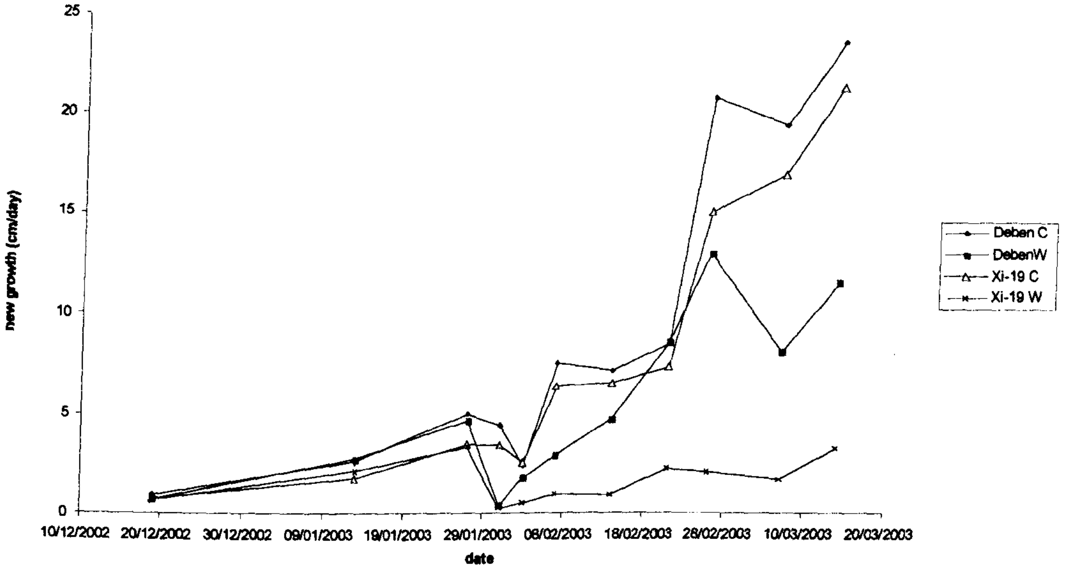

Figure 6.7. Growth rate in centimetres per calendar day of the root system of Deben and Xi-19 winter wheat grown in rhizotrons containing drained or waterlogged soil. The waterlogging period was from 27 January 2003 to 26 February 2003.

The growth of the controls of both varieties follows an exponential curve, as does that of the waterlogged Deben, albeit with a linear section during the waterlogging period (Figure 6.8). The growth of the waterlogged Xi-19 is much slower, showing a mainly linear pattern. Photographs of the intact, washed root systems at anthesis are included in Appendix IV. It should be noted that Deben has a more fibrous root system (like Claire in 2002) than Xi-19, which has a smaller number of main vertical roots, which have a tap root-like appearance. Waterlogged plants of all three varieties initiated nodal root axes in the upper soil layers in response to the loss of deeper seminal axes.

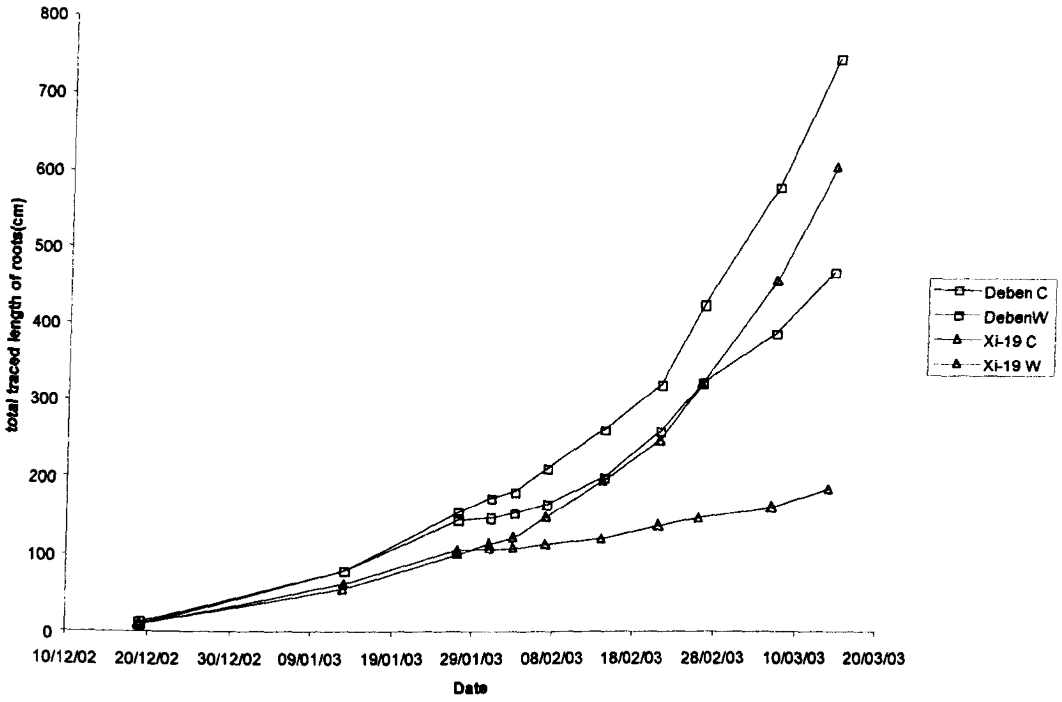

Figure 6.8. Total length of the root system of Deben and Xi-19 winter wheat grown in rhizotrons containing drained or waterlogged soil. The waterlogging period was from 27 January 2003 to 26 February 2003.

6.4. DISCUSSION

6.4.1. Effects of waterlogging on root growth and development

Waterlogging decreased root growth within the first few days of the treatment starting in both experiments. The restricted soil volume of the rhizotrons would mean that soil oxygen was quickly exhausted by root and microbial respiration. In these experiments all three varieties followed the same pattern of growth under drained control conditions, following an exponential curve, as described by Gregory *et al.* (1978), although total root length was used as the measurement of growth in these experiments, rather than the increase in dry weight.

6.4.2. Differences between varieties

Previous research has found that there was very little difference in root growth between varieties of winter wheat in normal conditions, and the results of these experiments do not suggest otherwise (Welbank *et al.*, 1973; Gregory *et al.*, 1978). The response of the varieties to waterlogging does appear to differ. Claire and Deben both resumed exponential growth after waterlogging, following a linear growth phase during waterlogging. The growth of Xi-19 appears to remain linear even after waterlogging has ended. Claire and Deben are closely related, so it would be expected that they would have a similar response to waterlogging. The growth of the root system of Xi-19 appeared to be more restricted by waterlogging than that of Deben and Claire, and the effects were more persistent. Xi-19 did appear less tolerant to waterlogging than the other varieties in some of the other experiments, such as the variety trials in the bins and tubes in 2002, but this trend was not consistent across all experiments. The growth of the root system of Xi-19 was slightly, but statistically significantly, slower than that of Deben, under control conditions. The interaction between waterlogging and variety was not statistically significant, although the responses of Deben and Xi-19 to waterlogging appeared to be different. The lack of statistical significance is most likely a result of the decreased and uneven number of replicates due to damage by mice.

6.4.3. Evaluation of the mini-rhizotron technique

Although pest damage made it impossible to make a statistically valid comparison of the response of different varieties to waterlogging, these experiments did demonstrate that the technique could be used to achieve useful data. As mentioned in the introduction to this chapter, the technique only allows the study of single plants, which will behave in a different way to plants grown as a population, so the data must be treated with some caution. The major problem with the method is the amount of time required to construct each rhizotron, and the care needed in harvesting the root systems intact. This restricts the amount of treatments and replicates that are feasible, especially when other experiments are being attempted at the same time. A choice must also be made between making harvests on several occasions, to observe rates of growth and development, and making one harvest the end of the experiment with sufficient replication to allow statistical analysis. A further problem with using this method to investigate waterlogging is that the waterlogging treatment caused the soil to slump in a similar way to that observed in the lysimeters (Chapter 4, section 4.3.3), buckling the roots, meaning that they had to be retraced onto fresh acetate.

Chapter 7: GENERAL DISCUSSION AND CONCLUSIONS

7.1. EFFECTS OF WATERLOGGING ON GROWTH AND YIELD

In all experiments where winter waterlogging reduced grain yield, this was as a result of a decreased number of fertile ears per unit area at harvest. This decrease was due to either a decreased plant population or decreased tiller production per plant. In the field experiment, waterlogging caused death of some plants over winter, and the decreased plant population of waterlogged plots had a positive effect on tiller number per plant, but not a great enough effect to compensate fully for the loss of plants. In the lysimeter experiments there was no effect of waterlogging on plant population, and so the decrease in tiller number per unit area was due to fewer tillers per plant. The most likely explanation for the differences in the effect of waterlogging on plant population between the lysimeters and the field is firstly that the glasshouse was sheltered, and secondly that the glasshouse plants were hand sown and evenly spaced, and tended to have a more erect growth habit, which would minimise competition between plants. In the field, varieties such as Hereward and Xi-19, with erect leaves, had a smaller decrease in plant population due to waterlogging, when compared to their more prostrate neighbours, such as Deben. There was no evidence of any effect of waterlogging on thousand grain weight (TGW); spikelet initiation or survival or fertility; or grain number per ear. These findings, that decreased ear number at harvest was the mechanism of grain yield reduction when waterlogging occurred during tillering, concur with the results of the lysimeter experiments at Letcombe (Cannell *et al.*, 1980). Yield loss was most severe when waterlogging coincided with the period of highest rate of tiller production, as illustrated by the waterlogging and sowing date interaction experiment. The September sown plants tillered in the autumn, and yield was decreased by the autumn waterlogging treatment, but not by the spring waterlogging, as by this time they already had an excess of tillers to that required to achieve maximum yield. In contrast the grain yield of plants sown in November was not affected by autumn waterlogging, as no tillering occurred until spring, but was severely cut by the spring treatment, during these plants' main tillering period.

Growth of the root system was affected before that of the shoot system, and to a greater extent, resulting in decreased root to shoot ratio (Chapter 3, tube experiments). In fact growth of the roots was almost halted within two days of the onset of waterlogging in the rhizotron experiments. This is to be expected, as it is the roots that are exposed to the hypoxic growth media, and it is the decrease in root growth that, in turn, decreases shoot growth. The decrease in nitrogen uptake resulted in a smaller canopy green area, both as a consequence of fewer tillers per unit area and a small decrease in leaf size, measured in the lysimeter and tube experiments. Therefore the decrease in grain yield may be attributed to the decreased resource capture of the smaller canopies of waterlogged crops.

Shorter straw of waterlogged plants, due to decreased internode elongation, was also observed in the field and lysimeter experiments. The most likely explanation for the decrease in straw length lies with the decreased availability of nitrogen in early spring. Withholding nitrogen fertilizer at this time is a strategy suggested to minimise lodging risk, by shortening the lower internodes (CPB Twyford, 2000). Another theory relates to the effect of hypoxia on plant growth substances – or 'plant hormones' – and their control of stem extension. Commercial PGRs act via the response mechanisms to gibberellin or ethylene. There is no evidence of a direct effect of hypoxia on gibberellin, although the flow of ABA, an inhibitor of gibberillin, in the transpiration stream is affected by hypoxia. However the effect of hypoxia in the roots is to decrease the supply of ABA (Else *et al.,* 2001). An increase in gibberellin activity would therefore be expected, and so hypoxia is unlikely to affect straw length via an interaction with gibberellin - although the decrease in leaf length due to waterlogging, observed in the tube and lysimeter experiments (see Chapter 3 and Chapter 4), would be consistent with a decrease in, or decreased sensitivity to, gibberrellin. Ethylene levels increase in response to waterlogging, as discussed in the literature review (chapter 1, section 1.6.4), and ethylene is a known inhibitor of internode extension. The enhanced rate of senescence of lower leaves due to waterlogging observed in all the experiments is further evidence of an increase in levels of ethylene in the shoot. Exposure to ethylene is known to inhibit cell elongation and enhance radial cell expansion, leading to shorter, thicker internodes (Waring and Phillips, 1970). The PGR 2-chloroethylphosphonic acid – as found in Terpal (BASF) - acts by breaking down to release ethylene. However waterlogging in all experiments finished some time before stem extension began, and no commercial PGR would be applied this early; anti gibberellins – such as chlormequat – should be applied at Zadoks 30-31, and Terpal after Zadoks 32. Thus it must be concluded that the mechanism by which waterlogging decreases straw length must be through decreased nitrogen availability during the early spring and a decrease in plant and shoot population, rather than any plant hormone interaction.

The effects of waterlogging on grain quality are far less clear, than the effect on yield. Grain proteins of all varieties in the variety screen in the bins, where all plots were waterlogged, were much lower than would be expected. Waterlogging also decreased the grain protein at harvest in the first lysimeter experiment. Total uptake of nitrogen was also decreased, leading to leaf chlorosis during waterlogging. In the following field variety screen total uptake of nitrogen by waterlogged plants was lower at the end of the waterlogging period and at anthesis, and percentage nitrogen content of the developing ears was lower at anthesis due to waterlogging. Therefore it was expected that grain protein would again be decreased at harvest. However this was not the case, and waterlogging had no effect on grain protein. Waterlogging would be expected to influence grain protein content both by the effect on the total uptake of nitrogen and by affecting the pattern of uptake during the season. The overall decrease in uptake would limit availability of nitrogen to the developing grains, thus reducing grain protein deposition. In contrast, limited nitrogen uptake early in the spring decreases tillering, meaning that surviving tillers would each be allocated a greater share of nitrogen applied as fertilizer top dressing later in the spring. Additionally the decreased green area of waterlogged plants would limit carbohydrate production, so that even if the total amount of grain storage protein deposited were decreased, there would be less dilution with carbohydrate, hence higher protein percentage.

7.2. EFFECTS OF WATERLOGGING ON DEVELOPMENT

There was some evidence that waterlogging delayed development, though the effect was not as great as that on growth. In the field variety trial the start of anthesis was delayed by about two days. Leaf emergence was delayed in the lysimeter waterlogging and drought trial and at one of the sampling dates of the second tube experiment. In the sowing date trial, the waterlogging treatments that had the greatest effect on grain yield, also had the greatest effect on development. For example, for the September sown plants, autumn and winter waterlogging decreased yield and delayed anthesis by two days, whilst the spring waterlogging had no effect on grain yield or development. For the October sowing date, autumn and winter waterlogging delayed anthesis by one and two days respectively and caused similar decreases in yield but spring waterlogging caused a greater loss of yield than both and delayed anthesis by four days. However there was no difference in harvest date due to waterlogging in any experiment (although there were differences between varieties in the first variety trial and between sowing dates in the sowing date experiment), and no difference in grain ripeness, as measured by moisture content. Therefore it may be concluded that waterlogging may shorten the grain filling period slightly, but not sufficiently to decrease TGW in these experiments. Delayed ear emergence and plant maturity, as a result of waterlogging, have also been reported by previous workers (Watson *et al.*, 1976).

7.3. RESPONSES AND ADAPTATIONS TO WATERLOGGING

As stated previously, when waterlogging decreased the plant population, the tiller number per plant increased to partially compensate. The proportion of tillers surviving to produce a fertile ear at harvest was also increased, when waterlogging decreased tiller number per unit area, in the field, bin and lysimeter experiments. As the differences in shoot biomass between drained controls and waterlogged plots were proportionally smaller at harvest than immediately after waterlogging it can be concluded that winter wheat has significant potential for recovery. Plants did show some ability to respond during waterlogging by adventitious production of nodal roots, able to penetrate more deeply below the water table due to their greater porosity. This adaptation of the root system by switching emphasis from seminal to nodal root production was observed in the rhizotrons, where root elongation almost ceased in the first few days of waterlogging and then increased again gradually, but never to the same level as the drained controls.

This study did not investigate the changes in gene expression and metabolism induced in the plant by waterlogging. However these processes are quite well understood, albeit using maize as the model species for monocotyledonous plants (see Chapter 1 section 1.11). Both the initiation of aerenchyma, signalled by elevated ethylene biosynthesis, and the initiation of anaerobic polypeptide (ANP) synthesis require oxygen to be present, and so occur in the period of hypoxia before the onset of anoxia (He *et al.*, 1992; Chang *et al.*, 2000). The waterlogging treatments used in all the experiments would allow a gradual decrease in soil oxygen levels, and total anoxia throughout the soil was probably never achieved, thus plants would be allowed the hypoxic acclimatisation required to initiate metabolic changes. Nodal root production in response to waterlogging was observed, and in the tube experiments (Chapter 3), the nodal roots were able to penetrate below the water level, and the root tips appeared white and healthy, in contrast to the seminal roots, which were brown and necrotic below the water level. Thus it is probable that the nodal roots possessed aerenchyma, at least to some extent, and that the mechanism of lysogenous aerenchyma production, involving ethylene signalling and enhanced cellulase activity had occurred. Plant death only occurred in situations where competition between plants was an additional factor, hence it may be hypothesised that the adaptations of the plants allowed them to survive the hypoxia caused by waterlogging. A caveat must be added that plant physiology studies tend to use model plants such as tobacco, castor bean and maize; to combine such experiments with agronomy work, such as this study, more molecular work is needed on wheat, rather than extrapolating from model species.

7.4. VARIETAL DIFFERENCES IN RESPONSE TO WATERLOGGING

There was very little evidence of difference in tolerance to waterlogging between varieties, in terms of a statistically significant interaction between variety and waterlogging, in the results of the experiments. The only time this did occur was in the first tube experiment. The statistical significance of this interaction may be merely a type two error as a result of analysing a large number of means (40) and must be treated with caution in the absence of evidence from other experiments. Certainly there was no interaction in the effects on final grain yield, even when varieties were chosen for the field experiment, because they appeared to have different responses in the screening experiments. That is not to say that there were no differences between the yields of varieties after waterlogging, but the highest yielding varieties under drained control conditions were the highest yielding after waterlogging and vice versa.

If there were differences in tolerance between varieties these would be expected to manifest themselves in the form of clearly identifiable characteristics, such as increased nodal root initiation or aerenchyma formation. The results of the second tube experiment showed no difference between varieties in their ability to produce nodal roots adventitiously in response to waterlogging, although such differences have been reported by other workers using US and Australian varieties (Huang *et al.*, 1994; Watkin *et al.*, 1998). Nor did the nodal roots of any one variety exhibit a greater ability than any other to penetrate below the water level. Therefore there was no evidence of differences in root porosity between varieties. By the last harvest however, nodal roots of all varieties were able to penetrate below the water level, whilst the seminal root system was largely restricted to above the water line. Thus it can be concluded that the nodal roots of all varieties have a greater porosity and hence penetration, than the seminal roots, in concurrence with previous findings (Trought and Drew, 1980; Huang *et al.*, 1997). It is believed that nodal roots have a greater ability to form lysogenous aerenchyma than seminal roots, as a result of the formers' greater sensitivity to ethylene. There was also very little difference between varieties in the severity of leaf chlorosis and premature senescence of lower leaves, although this has been suggested as a characteristic that could be used to screen varieties for tolerance (Villereal *et al.*, 2001). The field trial (Chapter 2, experiment 2) showed a decrease in nitrogen percentage content of leaves at the end of waterlogging, and this explains the chlorosis and premature senescence of older leaves. The differences in leaf chlorosis between varieties found by SPAD readings in the first variety screen were probably due to faster rates of development in varieties such as Xi-19, so that the rate of senescence of older leaves as new ones emerge, or leaf turnover, would be faster. Additionally, as there was no difference between varieties in the total uptake of nitrogen per area, varieties with a larger above ground biomass such as Xi-19 had a lower concentration of nitrogen in their leaves, and hence more chlorosis.

Of the varieties chosen for further testing in the field experiments there appeared to be different patterns of response to waterlogging, if not differences in tolerance, although the interaction between waterlogging and variety was not significant. Hereward had the smallest yield response to waterlogging, but also the lowest yield in drained and waterlogged conditions. The apparent tolerance of low yielding varieties, when the ability to maintain yield at a high percentage of the control is regarded as tolerance, has been identified by previous workers (Singh and Singh, 2003). However such tolerance is of little use to a farmer, if yields are still lower than a less tolerant variety with a higher yield potential. Low yielding but tolerant varieties would be of use in breeding programmes if traits to explain the tolerance could be identified. However no such traits were apparent in any of the varieties tested. The reason for the small response of Hereward was that this variety was sink limited, whilst waterlogging restricted the source, by decreasing nitrogen uptake and thus green leaf area. For all the other varieties this decrease in the source of photosynthates decreased yield; there being a positive correlation between green leaf area at anthesis and grain dry weight at harvest. This lack of yield response in Hereward to factors that affect the source (size and duration of green leaf area), such as foliar disease and fungicide application, has been observed previously (Dimmock and Gooding, 2002; HGCA, 2003b; Ruske *et al.*, 2003). Claire also had a small yield response to waterlogging but also a higher yield. This variety has strong winter dormancy, and is recommended for early drilling, so this lower growth rate during waterlogging would mean a lower metabolic demand for oxygen and perhaps this acted as a tolerance mechanism. Conversely, Xi-19, which includes spring wheat in its parentage and has a high winter growth rate, appeared to be more affected by waterlogging. Deben had a high tillering capacity, and whilst it was no more tolerant to waterlogging than the other varieties, had a good ability to recover in the spring. Riband was badly infected by *Septoria* disease in the field trial, so the data for this variety is of limited value.

7.5. STRESS TOLERANCE

Such avoidance of damage by stress due to the pattern of plant development, discussed in the previous paragraph, may be more important than physiological or morphological adaptations. For example barley is better able to 'tolerate' drought because it develops faster and has completed grain fill before the most likely time for drought to occur, later in the summer. In the same way, rye tolerates poor, low fertility or light drought prone soils by having a high winter growth rate, to produce a large biomass early in the season to provide a store of carbohydrate and nitrogen for drier conditions later on. A high early growth rate is associated with efficient uptake of nitrogen in some wheat varieties (Liaio *et al.*, 2004), and the growth of rye is more vigorous than any other cereal in the winter, as a result of its cold tolerance. In comparison with wheat, the leaves of rye during the vegetative stage are larger, but the flag leaf is much smaller. Wheat does the majority of its yield forming photosynthesis later in the season, relying much more heavily on its flag leaf, leaving it more vulnerable to yield loss due to drought and foliar disease. The price that must be paid for tolerance is that rye partitions a larger proportion of its biomass into vegetative growth, so that in unstressed conditions, modern semi-dwarf wheat, with its high harvest index will have a larger grain yield. A study of Australian wheat varieties, using a selection released over the last 150 years, found that modern varieties were – as would be expected – higher yielding, due to their higher harvest indices, but were less competitive against weeds (Vandeleur and Gill, 2004). The greatest decrease in competitiveness was associated with the introduction of Rht dwarfing genes, which not only decrease height, hence ability to shade out weeds later in the season, but also decrease seedling vigour. Dwarfing genes have been shown to interfere with gibberelin sensitivity, slowing elongation of seedling leaves, and thus the ability to smother weed seedlings in the seedbed would be decreased (Keyes and Paolillo, 1989). This illustrates that there is usually a yield penalty to be paid for stress adaptations; in the case of waterlogging tolerance the formation of structures such as nodal roots would divert resources away from grain yield. Some characteristics that confer tolerance to a particular stress may be disadvantageous in the face of another stress. High over winter growth rates allow winter cereals to build reserves to counter drought later in the season, but also put a higher demand on soil oxygen reserves, to facilitate the respiration needed to fuel this growth, so would be a disadvantage in waterlogged conditions. Erect leaves minimise competition between crop plants, and could help decrease plant death in stress situations, such as Hereward's response to waterlogging in the field experiment. However more competitive varieties such as Deben are better able to compensate for decreased plant populations by tillering, and a prostrate or planophile growth habit is more competitive against weeds (Richards and Davies, 1992; Davies *et al.*, 2002). Plant breeders must often make a compromise between yield potential and stress tolerance, for example triticale is an attempt to combine some of the characteristics of wheat and rye.

7.6. DIVERSITY FOR TOLERANCE

The lack of real differences in tolerance to waterlogging between the varieties tested is disappointing but perhaps not surprising when wheat's ancestry in the Middle East and subsequent centuries of inbreeding are considered. As discussed in the literature review, the genetic diversity of cultivated races of many crop species may be limited, as only the wild populations locally available to early farmers were used for domestication (Miflin, 2000). As undesirable agronomic characteristics were selected against, it is possible that genetic diversity for stress tolerance has been diminished in the process. In the evolution of wild plants and animals there is a general tendency for increasing diversity over time in terms of number of species within a group, but a decrease in disparity between species (Gould, 1989). Dominant groups will diversify, at the expense of less dominant groups (Darwin, 1859). Individual species are variations on a successful template, for example insects account for 80% of all animal species, so may be said to be extremely diverse, but all have a common body plan. Crop improvement by plant breeding may be considered to have worked in a similar way, as the most common strategy used by breeders in creating new varieties is to cross the best of the existing varieties and select the progeny with the best combination of the parental characteristics. For example Nickerson's two recent varieties, Nijinsky and Istabraq are both derived from crosses of Consort and Claire, which have been the two most popular biscuit wheats of recent years, and of the seven new varieties listed by this company as being in trials for the National List, five include Claire or Consort in their parentage, and one includes Flame, which was one of the parents of Claire (Nickersons, 2004).

However the selection pressure in the process of plant breeding has been much more intense than natural selection; the life of a commercial wheat variety is measured in years, not geological periods. An illustration of this is the fact that the oldest variety on the 2003 HGCA Recommended List is Riband, first registered in 1989, and most varieties are much more recent (HGCA, 2003a). So whilst there is reasonable diversity in terms of the number of varieties, most are merely variations on a theme. Modern UK wheat lines owe much of their ancestry to Cappelle Desprez, which at one time accounted for 80% of the UK wheat area, and in 1976, two thirds of the recommended varieties that year were Cappelle Desprez derivatives (Gill and Vear, 1980), and in their turn, modern varieties are derivatives of these. This is a good example of diversification by variation on a successful theme. The semi dwarf characteristic found in nearly all UK wheat varieties was derived from the Japanese variety Norin 10 in the 1970s, again an example of diversity based on a common ancestry. Additionally, nearly all wheat now grown in the UK (except for tiny amounts of Spelt and Durum grown for niche markets, such as health food) is of one species, *Triticum aestivum,* though there is a good diversity of varieties previously mentioned. This diversity of varieties, but lack of disparity of species, contrasts with the situation in Europe before the Agricultural Revolutions of the last two centuries. Iron Age and Medieval farmers grew the tetraploid Emmer (*Triticum dicoccum*), and rivet wheat (*Triticum turgidum*) and the hexaploid club wheat (*Triticum compactum*), Spelt (*Triticum spelta*), and Bread Wheat (*Triticum aestivum*). The *Triticum turgidum* variety 'Rampton Rivet' was grown up until the 1950's on poor, heavy soils (Gill and Vear, 1980). It would also be expected that limited communication would result in more disparity between populations of the same species grown in different localities, enabling landraces grown in marginal areas to develop tolerance. The modern wheat varieties used in the Henfaes experiments showed a very similar response to waterlogging as the Cappelle Desprez used at Letcombe; understandable as they are merely variations on a common theme. If it were possible to time travel back to Dark Ages Britain and collect the disparate species and land races of wheat it may be more likely that differences in tolerance to stresses such as waterlogging could be found. For diversity for stress tolerance to develop in crop plants, such as wheat, firstly the genes must exist within the genetic pool of the species, and then populations need to be isolated from one another, and subjected to different selection pressures in order for traits to diverge. Instead, as discussed above, the original gene pool of wheat was already restricted, and selection pressure is in favour of convergence, as traits for high yield characteristics are selected for, and marginal land (the source of selection pressure for stress tolerance in the crops grown on it) is removed from crop production - as has occurred in Wales over the last century.

Modern hexaploid wheat has a genome that originated from at least four wild ancestors. The A genome is identical to that of einkorn wheat *Triticum monococcum,* whilst the B genome is recombinant. Although the bulk of the B genome is believed to have originated from *Aegilops speltoides*, it is not identical to the S genome found in *Aegilops speltoides*; recently chomosome fragments that can only have come from *Aegilops searsii* have been identified in the B genome using molecular techniques (Liu, *et al.*, 2003). This ingression is believed to have occurred at the time of the hybridisation of *Triticum monococcum* and *Aegilops speltoides*, as the genomes of the raw amphiploids of the *Triticum-Aegilops* group are much more unstable than the diploids (Zohary and Feldman, 1962). The D genome is from *Aegilops squarrosa* (a.k.a. *Triticum tauscii*), resulting from a hybridisation with cultivated emmer when agriculture spread into the area that is modern day Iran. Therefore a small experiment was planned to investigate whether the ancestral species of wheat, which originate from the Middle East, were less tolerant to waterlogging than modern UK varieties, and if so could the increased tolerance be traced back to the incorporation of a particular genome. Additionally cultivated and wild barley species were included, from a range of habitats, and seeds were obtained from the Millennium Seed Bank at Kew. Unfortunately birds destroyed some of the wheat and barley ears, so final harvest data could not be obtained, and this experiment could not be used as a chapter in this thesis. Nonetheless a simple estimation of the percentage leaf area affected by chlorosis at the end of two weeks of waterlogging revealed some interesting results. Both accessions of *Triticum mononcoccum* and *Aegilops searsii* were badly affected, but *Aegilops speltoides* showed a similar level of tolerance to the wetland wild barley species, *Hordeum marinum* and *Hordeum secalinum*. The tetraploid *Triticum dicoccoides*, which includes most of the genome from *Aegilops speltoides*, was as tolerant as the UK hexaploid, Paragon, and more so than NIABWC10 from Pakistan. Genes for tolerance to other environmental stresses such as cold and salinity have been associated with the D genome from *Triticum tauscii*, and it was this hybridisation that allowed the cultivation of wheat to spread from the Middile East into Europe (Gill and Vear, 1980). However the results of this experiment suggest that enhanced waterlogging tolerance is found on that part of the B genome that originated from *Aegilops speltoides*. Indeed the ability of some tetraploid wheats to tolerate waterlogging to a similar or even superior degree as hexaploids has been previously reported (Davies and Hillman, 1988) and there is the example of the tetraploid Rampton Rivet, which was grown on heavy - and therefore waterlogging prone - land in the UK up until the 1950s (Gill and Vear, 1980).

Table 7.1. Percentage of leaf area affected by chlorosis and growth stage of a selection of *Triticum* and *Hordeum* species grown in drained or waterlogged conditions in an outdoor pot experiment.

Species	variety/Kew accession no	% leaf chorosis		Growth stage	
		control	waterlogged	control	waterlogged
Triticum monococcum	0033691	6	43	31	30
Triticum monococcum	0035444	2	39	31	30
Triticum dicoccoides	033369	2	15	41/45	39
Triticum aestivum	Paragon	2	15	39	39
Triticum aestivum	NIABWC10	2	31	51	45
Aegilops searsii	0151916	<1	61	45	39
Aegilops speltoides	0020161	<1	4	25	25
Hordeum vulgare	Optic	4	28	45	45
Hordeum spontaneum	0035455	12	28	51	51
Hordeum murinum	0057794	2	25	25	25
Hordeum marinum	0059020	<1	2	25	25
Hordeum secalinum	0057646	<1	1	25	25

statistics for leaf chlorosis

	treatment	species	interaction
P	<0.001	<0.001	<0.001
SED	2.1	5.0	7.1
LSD	4.1	10.0	14.2

Inbreeding of modern wheat may have reduced diversity for stress tolerance, but does not appear to have an affect on yield potential; illustrated by the observation that hybrid wheat varieties have not provided the improvements in yields demonstrated by hybrid maize since the 1970s, and to a lesser extent hybrid oilseed rape varieties. In an effort to counter the restriction of stress tolerance characteristics by inbreeding, genes from wild relatives or land races may be introduced, using plant collections and seed banks as a valuable genetic resource. Vavilov first proposed this strategy in the 1920s, but his rival Lysenko, who believed that inbreeding of the best varieties then available could increase Soviet yields, denounced him as a traitor (Juma, 1989, Hawkes, 1990). Lysenko's Lamarckian social beliefs, that learned behaviour could be inherited, found favour with the Stalinist regime; many leading geneticists were purged and the study of genetics virtually abandoned – the structure of DNA was yet to be discovered, and genetics could be dismissed as an unsubstantiated theory. Vavilov died in a prison camp, accused of agricultural sabotage, and progress in Soviet agriculture was curtailed for decades. Commercial plant breeding in the West has also followed the path of inbreeding of the best current varieties, as discussed previously. Now the genetic resources of wild relatives are recognised as an invaluable source of genes for stress tolerance, and there has been some success in selecting donors for waterlogging tolerance (Taeb, 1996, McDonald *et al.,* 2001; Garthwaite *et al.,* 2003). Synthetic hexaploids, (*Triticum turgidum* x *Aegilops tauschii*) developed by researchers at CIMMYT, have shown good tolerance to waterlogging, in respect of decreased levels of leaf chlorosis and ability to maintain a good thousand-grain-weight, when compared to sensitive *Triticum aestivum* varieties, although no yield data was provided (Villareal *et al.*, 2001).

It can be concluded that UK winter wheat varieties appear more tolerant of waterlogging than in other parts of the world. For example the average yield loss due to waterlogging in the UK is around 10-15 % (these experiments; Cannell *et al.,* 1980) compared to up to 50% in the Gulf Coast region of USA and parts of Western Australia (see Chapter 1, section 1.4). In part, this is due to the lower temperature at which waterlogging occurs in the UK. The growth habit of winter wheat also acts as a stress avoidance strategy, as growth is slowest in winter when waterlogging is most likely. Low growth rates have been identified as a stress tolerance mechanism in plants (Grime and Hunt, 1972; Lambers and Poorter, 1992) and specifically as an adaptation to waterlogging, by prioritising use of scarce energy to cell maintenance rather than growth (Greenway and Gibbs, 2003). As discussed previously all the varieties tested in the second tube experiment displayed an equally good ability to initiate nodal roots, able to penetrate more deeply than the seminal root system. Possibly some degree of waterlogging tolerance in the form of nodal root initiation has been inadvertently selected for in UK wheat varieties. The flip side of a lack of diversity in tolerance is that no variety may be considered as worse than the others.

7.7. SCREENING VARIETIES FOR TOLERANCE

At the start of this project it was hoped that it would be possible to identify characteristics that would allow varieties to be screened for tolerance at the seedling stage. However the results of these experiments cast considerable doubt on whether this will be possible. The characteristics suggested by previous workers include the extent of leaf chlorosis, decrease in dry weight due to waterlogging, as a percentage of that under control conditions, and the formation of aerenchyma. As discussed previously, varietal differences in leaf chlorosis may be as a result of different rates of growth and development so is unreliable as a screening method. There was no correlation between leaf chlorosis and yield after waterlogging in the variety screen in the bins, as shown in figure 7.1 below, so it can be concluded that the degree of chlorosis during waterlogging is of no value as a predictor of final yield. Previous workers have also found that leaf greenness during waterlogging is not a good indicator of final yield of wheat (Setter *et al.*, 1999).

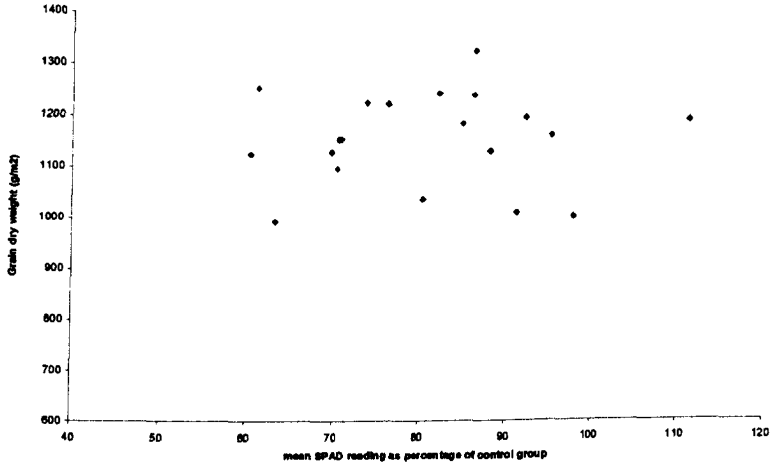

Figure 7.1. The relationship between mean SPAD reading, transformed as a percentage of the mean reading of four control varieties (Claire, Deben, Hereward and Xi-19) of leaf 1 and 2 taken during winter waterlogging of 20 varieties of winter wheat and grain dry weight per unit area at maturity. The values plotted are the means for each variety from all sampling dates when differences between varieties were significant according to ANOVA. The regression was not significant (P = 0.924).

There was no significant relationship between the ability to maintain plant dry weight during waterlogging at a high percentage of the drained control and the final grain yield of the varieties tested. Therefore it can also be concluded that measurement of plant dry weight during or immediately after waterlogging is not a valid screening tool for waterlogging tolerance either. The tube experiments found that the percentage plant dry weight decrease due to waterlogging was strongly correlated with plant dry weight under control conditions, with the varieties with a large vegetative biomass suffering a larger decrease due to waterlogging (see Chapter 3, Figure 3.12).

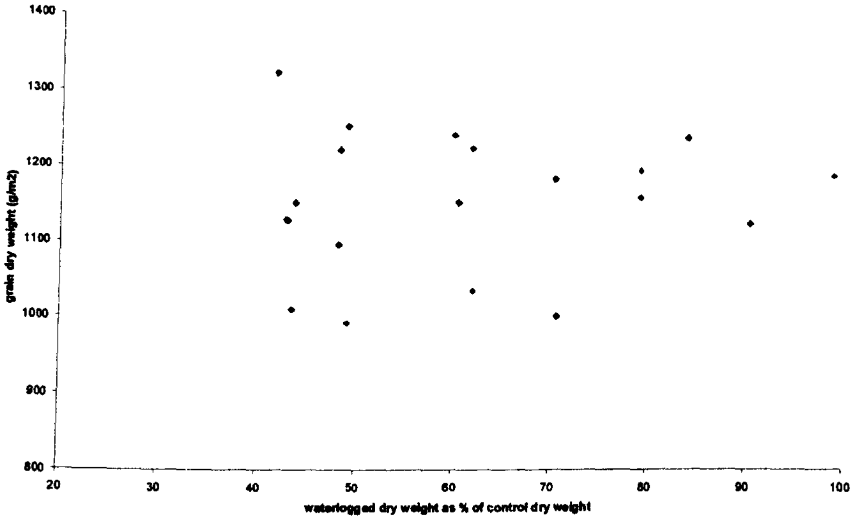

Figure 7.2. The relationship between plant dry weight after waterlogging in the 2002 tube experiment as a percentage of that of the control, and the grain dry weight m^{-2} of the same 20 varieties in the 2002 bin experiment. P = 0.837.

As discussed previously there was no evidence of varietal differences in the ability to form adventitious roots in response to waterlogging. Root porosity was not measured in this study, but can now be measured accurately using small samples of root tissue – with access to the required equipment (Visser and Bogemann, 2003), and aerenchyma formation has been associated with yield of waterlogged wheat (Setter *et* al., 1999). However in the tube experiment no variety was superior to any other in the ability of the nodal roots to penetrate below the water level, which if it had occurred, would have been indicative of varietal differences in root porosity. It can be concluded that the results of this study have got us no closer to finding a screening technique to identify tolerance to waterlogging at an early stage. As waterlogging tolerance appears to be a complex trait, involving the interaction of several genes, environmental factors and patterns of plant growth and development it may well be impossible to develop a simple screening technique.

7.8. INTERACTION OF WINTER WATERLOGGING WITH SUMMER DROUGHT

There has been speculation that winter waterlogging would leave plants more vulnerable to subsequent drought, by inhibiting the development of a deep and extensive root system. In the first year the drought treatment was too severe and masked the effect of waterlogging, accounting for the significance of the interaction, when droughted plants had no yield response to waterlogging; in the second the yield loss effects of the two treatments were additive, so it can be concluded that there was no interaction, of the type described above. The earlier work at Letcombe also found no interaction between waterlogging and drought (Cannell *et al.,* 1984, Gales *et al.,* 1984). Whilst waterlogging did restrict the size of the root system, as shown by the rhizotron experiments, transpiration demand must also have been decreased as a result of fewer tillers and, in some cases a small decrease in leaf elongation, hence a smaller canopy. Gales *et al.* (1984) reported decreased water use of previously waterlogged plants, as a result of decreased dry matter, and by implication, a smaller canopy and decreased transpiration. In the lysimeter experiment, waterlogged plants also had a slightly higher concentration of stem soluble carbohydrates, which can be used to aid the grain fill process during drought (data not shown). The most likely explanation for this increase is the slightly delayed development of these plants, especially as the concentration of carbohydrate in the ears of control plants was slightly higher than the waterlogged ones. An alternative theory is that decreased respiration demand by the roots led to a backlog of carbohydrate in the shoot.

Although waterlogging does not appear to affect wheat's ability to cope with subsequent drought, a wet winter and spring, when the soil remains at or near field capacity (but not waterlogged), may make plants more vulnerable to summer drought. Wheat roots will preferentially use water from the top 20cm or so of the soil when frequent rain replenishes the surface layers, rather than extracting water from the water table deeper down (Gregory, 1994). Approximately half of the total root dry matter is found in the top 20cm layer and easy availability of water here will discourage partitioning of resources into the deeper roots needed in the summer. The Letcombe work found that waterlogging changed the pattern of water extraction in spring, following winter waterlogging (Gales *et al.,* 1984). Previously waterlogged plants demonstrated increased water extraction from the top 20 cm of soil on clay (the top 40 cm on sand) and decreased extraction from the soil layers below this depth. The results of the Henfaes experiments and other published work suggest that this observation is due to increased reliance on nodal roots, which are formed in response to waterlogging. These roots form the root crown – a cone of roots which anchors the plant – which is found in the upper 20cm or so of soil. The deeper seminal roots are responsible for deep extraction of water, and it is these that are killed by waterlogging.

The other mechanism by which waterlogging and drought may interact is through stem base diseases such as eyespot (*Pseudocercospella herpotrichoides*), take-all (*Gaeumannomyces graminis* var. *tritici*), and *Fusarium* spp. stem blight, which are encouraged by wet conditions, and perhaps by weakening of the plants by waterlogging. Plants infected with these diseases, especially take-all, will have severely weakened root systems and will be much more vulnerable to subsequent drought (Hornby, 1998). The conclusion from the Letcombe work was that waterlogging was more likely to be a problem for cereal growers in the UK than drought, although climate change was not considered at that time (Cannell *et al.*, 1984). The reduction in yield potential due to waterlogging may be more serious than that due to drought. Drought generally causes a slow linear decrease in yield potential as the stress progresses, and once water becomes available significant recovery may occur, providing stress did not coincide with a sensitive stage in development; loss in yield potential due to hypoxia is sharper and recovery slower (Sojka, 1992). It would be unfair to compare the severity of the effects of waterlogging and drought in the lysimeter experiments, because of the high temperatures in the glasshouse during the drought period, which must have caused additional stress. To achieve a fair comparison shelters in the field, to exclude rain but maintain ambient temperatures, would be needed.

Following the hot summer of 2003, the media was full of reports that heat waves would become the norm, although after one of the wettest Augusts on record experienced in 2004, this has taken a back seat. If summer drought does become more prevalent in the UK as a result of climate change, feed grain production will probably move away from wheat and towards barley and triticale, which are both more tolerant of drought. In an extreme scenario, where winters became too wet and summers too dry for cereals currently grown to thrive, then grain maize, as already grown in France, may be adopted.

7.9. WATERLOGGING AND LODGING

As mentioned in section 1.10 of Chapter 1, some farmers believe that waterlogging may increase the susceptibility of crops to lodging, by restricting root growth thus reducing root anchorage. Two types of lodging have been identified: stem lodging occurs when the plant leverage is greater than the root anchorage, and stem lodging (or brackling) occurs when the leverage of an individual shoot is greater than the stem strength (Spink *et al.,* 2003). The finding that waterlogging tends to reduce straw length indicates that both plant and shoot leverage should be decreased by waterlogging. There is no reason to suppose that root anchorage should be decreased, because the nodal or crown roots produced in response to depleted soil oxygen, provide plant anchorage, not the seminal roots that are adversely affected by waterlogging. Therefore root lodging should not be made more likely by waterlogging; in fact the decrease in plant population due to waterlogging would increase root anchorage strength, by increasing the soil volume available for the root cone of each surviving plant (Hoad *et al.,* 2001). Haung *et al* (1995) observed a decrease in inorganic nutrient take-up, including a decrease in straw K, which could decrease straw strength, making stem lodging more likely. However the decrease in early season N uptake, would increase straw strength, by decreasing the production of unlignified 'soft growth'. In a field trial in 2004 (unpublished results) no lodging in control or waterlogged areas was observed, despite the very stormy summer and the varietal susceptibility to lodging of Deben and Xi-19, because of good crop management (a robust PGR programme applied at the correct timing, and delayed applications of nitrogen).

It is regularly mentioned in the farming press that some commercial plant growth regulators, such as chlormequat and trinexapac-ethyl (Moddus), may stimulate rooting. If this were so, then PGRs could be applied in the spring to help roots recover after waterlogging. However there appears to be very little published scientific literature to support these claims. Indeed a recent review (Hoad *et al.,*

2001) devoted a paragraph to these claims, without citing any specific work, after quoting work by Easson *et al.* (1995), which found that PGRs had no effect on root strength.

7.10. STRATEGIES TO COPE WITH WATERLOGGING

The finding that there is little difference between varieties in their level of tolerance to waterlogging, supports the views of Richards (1983, 1995) that the best strategy to cope with plant stress is to breed cultivars with high yield potential in non stressed situations. Selecting varieties that avoid serious damage, by the means of the most vulnerable developmental stages not coinciding with the times of greatest risk of waterlogging, is another strategy, possibly with a greater potential for maximising yields than trying to find cultivars with physiological tolerance. For example, in Australia, waterlogging on duplex soils often occurs during stem extension, causing a yield loss of 60%, but by sowing later maturing ‘long season’ varieties, which enter their reproductive stage after the most likely period for waterlogging, yield losses were cut to only 20% (Gardner *et al.,* 1992). The stages of development at which wheat is most vulnerable to waterlogging are establishment and early in the reproductive stage, stem extension and booting, and in UK winter wheat these occur before and after the highest risk period in winter. The results of the sowing date and waterlogging trial in the bins, suggest that an early autumn sowing date is able to ameliorate some of the effects of waterlogging. Firstly the higher unstressed yield potential of these plants gives them a higher yield from which the effects of waterlogging are subtracted, and secondly plants are more likely to be better established when waterlogging occurs and so are more likely to survive, and thirdly early sown plants have two potential tillering periods in autumn and spring. This last point means that plants can compensate in spring for autumn or winter waterlogging, and if waterlogging occurs in spring it will have little effect as the plants will have plenty of tillers from the autumn. This of course assumes that waterlogging is transient and not continuous from autumn to spring. However transient waterlogging is the most likely type on UK field soils, as a result of slow infiltration of water into heavy clay soils.

A solution to waterlogging in the UK may be to leave poorly drained or heavy soils uncropped. Orson (2003) suggests that in response to the introduction of reforms to CAP and the decoupling of subsidy from production, it makes economic sense to only cultivate those fields, or parts of fields, with sufficient yield potential to provide a profit above the value of the single farm payment on that land. This however, is a short-term solution, based on the assumption that grain production is in excess of requirements. This assumption is false; the worlds population is increasing, and barring disaster will continue to do so for the foreseeable future, the area of cultivatable land is decreasing due to urbanisation and environmental degradation, and as people become wealthier, consumption of grain per head increases as demand for meat increases, animal production being a less efficient use of grain. This process is currently happening in China, which is beginning to import grain to feed its large poultry and pig sector, despite this country being the World's largest wheat producer. Additionally, in Europe, non-food uses of cereals may become more important in future, for example bioethanol (Turley, 2003), especially in the face of decreasing security of oil supplies. Choosing not to produce food is not an option for subsistence farmers in the developing world. Here use of perennial species to lower the water table may be useful, for example an agroforestry system may be beneficial, or the new perennial *Triticum-Thynopyrum* hybrids currently being developed (Cai *et al.*, 2001). There is some limited evidence that Triticale may be a more waterlogging-tolerant alternative to wheat. Studies in Australia found the tritcale variety Muir to be more tolerant than the wheat varieties tested, in respect of biomass production and aerenchyma formation (Watkin *et al.*, 1998; Singh *et al.*, 2003). Two cautions must be considered before it can be said that triticale is more waterlogging tolerant as a species; firstly the studies used only one triticale variety and as variation in tolerance was found in the wheats tested, it may exist in triticale; secondly all the cereals used in the studies appeared to be of the spring type, and in the UK nearly all triticales are winter types. However, as triticale is already known to tolerate other marginal situations for cereal production, perhaps waterlogging tolerance of this crop deserves further study.

7.11. FUTURE PROSPECTS

As discussed previously, the results of these experiments offer very little hope that a simple screening method for waterlogging tolerance of winter wheat can be found. In other areas of plant science molecular techniques have proved useful, but in the case of a complex trait such as waterlogging tolerance the ability to identify and clone individual genes may be of limited value. Genetic modification is not a 'magic bullet', which can solve all the world's food problems. Genes for tolerance of anoxia have been identified in maize – those coding for ANPs – but unfortunately the mechanism of their selective expression is not well understood (Sachs *et al.,* 1996). The proteins that are produced by these genes are enzymes that regulate alternative metabolic pathways, fermentation for example, and enzymes active in forming lysogenous aerenchyma - mechanisms that will aid survival of the plant during waterlogging. However the results of the experiments reported in this thesis suggest that when transient waterlogging occurs, as might be experienced in a field over winter, the ability of plants to recover from damage may be more important in determining final yield than tolerance whilst waterlogged. Furthermore the role of plant adaptations to waterlogging, such as aerenchyma, in improving performance is not clear. Yield of a range of Australian spring wheats was found to be correlated with root porosity (Setter *et al.,* 1999); Haung *et al* (1994) reported that wheat varieties with greater root porosity suffered a smaller decrease in growth and less leaf chlorosis as a result of waterlogging; but Watkin *et al* (1998) found that, whilst aerenchyma allowed greater root growth, this was not always translated into more shoot growth. Boru *et al* (2003) observed that tolerant wheat varieties could increase the rate of oxygen uptake in response to hypoxia, but these differences in oxygen use between tolerant and sensitive varieties were not always related to differences in root structure. Additional factors, such as the supply of carbohydrate to the roots were cited as important in determining waterlogging tolerance. So unfortunately adding or enhancing expression of genes for aerenchyma alone is unlikely to improve waterlogging tolerance in wheat.

Considering these difficulties it is unlikely that significant breakthroughs in breeding for waterlogging tolerance can be made in the near future. The production of crop varieties with salt tolerance in the field, a complex trait like waterlogging, has also been very slow, considering the amount of research effort expended on the problem (Flowers and Yeo, 1995; Flowers 2004). Work in Australia has identified the wild grass *Hordeum marinum* as a potential source of tolerance and this has been successfully hybridised with wheat (McDonald *et al.*, 2001; Garthwaite *et al.*, 2003). However such wide hybridisations will always introduce unwanted 'weedy' characteristics from the wild parent, that require extensive back crossing to remove. UK farmers are now encouraged to produce quality grains for specific markets, such as NABIM group 1 and 2 milling wheats, so grain quality is as important as yield. Wheat storage proteins are extremely complex and introducing genetic material from other species often has a negative effect on grain protein quality. For example the 1B1R chromosome substitution from rye has been introduced into wheat, and increases yield by allowing more grain sites on the spike to be filled and prolonging green area retention. However the storage proteins from rye introduced with the 1R chromosome cause these varieties to have poor bread making quality, restricting their use to the animal feed market.

7.12. BREEDING FOR STRESS TOLERANCE

A recent report into crop science in the UK by a review committee of the BBSRC highlighted the need for 'public good' plant breeding to produce cereals able to cope with some of the effects of climate change, such as winter waterlogging (BBSRC, 2004). The findings of these experiments strongly suggest that such a project would have to compare the effects of single 'stress genes' and crop growth patterns. Crop science has been criticised for taking a reductionism approach, whereby scientists explain a factor by looking at the layer of organisation below it (Wiener, 2004). For example yield - a product of the population of plants in the field - is investigated on the plant physiology level. Considering the resource capture and canopy management models proposed by Scott and Monteith (Monteith, 1994) and work in plant ecophysiology, this criticism is not entirely fair. However whilst reviewing literature for my own thesis it became apparent that most work on waterlogging was done as pot or solution culture experiments; field trials were rare. Therefore stress tolerance needs to be investigated on multiple levels; the molecular, whole plant physiology and population ecology as part of the field plant community.

Plant breeding over the last half century has made huge advances in yield possible by increasing the harvest index of the plant, with some losses in stress tolerance as mentioned previously, and greater reliance on chemical inputs. The highest yielding NABIM group 4 varieties such as Tanker and Access at the moment are 'dirty barn-fillers', short strawed, with high yield potential, but with poor disease resistance and requiring high levels of inputs. Climate change may place greater emphasis back onto stress tolerance, due to greater unpredictability of weather. If climate change increases the incidence of extreme weather events, such as heat waves, droughts and storms it is very unlikely that cereal production will cease in the arable areas of east England, as predicted by Prof. Edwards-Jones (Poster for the RWAS Show, July 2004). Instead management will switch to a low input-low output system, more akin to USA or Australia. As fungicides will not be economically justifiable plant resistance to disease will be much more important. Already there is pressure to decrease chemical inputs due to resistance (black grass to 'fop' and 'dim' graminicides, *Septoria* and mildew to strobilurins) and environmental concerns (VI, NVZs etc). Therefore the cereal ideotype may switch to a disease resistant plant, tolerant to late season drought, able to compete with weeds and efficiently scavenge lower nitrogen inputs, such as triticale. Any breeding project, to cope with climate change, will have to decide whether it is best to adapt wheat to the new conditions or look at different cereals. There will always be a demand for bread wheat, but as most grain is used as animal feed, other cereals could be substituted. Until the 1980s barley was the major feed cereal grown in UK.

In the case of complex multi gene traits such as drought or waterlogging tolerance wheat varieties can be screened and PCA used to find the traits with the strongest positive effects of performance under stress. These genes could be identified and used in stress breeding. Hence molecular biology and field-testing of crops in a realistic environment could be combined. This approach could be compared to simply improving other crops with better tolerance to specific stresses such as barley, oats, rye and triticale.

Current plant breeders try to achieve Recommended List status with their new varieties. The Recommended List system may discriminate against lower yielding but stress tolerant varieties. To qualify, a variety must offer a yield improvement over existing equivalent varieties. Perhaps a positive step is the inclusion this year of the variety Welford, despite a lower yield potential, because of its resistance to orange blossom midge (HGCA, 2004). The List now also includes information on performance on light and heavy soils, in different rotational positions and after late drilling.

For the short-term, in the absence of tolerant varieties the best approach appears to be to select varieties with characteristics, which make them less susceptible to damage by waterlogging. For example Claire has a strong winter dormancy, which lowers the metabolic demand for oxygen when it is most likely to be restricted by waterlogging. Deben has a very high tillering ability which allows it to recover from damage. Alternatively bread making varieties such as Hereward, Malacca and Soissons can be grown with a specific market in mind, with the knowledge that their lower yield potential will be less affected by waterlogging.

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UK RECOMMENDED LIST OF WINTER WHEAT 2001

The control for yield comparisons is the mean of Consort, Hereward, Madrigal, Rialto and Savannah. Differences of less than 3% for the fully recommended varieties, and less than 4% for comparisons involving provisionally recommended varieties, should be treated with reserve.

	Fully Recommended												Provisionally Recommended					Bec. Out.
													NEW	**NEW**		**NEW**	**NEW**	
Recommendation categories: G General Use S Special Use R Regional Use P Provisional Use O Becoming Outclassed	Savannah	Claire	Equinox	Consort	Malacca	Shamrock	Hereward	Charger	Madrigal	Riband	Buchan	Soissons	Tanker	Deben	Napier	Biscay	Option	Rialto
	G	G	G	G	G	G	G	S	RG	RG	RG	RS	PG	PG	PG	PG	PG	O
Region of use	UK	UK	UK	UK	UK	UK	UK	UK	NE	NE	NE	C,SE SW	UK	UK	UK	UK	UK	UK
UK yield as % treated control (10.09 t/ha)																		
With fungicide treatment	105	102	102	102	98	96	91	99	102	101	100	91	107	106	105	104	103	99
Without fungicide treatment	68	75	71	65	72	76	72	73	71	59	73	70	70	81	75	74	77	76
Standing power	7	8	9	8	8	8	8	5	8	8	9	6	8	6	7	6	7	6
Shortness of straw	7	7	9	8	8	8	7	8	8	7	8	7	8	6	8	7	7	6
Earliness of ripening	6	7	7	6	8	7	7	8	6	7	6	9	7	7	7	7	7	7
Resistance to shedding	7	7	6	6	7	7	6	5	7	6	7	6	–	–	7	–	–	5
Resistance to sprouting	6	4	5	6	6	5	5	2	6	6	6	7	–	–	5	–	–	6
Latest safe sowing date	Mid Feb	End Feb	End Jan	End Jan	End Jan	End Jan	End Jan	End Jan	End Jan	End Jan	End Jan	Mid Feb	Mid Feb	Mid Feb	End Jan	End Jan	End Feb	End Jan
Resistance to disease																		
Mildew	8	4	5	6	7	8	6	7	6	6	7	8	7	5	6	5	4	6
Yellow rust	5	9	6	9	9	8	7	9	3	6	4	8	7	9	4	5	9	6
Brown rust	9	9	9	5	8	4	8	6	9	3	9	2	8	7	9	9	7	4
Septoria nodorum	5	7	6	6	7	7	7	6	6	4	5	5	5	7	6	6	5	6
Septoria tritici	4	7	5	4	6	6	6	5	5	3	5	6	4	7	5	6	5	5
Fusarium ear blight	6	6	6	6	6	6	6	4	6	5	6	5	(5)	(6)	4	(8)	(6)	5
Eyespot	6	7	6	6	5	4	4	5	6	6	6	4	6	5	5	5	6	6
Grain quality																		
Bread-making quality	–	–	–	–	8	8	8	6	–	–	–	6	–	–	–	–	6	6
Biscuit-making quality	–	7	–	7	–	–	–	–	–	7	–	–	–	5	–	–	–	–
Endosperm texture	Hard	Soft	Hard	Soft	Hard	Hard	Hard	Hard	Soft	Soft	Soft	Hard	Hard	Soft	Hard	Hard	Hard	Hard
Protein content (%)	11.0	11.9	11.8	11.8	12.3	12.7	13.2	12.1	11.9	11.6	11.7	13.1	11.7	11.5	11.6	11.6	12.1	12.7
Hagberg Falling Number	246	269	241	241	346	260	267	248	236	209	270	284	282	234	176	301	294	220
Zeleny volume	24.1	21.0	25.9	21.5	47.4	54.7	51.5	49.0	17.9	15.0	19.5	58.6	(24.9)	(26.6)	(20.1)	(27.5)	(49.9)	46.9
Specific weight (kg/hl)	77.0	77.5	75.0	77.0	75.9	79.0	79.2	76.5	77.8	75.3	78.6	79.0	75.9	76.3	76.1	77.4	78.4	77.8
1000 grain weight (g)	51.4	44.4	51.0	46.0	42.1	42.0	45.3	43.6	45.2	49.5	45.7	42.6	50.0	49.7	50.6	50.5	43.6	48.7
Year first listed	1998	1999	1997	1995	1999	1999	1991	1997	1997	1989	1999	1995	**2001**	**2001**	2000	**2001**	**2001**	1995

The yield figures presented contain data from the 1997 trials in the North East region in which some varieties were affected by poor grain set.
A high figure on the 1–9 scale indicates that a variety shows the character to a high degree.
( ) = Limited data.

Funding for Recommended List trials is provided by HGCA

RECOMMENDED LIST OF WINTER WHEAT 2002

The control for yield comparisons is the mean of Consort, Claire, Malacca, Rialto and Savannah. Differences of less than 3% for the fully recommended varieties, and less than 4% for comparisons involving provisionally recommended varieties, should be treated with reserve.

	Fully Recommended											Provisionally Recommended							Becoming Outclassed	
												NEW		**NEW**				**NEW**		
	Napier	Savannah	Claire	Consort	Malacca	Shamrock	Hereward	Charger	Buchan	Riband	Soissons	Access	Deben	Xi 19	Tanker	Biscay	Option	Solstice	Madrigal	Equinox
Recommendation categories: G General Use S Special Use R Regional Use P Provisional Use O Becoming Outclassed	G	G	G	G	G	G	G	S	RG	RG	RS	PG	PG	PG	PG	PG	PG	PG	O	O
Region of use	UK	UK	UK	UK	UK	UK	UK	UK	NE	NE	C,SE SW	UK	UK	UK	UK	UK	UK	UK	NE	UK
UK yield as % treated control (9.99 t/ha)																				
With fungicide treatment	104	103	101	101	98	94	90	98	99	99	89	105	104	104	104	103	102	100	101	100
Without fungicide treatment	74	67	74	64	72	74	72	72	72	58	68	72	79	73	70	74	76	75	69	70
Standing power	7	7	7	8	8	8	8	5	9	8	6	8	6	6	8	6	7	9	8	8
Shortness of straw	8	7	7	8	8	8	7	8	8	7	7	9	6	6	8	7	7	6	8	9
Earliness of ripening	7	6	7	6	8	7	7	8	6	7	9	7	7	8	7	7	7	7	6	7
Resistance to shedding	7	7	7	6	7	7	6	5	7	7	6	–	6	–	6	7	7	–	7	6
Resistance to sprouting	5	6	4	6	6	4	5	2	6	6	7	–	5	–	6	7	8	–	6	4
Latest safe sowing date	End Jan	Mid Feb	End Feb	End Jan	End Jan	End Jan	End Jan	End Jan	End Jan	End Jan	Mid Feb	–	Mid Feb	–	Mid Feb	End Jan	End Feb	–	End Jan	End Jan
Resistance to disease																				
Mildew	7	7	4	7	7	6	5	8	7	7	8	7	6	8	6	5	4	5	6	5
Yellow rust	4	5	9	6	9	8	7	9	3	7	8	3	9	9	7	5	9	9	3	5
Brown rust	9	9	9	5	8	5	8	6	9	3	2	9	7	8	8	9	7	5	9	9
Septoria nodorum	6	5	7	6	7	7	7	6	5	4	5	5	7	5	5	7	6	6	6	6
Septoria tritici	5	4	7	4	6	6	6	5	5	3	6	5	7	6	4	6	5	6	4	4
Fusarium ear blight	5	6	6	6	5	6	5	4	6	5	5	(5)	6	(4)	5	8	6	(7)	5	5
Eyespot	5	6	7	6	5	4	5	5	6	6	4	6	6	6	6	5	6	5	6	6
Grain quality																				
Bread-making quality	–	–	–	–	8	8	8	6	–	–	6	–	–	7	–	–	6	7	–	–
Biscuit-making quality	–	–	7	7	–	–	–	–	–	7	–	–	5	–	–	–	–	–	–	–
Endosperm texture	Hard	Hard	Soft	Soft	Hard	Hard	Hard	Hard	Soft	Soft	Hard	Hard	Soft	Hard	Hard	Hard	Hard	Hard	Soft	Hard
Protein content (%)	11.6	11.1	11.8	11.6	12.3	12.7	13.2	12.2	11.7	11.6	13.0	11.2	11.4	11.8	11.8	11.6	12.1	12.3	11.9	11.8
Hagberg Falling Number	166	232	259	232	331	243	253	235	259	200	268	179	215	299	260	297	288	276	213	225
Zeleny volume	22.5	22.1	21.0	21.4	47.3	54.5	51.4	47.1	18.7	15.4	56.5	(19.8)	26.4	(41.0)	24.0	26.1	48.6	(45.4)	17.8	23.7
Specific weight (kg/hl)	75.7	76.7	77.1	77.0	75.6	78.7	79.1	76.0	78.3	75.1	78.6	76.0	76.2	76.2	75.4	77.0	78.2	77.5	77.3	74.3
1000 grain weight (g)	52.3	53.6	46.7	48.0	44.2	43.7	47.4	45.4	47.7	51.4	44.1	49.2	51.8	49.9	52.1	52.4	45.8	49.0	47.1	52.9
Year first listed	2000	1998	1999	1995	1999	1999	1991	1997	1999	1989	1995	**2002**	2001	**2002**	2001	2001	2001	**2002**	1997	1997

The yield figures presented contain data from the 1997 trials in the North East region in which some varieties were affected by poor grain set.
A high figure on the 1–9 scale indicates that a variety shows the character to a high degree.
( ) = Limited data

NIAB acknowledges trial funding from HGCA.

APPENDIX II. SOWING DATE X WATERLOGGING DATE EXPERIMENT

CHAPTER 5

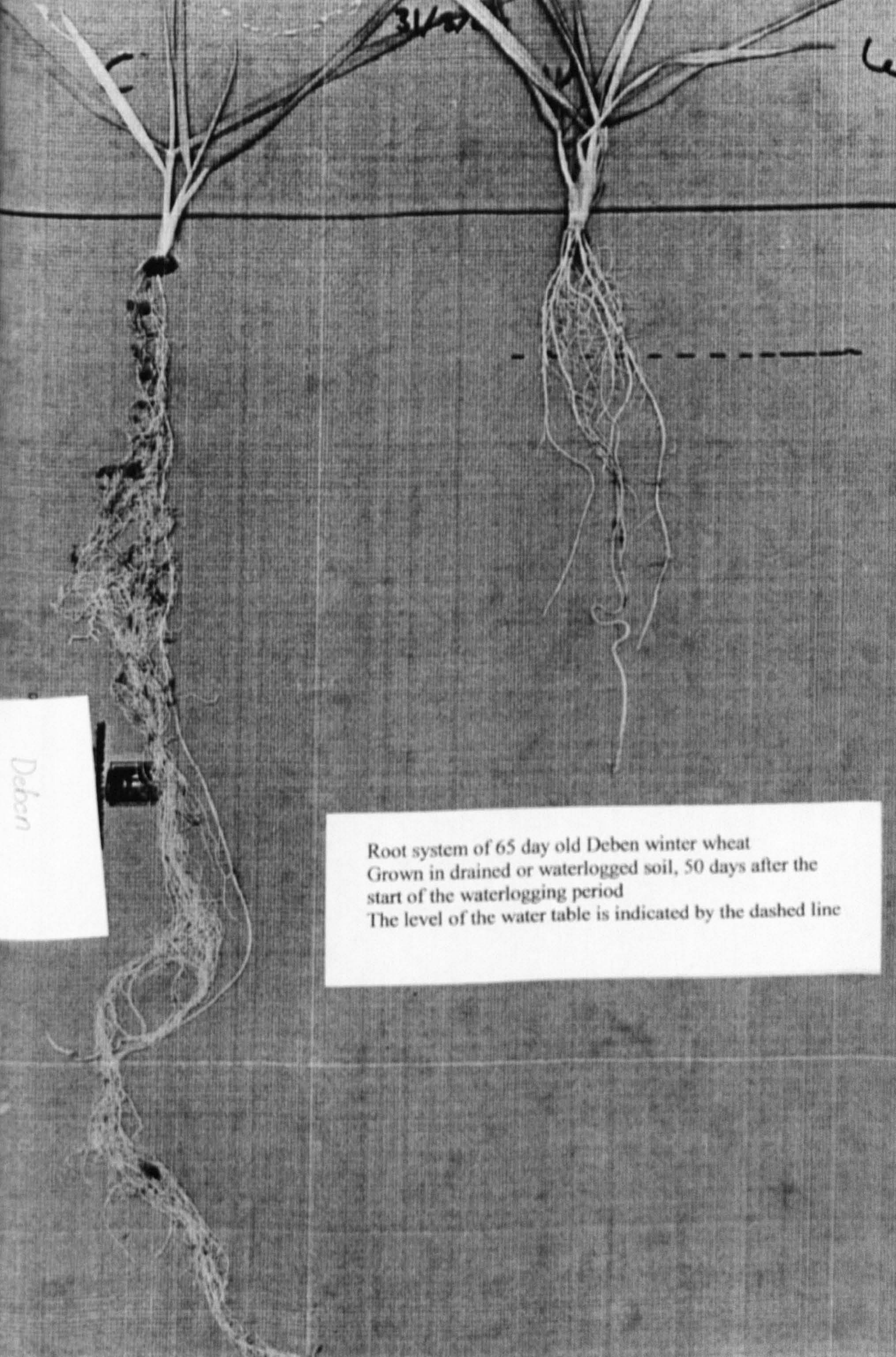
Growth analysis at Maturity, with BYDV affected plots included in the analysis.

Table A2.1: Yield and Yield Components. Statistical analysis was a two factor analysis of varience, with randomised blocks, using Genstat. Seds and lsds are given at the 5% level.

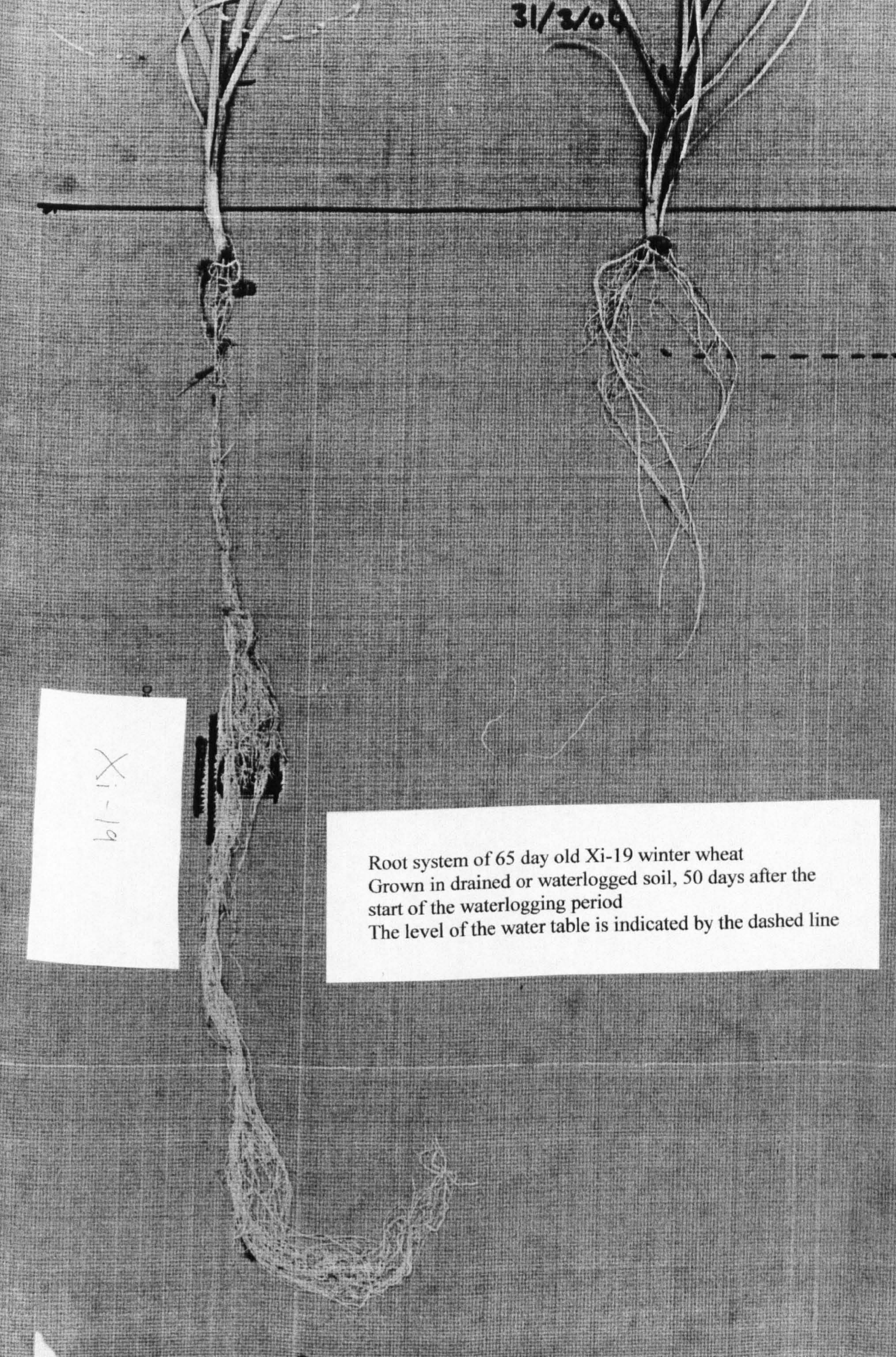
	Grain gm^{-2}	DW	Ears m^{-2}	Grains Ear^{-1}	TGW (g)	Spikelets ear^{-1}	Grains spikelet^{-1}
Sowing Date							
Early		930	409	47.4	47.7	21.1	2.42
Middle		722	408	39.4	44.9	22.9	1.73
Late		616	431	35.4	39.4	21.3	1.66
Waterlogging Period							
Control (C)		821	461	40.5	43.1	20.6	2.16
Autumn (A)		766	414	41.8	44.1	22.5	1.85
Winter (W)		757	394	41.9	46.3	22.0	1.92
Spring (S)		680	394	38.8	42.5	21.8	1.81
Interaction							
Early C		1058	449	48.1	49.0	18.8	3.10
Early A		887	409	45.2	48.0	22.4	2.02
Early W		841	386	48.0	46.0	21.7	2.22
Early S		934	394	48.4	47.9	21.5	2.33
Mid C		763	458	42.6	42.0	21.9	1.75
Mid A		718	400	38.4	42.9	23.7	1.80
Mid W		741	378	39.1	50.3	23.3	1.68
Mid S		665	399	37.5	44.5	22.6	1.67
Late C		642	479	34.9	38.3	21.2	1.64
Late A		692	436	37.5	41.5	21.5	1.74
Late W		689	420	38.6	42.6	21.1	1.85
Late S		441	391	30.7	35.1	21.3	1.43
P							
Sowing date		<0.001	0.156	<0.001	<0.001	0.053	<0.001
Waterlogging		0.112	<0.001	0.331	0.361	0.207	0.448
Interaction		0.193	0.879	0.275	0.314	0.800	0.363
SED							
Sowing date		48.8	ns	1.61	1.94	0.79	0.202
Waterlogging		ns	15.4	ns	ns	ns	ns
Interaction		ns	ns	ns	ns	ns	ns
LSD							
Sowing date		98.3	ns	3.24	3.91	1.58	0.408
Waterlogging		ns	31.1	ns	ns	ns	ns
Interaction		ns	ns	ns	ns	ns	ns

Table A2.2 Other harvest measurements

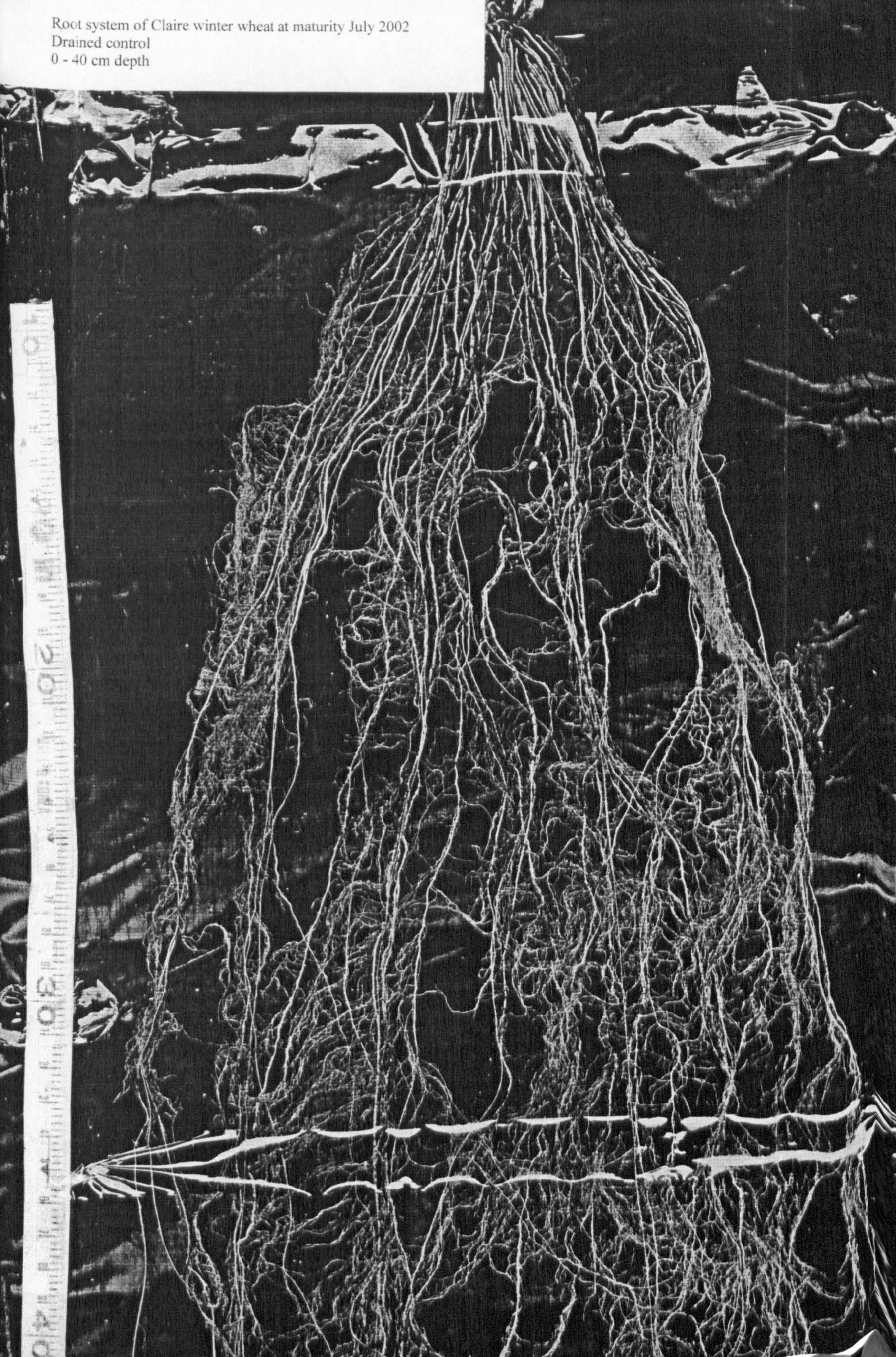
	Plants m^{-2}	Ears plant^{-1}	Shoots plant^{-1}	Straw Length (cm)	Straw DW (gm^{-2})	Straw Density mgcm^{-1}
Sowing Date						
Early	246	1.67	1.85	76.1	728	23.67
Middle	242	1.69	1.84	75.4	626	20.43
Late	233	1.86	2.09	69.4	559	18.61
Waterlogging Period						
Control (C)	248	1.86	2.07	73.9	664	19.73
Autumn (A)	234	1.78	2.04	74.7	651	21.05
Winter (W)	236	1.67	1.86	73.7	645	22.33
Spring (S)	242	1.64	1.76	72.2	590	20.49
Interaction						
Early C	248	1.81	1.98	77.5	731	21.66
Early A	234	1.75	1.96	75.8	743	24.10
Early W	241	1.90	1.75	74.7	741	26.02
Early S	259	1.52	1.72	76.2	696	22.88
Mid C	244	1.88	2.04	72.8	671	20.28
Mid A	240	1.67	1.91	79.0	638	20.19
Mid W	238	1.59	1.73	75.6	591	20.71
Mid S	247	1.62	1.69	74.2	607	20.52
Late C	253	1.90	2.17	71.3	591	17.26
Late A	230	1.92	2.23	69.3	573	18.87
Late W	230	1.83	2.09	70.8	602	20.24
Late S	221	1.77	1.87	66.1	468	18.07
P						
Sowing date	0.008	0.008	0.002	<0.001	<0.001	<0.001
Waterlogging	0.014	0.011	0.001	0.415	0.096	0.077
Interaction	0.010	0.802	0.904	0.184	0.559	0.786
SED						
Sowing date	3.9	0.062	0.072	1.30	26.6	0.857
Waterlogging	4.5	0.072	0.083	ns	ns	ns
Interaction	7.8	ns	ns	ns	ns	ns
LSD						
Sowing date	7.8	0.126	0.145	2.63	53.5	1.729
Waterlogging	9.0	0.146	0.168	ns	ns	ns
Interaction	15.6	ns	ns	ns	ns	ns



Root system of 65 day old Deben winter wheat
Grown in drained or waterlogged soil, 50 days after the start of the waterlogging period
The level of the water table is indicated by the dashed line

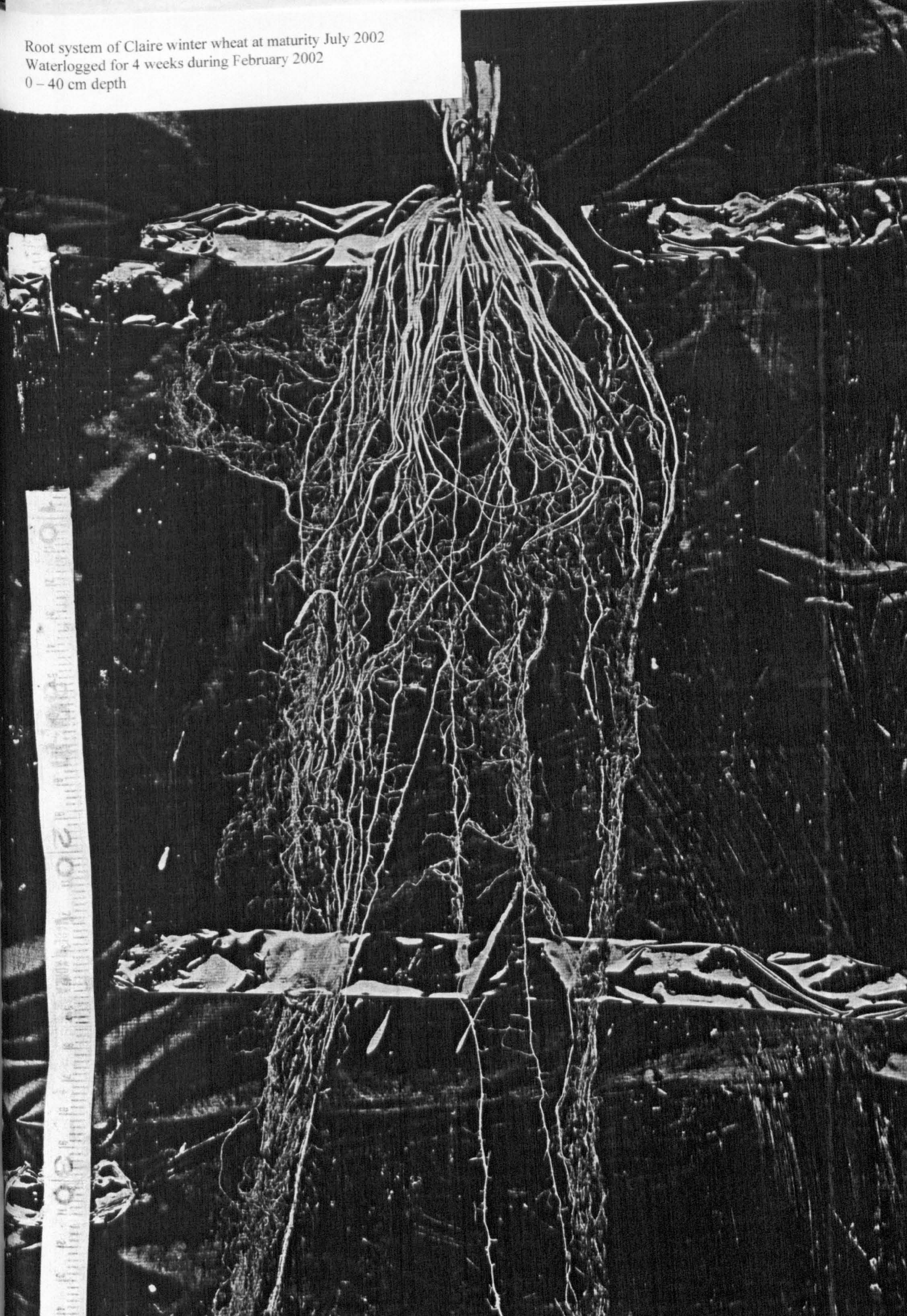


Root system of 65 day old Xi-19 winter wheat
Grown in drained or waterlogged soil, 50 days after the start of the waterlogging period
The level of the water table is indicated by the dashed line



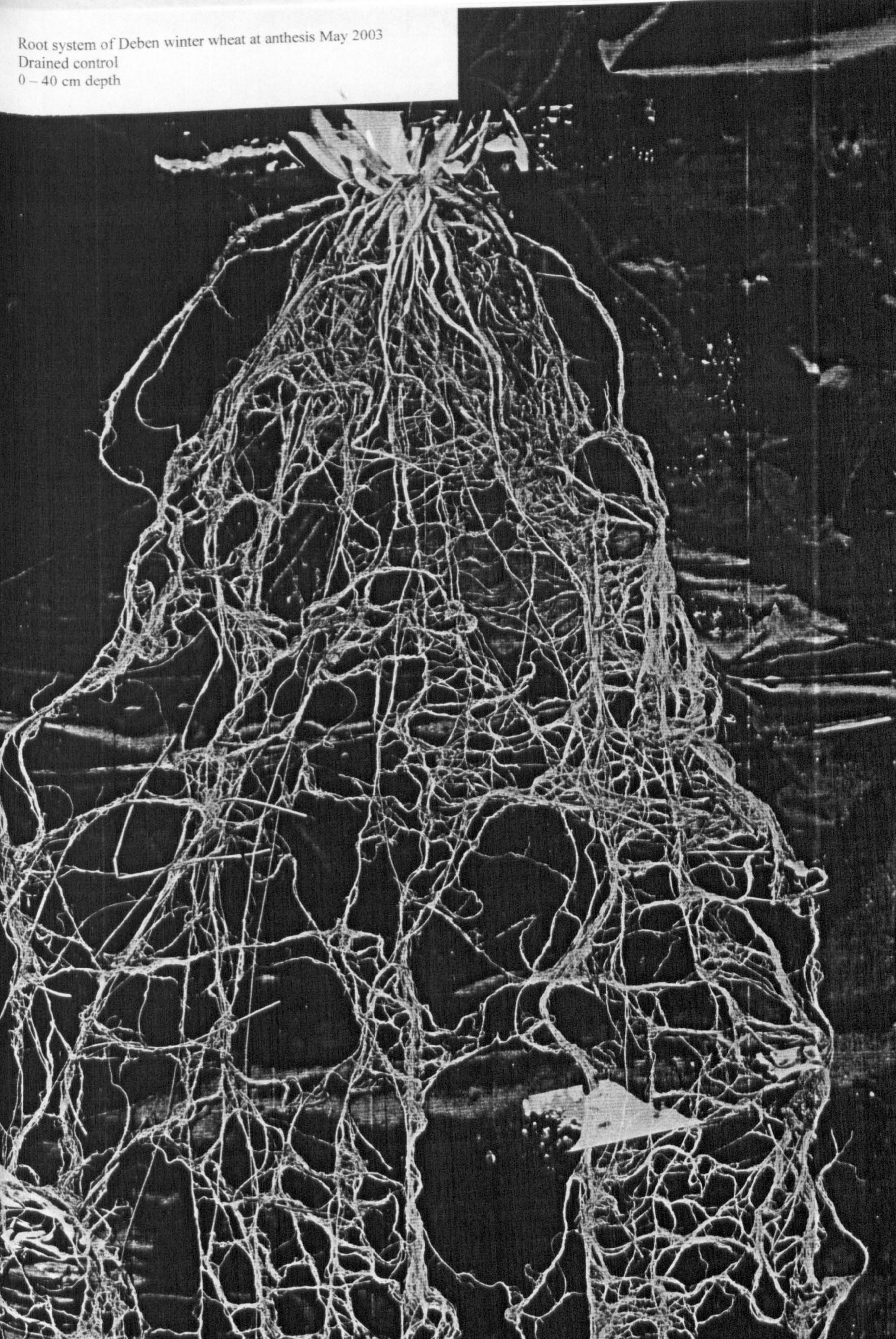
Root system of Claire winter wheat at maturity July 2002
Drained control
0 - 40 cm depth

Root system of Claire winter wheat at maturity July 2002
Drained control
40 - 80 cm depth



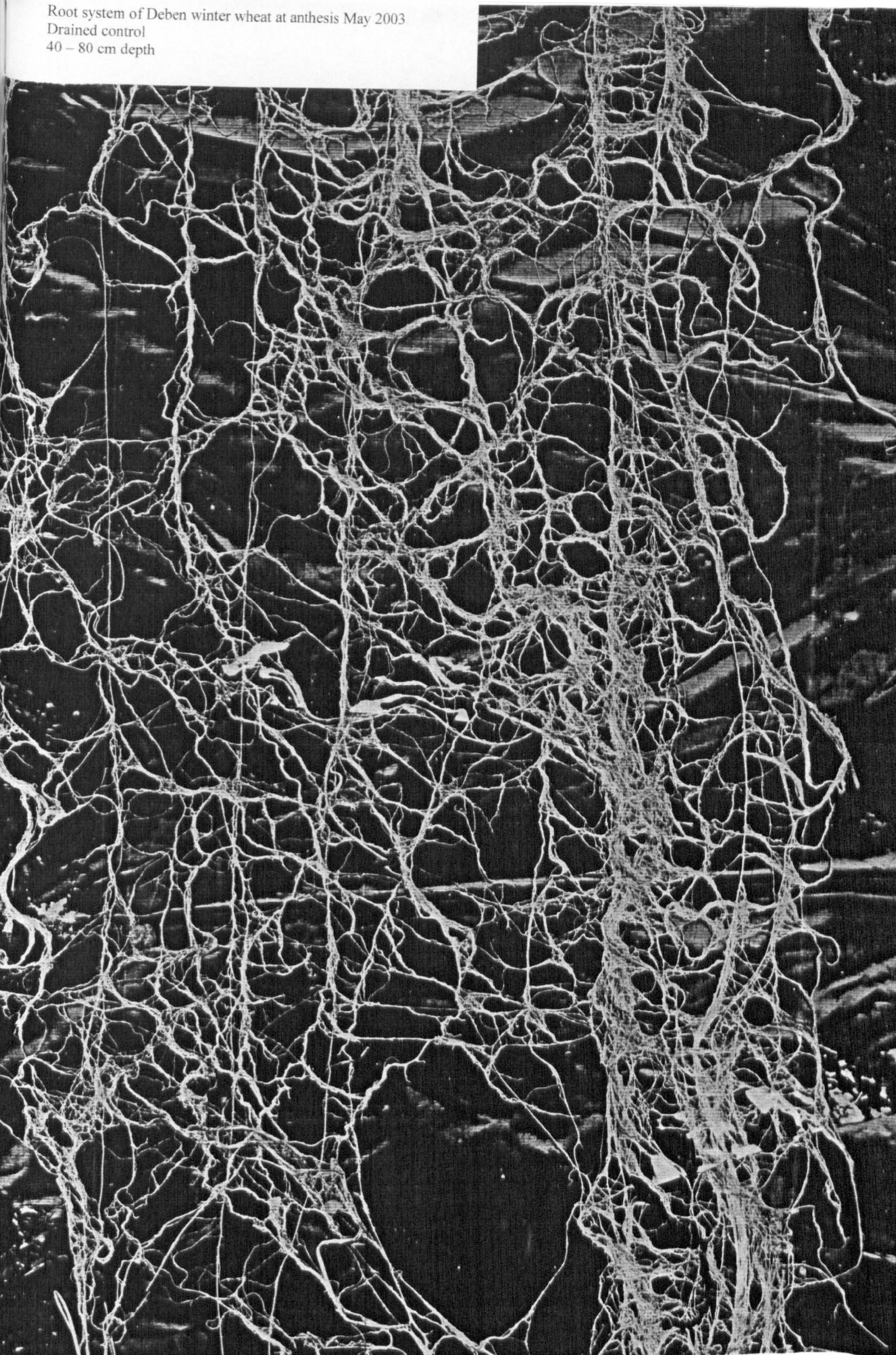
Root system of Claire winter wheat at maturity July 2002
Waterlogged for 4 weeks during February 2002
0 – 40 cm depth

Root system of Claire winter wheat at maturity July 2002
Waterlogged for 4 weeks during February 2002
40 – 80 cm depth

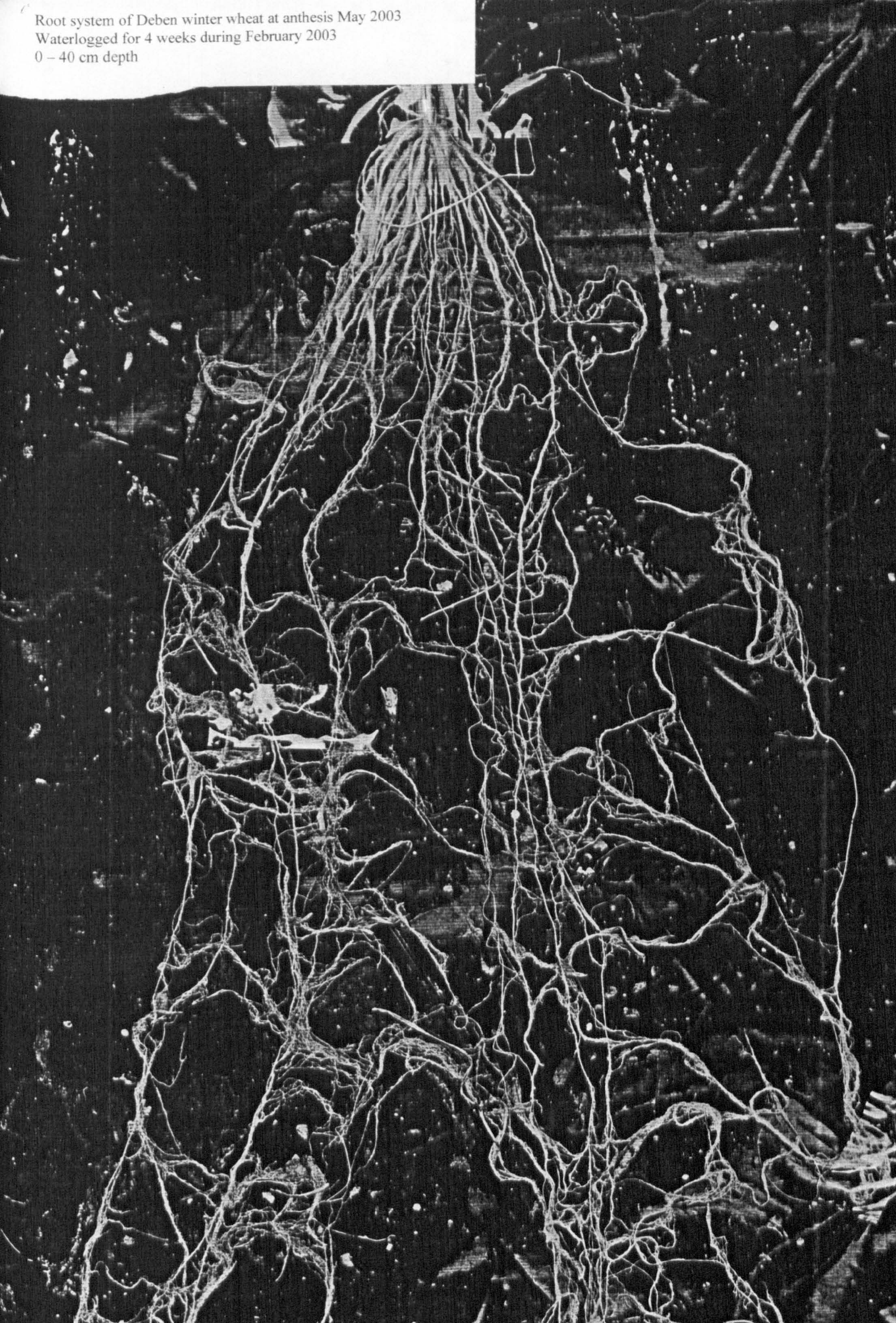


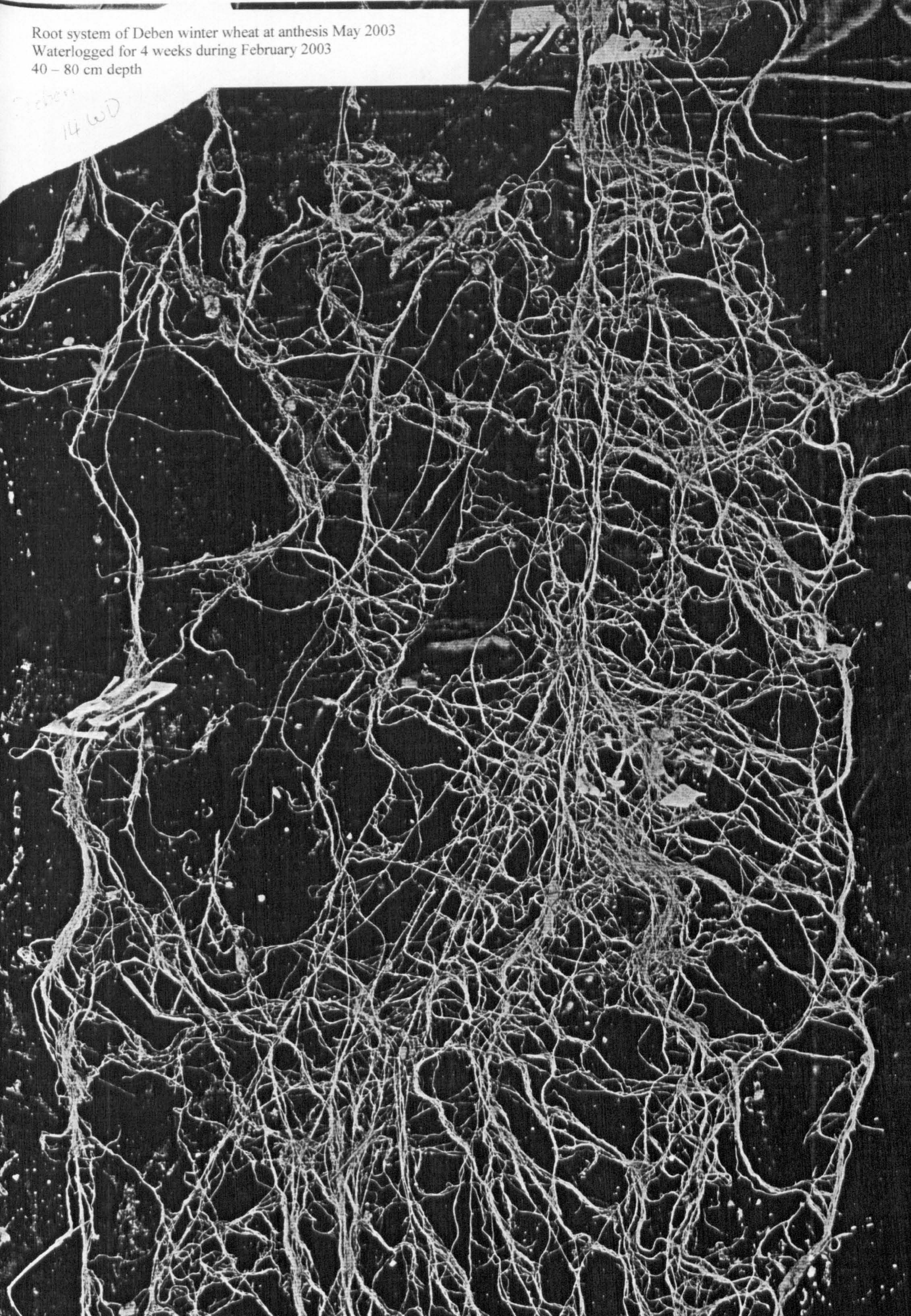
Root system of Deben winter wheat at anthesis May 2003
Drained control
0 – 40 cm depth

Root system of Deben winter wheat at anthesis May 2003
Drained control
40 – 80 cm depth



Root system of Deben winter wheat at anthesis May 2003
Waterlogged for 4 weeks during February 2003
0 – 40 cm depth





Root system of Deben winter wheat at anthesis May 2003
Waterlogged for 4 weeks during February 2003
40 – 80 cm depth

Deben
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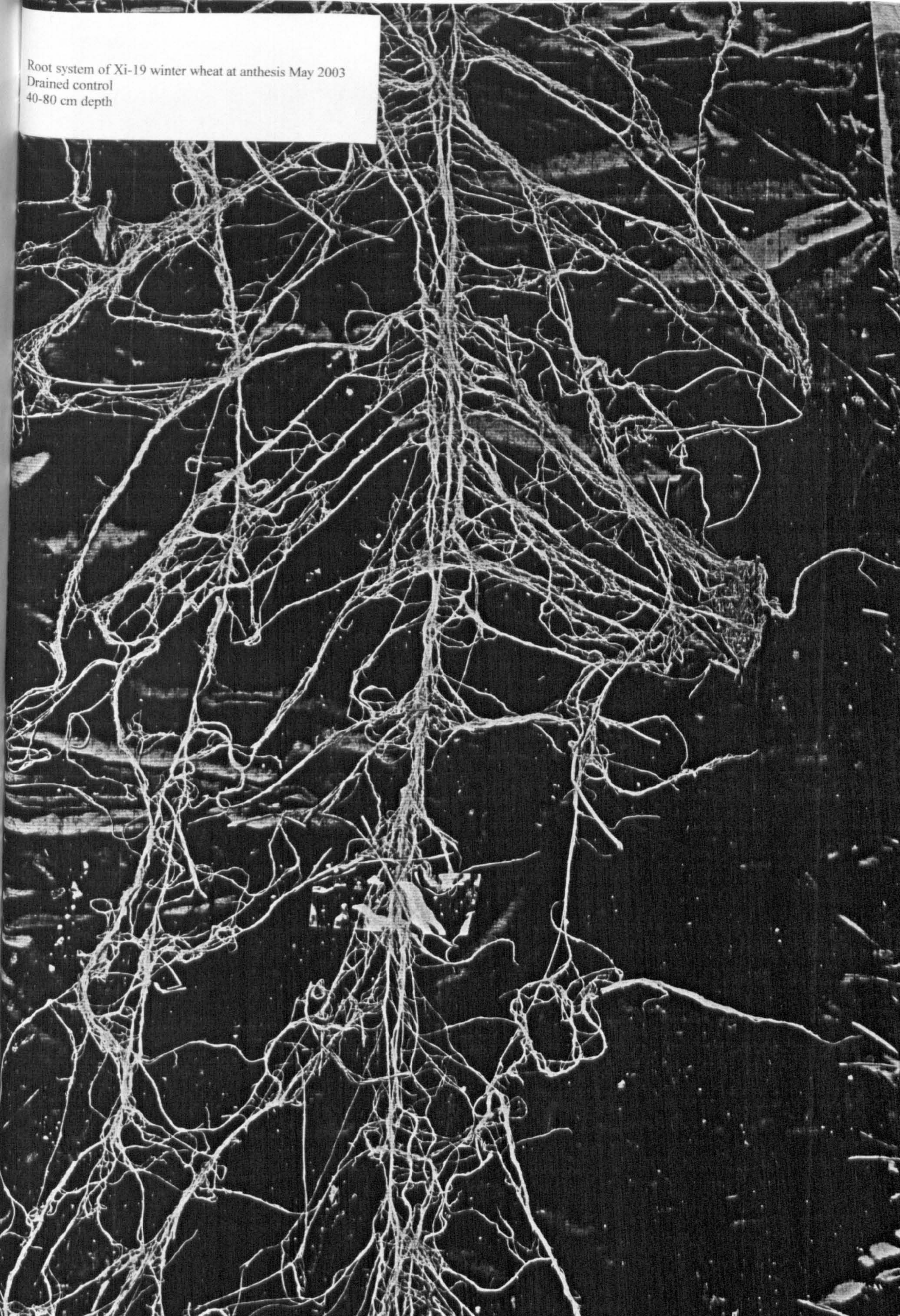
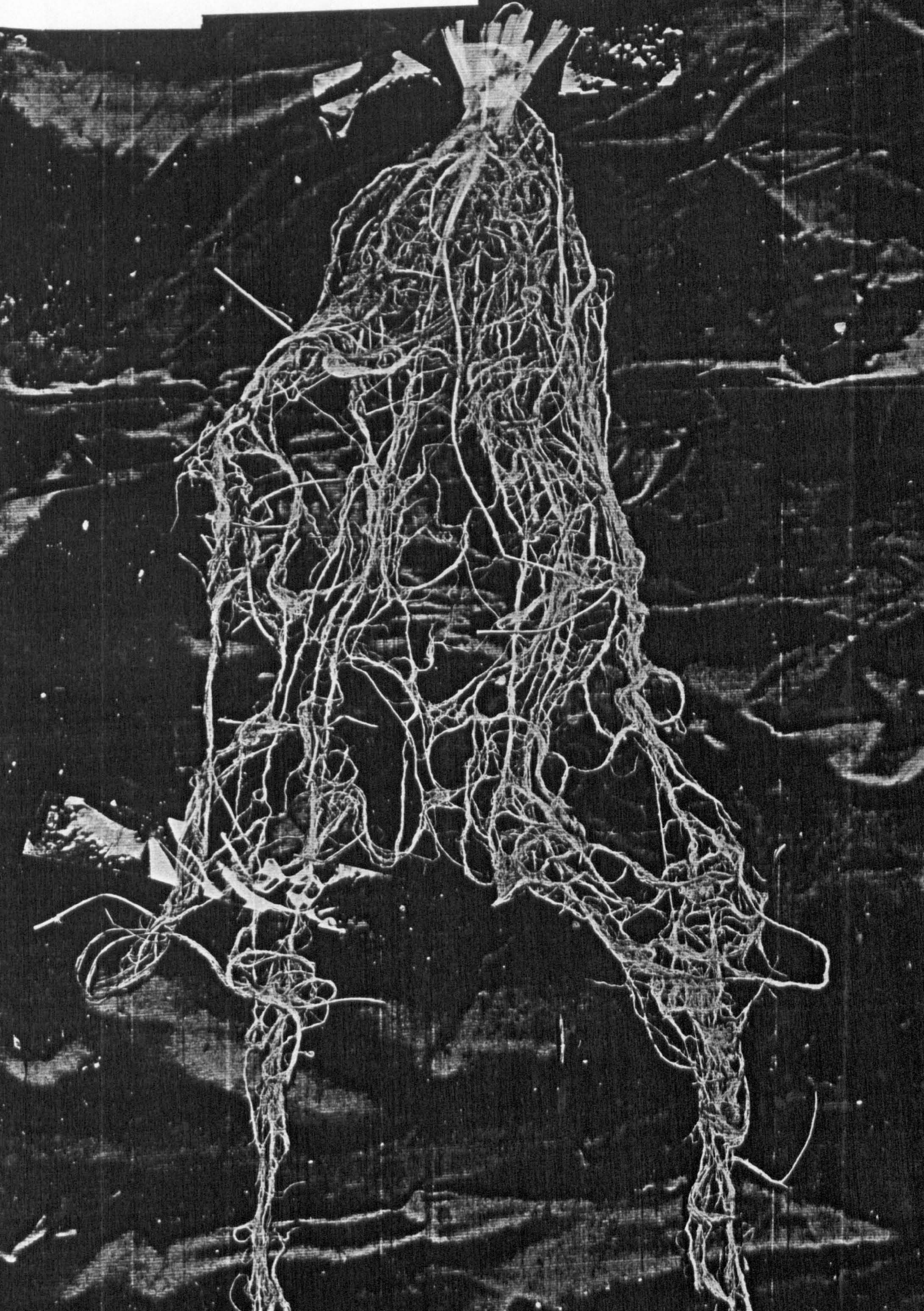
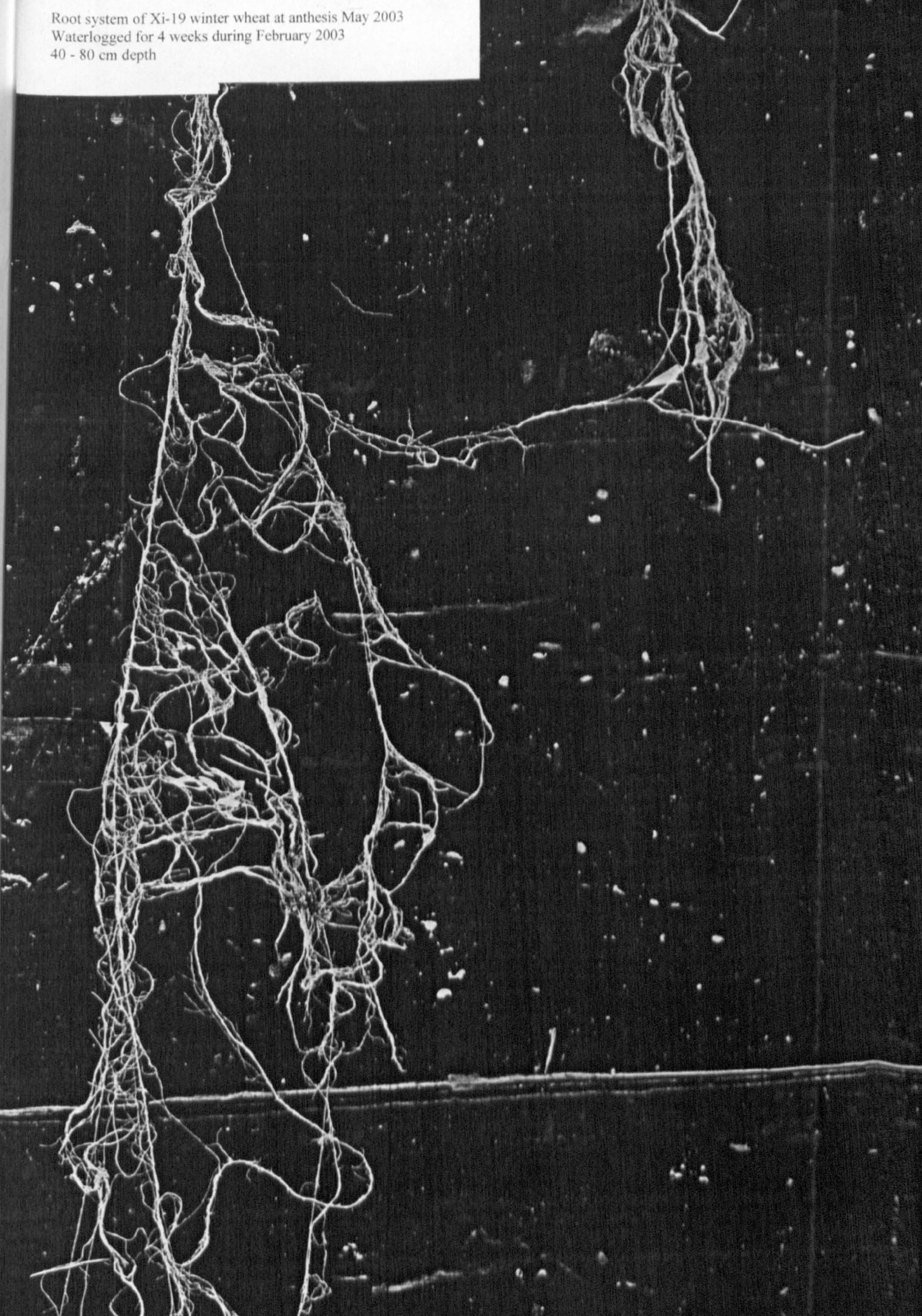
Root system of Xi-19 winter wheat at anthesis May 2003
Drained control
0 – 40 cm depth



Root system of Xi-19 winter wheat at anthesis May 2003
Drained control
40-80 cm depth

Root system of Xi-19 winter wheat at anthesis May 2003
Waterlogged for 4 weeks during February 2003
0 - 40 cm depth





Root system of Xi-19 winter wheat at anthesis May 2003
Waterlogged for 4 weeks during February 2003
40 - 80 cm depth