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Effects of water stress and salinity on contrasting wheat genotypes.

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EFFECTS OF WATER STRESS AND SALINITY ON CONTRASTING WHEAT GENOTYPES

A Thesis submitted to the University of Wales

By

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DEDICATION

This thesis is dedicated to my father's name, Mr Taybuddin Mallah, who died suddenly whilst I was in Bangor during by Ph.D. study period. He missed me a long time during my stay in Bangor. Also I miss him always. He was a very poor person, always himself eating his morning meal with whey (lassi) and raw sugar (mithai) and wearing only one dress, because he wanted his sons to get higher education, and save money to help them. I will always be in debt to him.

ABDUL NABI MALLAH

CONTENTS

بسم الله الرحمن الرحيم

شروع الله جي نالي سان جيڪو تمام ٻاجهارو ۽ رحم وارو آهي.

In The name of God, Most gracious Most Merciful

وَتَرَى الْأَرْضَ هَامِدَةً فَإِذَا أَنزَلْنَا عَلَيْهَا الْمَاءَ اهْتَزَّتْ وَرَبَتْ وَأَنبَتَتْ مِن كُلِّ زَوْجٍ بَهِيجٍ

تون ڏسين ٿو زمين سڪي پئي آهي پر جڏهن اسان ان تي مٿان برسات جو پاڻي وسايون ٿا ته اها ساوي ٿي ۽ باغ بهار ٿي پوي ٿي ۽ هر قسم جي ٻوٽن کي پيدا ڪري ٿي

You see The earth barren and lifeless, but when we pour down rain on it, it is stirred (to life) it swells, and its puts forth every of beautiful growth (in pairs).

مضمون: ڪڻڪ جي مختلف جنسن تي پاڻيءَ جي اسوڪهڙي ۽ ٻوٽن جا اثر

تت پانيوڙ

پاڻيءَ جي اسوڪهڙي ۽ ٻوٽن جي اثر تحت ڪڻڪ جي پيداوار جو اندازو لڳائڻ لاءِ ايوب ريسرچ ڪاليج انڊ ويلس لوڊيڪي جي زرعي شعبي ۾ چار تجربن جي ڪيا تا حصن ۾ ڪيا. مهڙ ١٩٨٦ تان سپٽمبر ١٩٨٩ تائين ڪيا ويا. ٻه تجربا پاڻيءَ جي اسوڪهڙي ڏيڻ وارا ۽ ٻه تجربا ٻوٽن جي اثر ڏسڻ لاءِ ڪيا ويا.

مقصد اهو هو ته پاڻيءَ جي نه ڏيڻ جو اثر (اسوڪهڙي) ۽ ٻوٽن جو اثر ڪڻڪ جي مختلف مرحلن ۾ مختلف جنس. آبپاشي (نارمن) ڇوهاري عرصي (فيمنين) ۽ پاڇائي جنس (فيمبلي) جي مختلف ٢ ڀڃائين ۾ ٢ زماني پاڻيءَ جي اسوڪهڙي جو تجربو ڏکيو پيدا ڪرڻ جي ڪوشش ۾ مختلف ڏينهن ۾ ڪيو ويو. ٻوٽن جي اثر جو تجربو ڪرڻ طاقتور ڪيمر (ٻوٽي) کي صرف پاڻيءَ ۾ طاقتور ساڳيا ڏنا ويندا آهن جهڙوڪ فاسفيٽ ٻيهن) ۾ ٢ زمانو ڪيو ويو. ٻنهي تجربن ۾ ڪڻڪ جي ٽن اهم مختلف

مرحلن ۾ (فونهڙي کان ڦٽڻ ۽ گني تائين) (ڦٽڻ کان بعد کان ڏري تائين)
۽ (ڏيڻ کان پچڻ وقت تائين) سوڪهڙو ڏئي ويو هو ۽ ان وارين ٻوٽن
۾ لوڻ ڏنا ويا.

ھرھڪ جنس ۾ اهي مختلف مرحلا ۲ ڀيرا ڏنا ويا ۽ هر
هڪ جنس جي ڪنٽرول وارن ٻوٽن سان (ڪنٽرول جي ٻوٽن کي
ٻوٽي پوکڻ کان پوءِ هر وقت ڏنو پئي ويو ۽ پاڻي ڏنو ويو. ان مرکوز سوڪهڙو
يا لوڻ نه ڏنو) پيٽ ڪئي وئي. اهن مختلف مرحلن ۾ آزمائش
لاءِ ٻوٽي جون وڌندڙ ماپون ورتيون ويون جهڙوڪ پن جي ڊيگهه،
ڏانڊي جي ڊيگهه، فونهڙي ۾ تيلن جو تعداد، ٻوٽي جي ڊيگهه، نائٽروجن
جو تناسب، نائٽروجن جو ٻوٽي ۾ داخل ٿيڻ ۽ ٻوٽي جي اسڪل هر هڪ
مرحلي ۾ معلوم ڪئي وئي. هر هڪ مرحلي ۾ سوڪهڙو ۽ لوڻ
ڏيڻ سان معلوم ڪيو ويو ته ڪيترو وڌندڙ ماپون گهٽيون آهن ۽
ڪهڙي مرحلي ۾ لاباري جي دوران اهو ڏنو ويو ته ڪيتري پيداوار ۾ پيداوار
جا حصا گهٽجن ٿا. اهڙي نموني ڏنو ويو ته آچاري جنس (نارمن) ٻين
کان فونهڙي تائين وڌڻ ۾ گهٽ عرصو وٺي ٿي بنسبت ٻين جنسن
وچواري ۽ پاڇاري جي کان. آچاري جنس وڌيڪ ڏيئي ٿي ٻوٽي جي ڊيگهه
سڪل ٻوٽي جي لوڻ گهٽائڻ ۾ پيداوار بنسبت پاڇاري جنس جي. آچاري
جنس گهٽ پيداوار ڏيئي ٿي وچواري ۽ پاڇاري جنس جي پيٽ ۾،
جيڪا ان جهڙي ڏڪندا رهڻ، گڏندا لوڻا رهڻ ۾ گهٽ داڻا رهڻ ۾ ۽
گهٽ داڻن جو وزن سنگ جي لوهه ۾ آهن.

ٻنهي تجربن ۾ سارين جنسن

پهرين ڦٽڻ کان ٻڌي دوران ۽ پچڻ کان پوءِ واري مرحلي گهڻي گرمي
هوا جي ڪري ڏکيا ڏينهن حاصل ڪيا. ٻنهي تجربن ۾ سارين جنسن جي
وچهر، سارين مرحلن جي ڏيکهڙي لاءِ تمام فرق رهيو. سوڪهڙي ڏيڻ واري
ٻنهي تجربن جي مٽيءَ ۾ ڪاٺ جو گهڻيل پورو ملايو ويو. اها ڪاٺ جي ٻوري
واري ملايل مٽي عام زمين جي مٽيءَ کان پهرين سوڪهڙي ڏيڻ واري
تجربي جي پيٽ ۾ جلدي سڪي لڳي ۽ سوڪهڙي جي دوران مٽيءَ
جي هيٺين حصي جي پيٽ ۾ مٽيءَ جو مٿيون حصو جلدي ۾ سڪي ويندو ويو
پيئي رهي. پاڻي نه ڏيڻ جي ڪري پهرين ڦٽڻ کان ٻڌي واري
مرحلي ۽ پچڻ کان پوءِ واري مرحلي جي مٽي جلدي سڪي پيئي رهي.
ٻنهي سالن ۾ پاڻي ڏيڻ سيڪڙو ڏسڻ لاءِ جپسم بلاڪ استعمال ڪيا
ويا. سارين جنس ۾ ٻڌي کان پوءِ دوران سوڪهڙي جي ڪري
ڏيڻ هڪڙي مان پنج مٽي بلڪل سڪي ويئي، ان جو سبب پوءِ جي
ڏکيو هجڻ، گهڻي گرمي جو درجو، لئي ۽ زمين مان پاڻي جو گهڻو
خارج ٿيڻ. ان سبب ڪري ٻڌي کان پوءِ تائين ٿوري وقت لڳو. ٻنهي
تجربن ۾ پاڻي نه ڏيڻ جي سوڪهڙي ڏيڻ ڪري سارين جنس ۾ سارين مرحلن جي
لئي جي وڌ ۽ پيداوار ۽ پيداوار جا حصا گهٽ ٿيا. جهڙي نار من لئي
ڦوٽهڙي کان پهرين ڏڳنيءَ تائين سوڪهڙي جو گهڻو عرصو رهيو.
چاڪاڻ جو تمام گهڻي سرد ٿي ڪري ٻهسٽي وڌي پئي ان سبب
ڪري پهرين گٻيءَ ٻيڙ سان ٿي ٿي. بهرحال سارين جنس ۾ ڦوٽهڙي کان
پهرين ڦٽڻ واري مرحلي ۾ هڪ جهڙو نقصان ٿيو. ٻنهي تجربن ۾
پاڻي نه ڏيڻ ڪري سارين جنس ۾ پهرين ڦٽڻ کان ٻڌي واري مرحلي

تاڻي تمام گهٽ وڌندڙ مايون ملنديون. ڇاڪاڻ ته هن مرحلي تي لوڻي
جي پکيڙ تمام وڌي ويندي. گرمي جي درجي جو گهٽجڻ هليو ان ڪري پاڻي
مٽي ۾ مان جلدي سڪي ويو. پر هن مرحلي تي اسو ڪهڙي جو عرصو
لڳ ڀڳ ٽي هفتا رهيو. بهرحال ڏيڍ سان پيڻ واري مرحلي کي اسو ڪهڙو
ڏينهن ڪري پيداوار ۽ پيداوار جا حصا تمام گهٽ ٿيا، ان جو سبب
ڏاڍي جي ٽنڊي ڊسائيز، لڳ ڀڳ پڌري نظرها، وسنگ جي ٽنڊي ڊسائيز
پڻ جو پکڙجڻ سڪي وڃڻ گهٽ گرمي جو درجو، لڳ ڀڳ عرصي ۾
ڏيڍ، ڏاڍي جي پڌري لاءِ گھربل ڪاربوهيڊريٽ ذخيري مان لڳ ڀڳ
اڳ ۾ لوڻ جي وقت جو ڳپ جو مسئلو هيو.

لوڻي جا تجربا ۽ لوڻي جو اثر

پلنڊي لوڻي جي ذريعي ٻوٽين ۾ ڌنڌي ۾ نسيدي جنس تمام وڌي پئي جي
پکيڙ، گهٽ فوٽوسنٿيسز هيو ۽ نسيدي جنس جا ٻوٽا ٻوٽين ۽ گهڻي سان
لوڻ مضبوط هيا. ٻنهي اسو ڪهڙي وارن تجربن جي. ڇاڪاڻ ته جو ٽوٽي
تجربن ۾ گهربل طاقتور ڪاڌو پاڻي ۾ ملايو ويو هيو. ناڙ من
جنس تمام گهڻي مضبوط هئي، ڇاڪاڻ ته جو ڏکيو عرصو گهربل طاقتور
سيني جنس ۾ فوٽوسنٿيسز سان ٻوٽين ۽ گهڻي واري مرحلي ۾ لوڻي گهڻو
اثر ڪيو. لوڻي جي اثر ڪري ارڙهين مرحلي ۾ لوڻي جي واڌ پڻ
جي پکيڙ، ذخيري جي پکيڙ، لوڻي جي ڏيگهه ۽ في لوڻي جي مسئلن
تمام گهٽ ٿي. ٻين حصن جي گهٽ وڌ ڪري، ڏاڻي جي
تعداد، ڏاڻي جو وزن في لوڻي ۾، في وسنگ ۾ پيداوار لوڻي ۾

تمام گهٽ ڏٺو. پهرين ڏينهن کان ڏهين ڏينهن واري مرحلي ۾ ڏهين ڏينهن کان
ويهن واري مرحلي جي ڀيٽ ۾ اثر ڪيو پر گهٽ پسيت ڦوٽهڙي
کان پهرين ڏينهن واري مرحلي جي، انهن ٻنهي مرحلن ۾ ٻوٽي
جي واڌ گهٽ ڏني، انهن ٻنهي مرحلن دوران ٻج لڳڻ ۽ لاباري
جا ٻيا مرحلا پڻ گهٽ ڏٺا ويا.

ٽئين ۾ سڀني جنسن ۾ ڏهين ڏينهن کان

ويهن ڏينهن واري مرحلي کي ٻين مرحلن ۾ ڪنٽرول جي ٻوٽن کان گهڻو
ڪن اڳ ۾ لاباري ڪئي ويئي. ان جو سبب گرمي جو گهڻو ڏرڪو
هليو. ڦوٽهڙي کان پهرين ڏينهن واري مرحلي ۾ نارمن تمام ناڪ
هئي. جيڪا ان جو گهڻو عرصو لاڳاپيل آهي ته تمام رهي.

پهرين ڏينهن کان ڏهين ڏينهن جي مرحلي ۾ ڏهين ڏينهن کان ويهن واري
مرحلي دوران نارمن تمام مضبوط رهي. ٽيهين جنس ڏهين
ڏينهن ويهن واري لاڳاپيل پيداوار جا لاڳاپا گهٽ ڏٺا،
نسبت ٻين جنس جي ساڳئي مرحلي ۾.

SUMMARY

A series of experiments was carried out in the Department of Agriculture, University College of North Wales, Bangor, during October 1987 to September 1989. The purpose of these was to study the effects of water stress and salinity stress at different stages on long (Norman), medium (Fenman) and short duration (Wembley) wheat varieties in different environments. Effects of water stress were tested in large pots in different types of soil. Effects of salinity were tested by growing plants in solution culture. In both experiments water stress and salinity stress were imposed at three major stages, tillering to stem extension (TL-SE), stem extension to booting (SE-BG) and booting to maturity (BG-MT). These were tested in each variety in comparison with a control of each variety. Growth measurements, leaf number and area, stem area, shoot number, plant height, nitrogen %, nitrogen uptake, dry weight per plant were determined at the end of each stage. Soluble carbohydrates were determined at anthesis. This was done to find out how much these growth measurements were decreased during each stress period. Yield and yield components were determined at harvest.

In these experiments the long duration variety took a long time in growth during TL-SE, in comparison to mid winter and spring wheat varieties. The long duration variety gave a higher plant, more straw dry weight production and more leaf number than the short duration variety. The long duration variety also gave a higher yield than the medium and short duration varieties, due to larger ears, more spikelets

per ear, more grain number per ear and more grain number per spikelet. All varieties experienced higher temperatures and longer days during SE-BG and BG-MT in both experiments. The lengths of these stages therefore showed smaller variation between varieties.

In water stress experiments the mixed peat-soil used in Experiment 2 dried out quicker than the normal field soil used in Experiment 1. The upper portion of the soil was dried before the lower portion of the soil during the stress period. With water stress at SE-BG and BG-MT the soil dried out quicker in both years. Gypsum blocks were used to give readings of water stress. With water stress at BG-MT the soil was completely dried out after the third week, in all varieties, due to higher plant height, higher temperature and more evaporation. Because of this water stress at BG-MT resulted in a short duration for ripening. In both water stress Experiments 1 and 2, in all varieties all water stress treatments decreased the growth measurements, decreased yield and yield components. In Norman water stress at TL-SE had a long stress period due to slow growth processes during cold winter. However, this stage had a similar effect on yield in Norman, Fenman and Wembley. In both water stress experiments in all varieties, water stress at SE-BG caused the largest reductions in growth measurements, because at this stage the plant had the greatest leaf area and temperature was higher, although the period of stress was only a few weeks. However, water stress at BG-MT caused the greatest decreases in yield. This stage showed the greatest

decreases in yield and yield components, due to small grain size, fewer fertile spikelets, small size of ear, earlier leaf senescence, short duration for ripening, higher temperature, lack of soluble carbohydrate for grain filling from stem and pollination problems at anthesis time.

In both salinity Experiments 1 and 2, all varieties had a larger green leaf area, more tillers and all varieties were much stronger after stem extension than in the water stress experiments due to the solution culture technique. Norman was more strong than the other varieties because of its long period grown in solution culture. Salinity at TL-SE was more damaging than other stages in all varieties. Salinity at TL-SE decreased the growth measurements, such as leaf area, stem area, plant height, dry weight per plant. Because of the growth measurement reduction, grain weight per plant, grain number per plant, grain number per ear, grain number per fertile spikelet and fertile spikelet per ear were decreased by salinity at this stage. Salinity at SE-BG and BG-MT also decreased growth measurements, decreased grain yield and yield components. Salinity at BG-MT decreased grain yield and yield components more than salinity at SE-BG. In Experiment 2 in all varieties with salinity at BG-MT plants were harvested a few days before other stages and the control. Norman was more sensitive with salinity at TL-SE than the other varieties because of its long period grown under salt stress. Norman was much stronger with salinity at SE-BG. Norman gave lower yield, yield components at BG-MT than other varieties at this stage.

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LIST OF TABLES

CHAPTER 4 SALINITY EXPERIMENTS

PAGE

NUMBERING

AS ORIGINAL

LIST OF FIGURES

CHAPTER 4: SALINITY EXPERIMENTS

ABBREVIATIONS

TL-SE	=	Tillering to stem extension
SE-BG	=	Stem extension to booting
BG-MT	=	Booting to maturity
g	=	Gram
mg	=	Milligram
/	=	Per
%	=	Percentage
NaCl	=	Sodium chloride
cm	=	Centimetre
NS	=	Not significant
^{o}C	=	Degree centigrate
m^2	=	Metre squared
>	=	Greater than
<	=	Less than
mm	=	mili metre
ha	=	hectare

CHAPTER 1

GENERAL INTRODUCTION

1.1 GENERAL INTRODUCTION

Drought and salinity are two major environmental factors limiting agricultural crop production in many parts of the world.

These two environmental factors are affecting arid and semi-arid zones, where there is a natural shortage of rainfall. Wheat, the plant studied in this thesis and other cereals such as rice, maize, sorghum and millets, are particularly grown in these arid and semi-arid regions. Wheat is grown more than other cereals on a large scale for consumption by human beings and animals in all parts of the world.

In 1987, 220689 thousand hectares of land were used for wheat production and 516780 thousand metric tonnes of grain were harvested (F.A.O. statistics). About one third of the earth's land surface (47 million square km) is classed as arid or semi-arid. More than 20% of the earth's surface is directly threatened by shortage of water and inadequate rainfall. It is estimated that eighty million people or one-tenth of the total world population is counting for survival or endurance on these areas (Shakoor, 1983; Grainger, 1986).

Drought and salinity are related to each other. Drought occurs in areas of low rainfall, or where there is a shortage of irrigation water. Salinity is most pronounced in arid and semi-arid regions because of insufficient annual rainfall to flush accumulated salts from the crop root zone. Some parts of the world where there is no shortage of irrigation water are also affected by salinity. In such areas, e.g. Iraq, Iran, Pakistan, India, U.S.A., etc, the salt problem arises

from the combination of high evaporative demand and shallow depth to ground water. Considerable amounts of salts are moved to the soil surface and accumulation occurs during evaporation. The term saline soil is normally used in plant physiology to indicate a soil with an electrolyte concentration which is inhibitory to the growth of crop plants. A large area is affected by soil salinity in Pakistan. About 10 million hectares from the 15 million hectares of canal irrigated land is affected by salinity and sodicity. Quite a large part of the salt affected area (40,000 hectares) belongs to the only irrigated land which is most used for agricultural production (Muhammed, 1978, 1983). According to Qayum and Malik (1985) wheat yield was 2.28 tonne/h on normal soil, but it was decreased under saline soils respectively to 1.43 tonne/h and 0.72 tonne/h, from slightly and moderately salt affected soils respectively.

One way to solve these problems is to choose much more water stress and salt tolerant varieties.

There is also a need to study how different agronomical characteristics, such as average grain weight per plant, grain number per plant, plant height, leaf number, dry matter production are affected by stress.

Water stress and salinity decrease crop production particularly when they occur at sensitive stages. Many workers have determined that water stress has its greatest effects, if it occurs during grain filling. Wheat is most sensitive to salinity, during germination and during tiller appeance (Ayers, Brown and Wadleigh, 1952; Slayter, 1969, 1973; Morgan and Riggs, 1981).

The purpose of this study was to determine the relative effects of drought and salinity at different stages on contrasting wheat varieties. The drought and salinity stress were imposed at specific growth stages with a view to them having effects on specific growth and development processes. The experiments tested winter and spring wheat varieties which were sown at their normal time. The different varieties attained various growth stages at different times and as a consequence the weather conditions during the stress periods were not the same for each variety. Although this complicated the interpertation of results, the main purpose of the experiments was to determine the effects of these stresses on the varieties when grown under their normal conditions

The varieties chosen were: Norman, a winter wheat with a high vernalisation requiement which normally experiences cool moist growing coditions for more than half of its life cycle; Fenman a winter wheat with a low vernalisation requirement and which is suitable for sowing in early spring; Wembley a spring wheat, which normally experiences higher temperatures, long days during most of its growing period.

CHAPTER 2

REVIEW OF LITERATURE

2.1 INTRODUCTION

The topics of drought and salinity and plant and crop reactions to water stress and salinity have been the subject of many investigations by scientists. As well as numerous individual research papers, there are books and comprehensive literature reviews on these subjects. Therefore it is impossible in one thesis to review all this work.

In this literature review only that work which is relevant to this project will be summarised.

2.2 DROUGHT STRESS AND WATER STRESS COMPARED

2.2.1 Drought stress: The terms drought stress and water stress are defined in different ways. The word drought belongs to meteorological terminology. It is a result of weather of hot dry wind, high temperature and low atmospheric humidity. It is mostly defined as a period with no significant rainfall. It is not a uniform phenomenon. Drought is a seasonal phenomenon and the time at which it occurs depends upon the seasonal distribution of evaporation and rainfall. Plants reaction to drought depends on the stage of development at which drought occurs, the water storage capacity of the soil in the root zone and atmospheric conditions affecting the rates of evaporation and transpiration. Drought may be essentially permanent, as in desert areas; seasonal, in areas with well defined wet and dry seasons; or random as in humid areas. Some plant processes are relatively insensitive to drought stress, others are distinctly affected (May and Milthorpe, 1962a; Turner, 1979).

2.2.2 Water stress: Water stress is a condition experi-

enced by plants when cells lose turgidity and have not enough water to carry out normal metabolic activity. It occurs when available soil moisture is reduced to the point where the plant cannot absorb it rapidly enough to compensate for transpiration losses. It is clear that water stress is increased by weather drought. If the plant is subjected to an artificially induced evaporative loss of water this is called desiccation stress. A stress that is capable of inducing a loss of water in the liquid phase is called an osmotic stress, e.g. soil salinity.

2.3 CAUSES AND DEVELOPMENT OF WATER STRESS

There are many factors which cause water stress by different ways and at different times. These depend on the plant, crop structure, size of plant, soil structure, type of soil and climatic conditions. These factors all interact to control the rate of water absorption and water losses (Kramer, 1959, 1963; Vaadia et al., 1961). Solar radiation is the source of energy, supplying the latent heat requirement for the vaporization of water. Secondary sources of energy include scattered and reflected radiation from the sky and clouds which is known as sensible heat and which is transferred from the adjacent air, crops and soil (Slatyer, 1967). Water moves through the soil plant atmospheric pathway along a gradient of decreasing water potential (Gradman, 1928; Vanden Honert, 1948; Weatherley, 1965; Slatyer, 1967; Kramer, 1969; Van Haveren and Brown, 1972; Gardner et al., 1975). Water is lost from the leaf as the stomata open to allow the uptake of carbon dioxide from the

atmosphere for photosynthesis. The water loss by transpiration from the leaf mesophyll cells is replaced by water drawn from the soil through the root, stem and leaf via the xylem (Passioura, 1980; Weatherley, 1982; Turner and Burch, 1983). An internal water deficit can develop either due to excessive loss of water or by slow absorption of water or by a combination of both. Periods of excessive transpiration are usually shorter and less severe than periods of inadequate absorption due to low soil water availability. However, periods of hot, dry windy weather can cause severe damage, even to plants in moist soil, by causing excessive transpiration. A decrease in photosynthesis occurs in plants of many species at mid day on sunny days. This decrease is usually attributed to closure of stomata (Polster, 1950; Nutman, 1973). It does not occur on cloudy days. Stocker et al. (1954) regard midday sprinkling of crops in hot weather as very beneficial by keeping leaves turgid and stomata open, preventing this midday decrease in photosynthesis. Conversely, during foggy, showery, or humid weather even plants in dry soil may be subjected to relatively small water deficits. Thus the effect of soil moisture supply may be greatly modified by atmospheric conditions that affect the rate of transpiration (Hagan, 1955; Latey and Peter, 1975). During the morning plants transpire at normal rates, but transpiration becomes rapid in hot and sunny weather around midday. Under these circumstances plants can be water stressed even though there is plenty of moisture available in the soil. According to Turner and Begg (1981), water absorption sometimes exceeds transpiration in the afternoon and at night because an internal water deficit still

exists. Hence plants can often recover from water stress at night-time provided that the soil moisture content is high enough. In different crops at different stages of growth, the rates of water transpiration and absorption are different in different climates (Salter and Goode, 1967). For example, in wheat crops the rate of transpiration is greater at anthesis than at the tillering and stem extension stages. This is because at anthesis plants have got more leaves, ears, a large stem and also a larger rooting system. A study of how internal water deficits develop requires a more detailed examination of the diurnal and day to day changes which occur in transpiration, absorption and soil and plant water potential. The level of plant water stress and hence of internal water deficits is influenced by two main factors: (i) the level of soil water potential and (ii) the diurnal lag of absorption behind transpiration. In turn each of these factors is influenced by other factors, both environmental and physiological (Slatyer, 1969).

2.4 CLASSIFICATION OF ADAPTATIONS TO WATER STRESS

Different types of plant can be classified according to their adaptation to water stress. Plants which are adapted to grow in dry places cannot survive for long in wet habitats and vice versa. Ecologists classify plants according to the environmental water supply required for the normal completion of their life cycle (Levitt, 1972; Seddon, 1974). They have distinguished three major classes; hydrophytes, mesophytes and xerophytes. Each group is characterized by a combination of structural adaptations to their environment.

2.4.1 Hydrophytes: Hydrophytes grow where water is always available. The plants grow either immersed in water or completely submerged in free water such as in ponds or marshes. Hydrophytes include marine algae and sea weeds, and plants found in fresh water such as aquatics ranging from free floating ferns, e.g. Azolla filiculoides, duck weed (Lemma minor) to water lilies (Nymphaea alba and Nuphar lutea).

2.4.2 Mesophytes: These types of plant normally grow where water availability is intermediate. These plants have a need for well drained soil because their leaves are exposed to moderately dry air. Most crop species, quite a big proportion of forestry trees, and those crop plants who belong to the temperate and tropical regions come into this category.

2.4.3 Xerophytes: Xerophyte plants usually grow in areas affected by natural climatic drought, mainly in deserts or rocky places. Some xerophyte species normally found in deserts and rocky areas can also survive in areas where mesophytes grow (Hickel, 1967). Chamaegigas intrepidus normally grows as a mesophyte in shallow water pans in South Africa. However, during the dry season it exists in the air dried condition (Walter, 1950).

No traditional crop plants are classed as xerophytes. However, some xerophytes can be useful for providing grazing in desert areas.

2.5 DROUGHT RESISTANCE

Levitt (1972) divided drought resistance into drought avoidance and drought tolerance. A drought resistant plant can survive periods of environmental water stress.

Basically, plants are drought resistant either because their protoplasm is able to endure dehydration without permanent injury or because they possess structural or physiological characteristics which result in avoidance or postponement of a lethal level of desiccation.

A drought resistant crop variety or species can grow and complete its development in areas subject to periodic water deficits. For example some wheat varieties can produce a good yield by completing their development processes before drought starts (Chinoy, 1960).

2.5.1 Identification of drought resistance for breeding purposes.

In a drought resistance breeding programme the breeder must decide on the stage at which water stress will be imposed and the severity of water stress. Lewis and Christiansen (1981) suggest that stress environments be selected at a level that differentiates between stress susceptible and stress resistant genotypes.

Quizenberry (1981) suggested that characters such as earliness of maturity, extensive root growth, stomatal control, cuticular resistance (Tazaki, 1960), stomatal number, cell turgor and proline accumulation have been associated with drought resistance (Boyer, 1982; Williams, 1984). They have suggested that for farmers drought resistance could be assessed on the basis of economic returns or on the farmer's own survival when his crops fail to grow to maturity. Levitt (1972) used a different approach. He defined the drought resistance of a plant as the water stress that is just sufficient to kill half of the plants.

2.6 DROUGHT AVOIDANCE

In dry regions where soil moisture availability is low, plants can grow in the wet season, particularly in winter. At the end of the wet season plants can also complete their life cycle on water stored in the soil. May and Milthorpe (1962a; 1962b) reported that when seasonal drought occurs plants with a short life cycle can mature before the soil water is exhausted. Levitt (1972) describes drought avoiding plants as those which maintain a high internal water potential, in spite of low environmental water availability. According to Cooper (1963) some Mediterranean grasses can grow better in cool weather, and they mostly complete their development before the summer drought. Reitz (1974) stated that each day by which certain varieties of wheat in Kansas and Nebraska matured earlier than the Kharkof variety resulted in an average increase in yield of 60 kg/ha or more. Where early maturity is important, tolerance of low temperature for seed germination and seedling establishment is a valuable characteristic. This is because it permits planting early enough to ensure maturity before water becomes seriously limiting.

2.7 DROUGHT TOLERANCE

Drought tolerant plants can tolerate drought without serious loss in yield. Drought tolerance is divided into two main groups: (i) postponement of dehydration, (ii) tolerance of dehydration.

2.7.1 Dehydration postponement: In this type injury due to dehydration is postponed by morphological or physiological

characteristics which either reduce the water loss by transpiration or increase water absorption. Prescence of waxy cuticle, responsive stomata and leaf rolling can reduce water loss and deep root systems increase water absorption. In postponement of dehydration roots play a major role. There are different rooting systems in different types of soil according to the crop or plant species (Turner, 1986). Gulmon and Turner (1978) mentioned the importance of maintenance of water for development of roots into soil and their continued extraction of water in the absence of rain. The growth of roots in deep soil layers is clearly a function of both genotype and environment. The interaction between these two often makes it difficult to distinguish genotype differences in root growth. Begg and Turner (1976) reported that an increase in water deficits usually leads to a greater root:shoot ratio. Shallow rooted crops, e.g. onion, potatoes, lettuce, tomatoes, are usually injured before deep rooted crops. They usually suffer from both the direct environmental effects on plant growth and also because the roots are not capable of getting enough soil moisture from the top layers of the soil. According to Hurd (1974), differences in drought tolerance of wheat in the Canadian wheat belt are related principally to differences in root development. Generally extensive root systems are effective in postponing dehydration, especially in deep soil. However, Kummerow (1980) suggested that the root system is less important than leaf adaptations in drought tolerance of shrubs of the California Chaparrals where soils are typically shallow.

2.7.2 Dehydration tolerance: When drought occurs for a

long time and plants can no longer postpone dehydration, then most plants are injured or die. However, a few remaining plants show tolerance. Blum and Ebercon (1981) observed that plants with poor dehydration postponement characteristics appear to have greater dehydration tolerance. Postponement of dehydration allowed little selection for dehydration tolerance. This tolerance of dehydration is considered to appear at the molecular level and depends on membrane structure and enzyme activity (Gaff, 1980; Levitt, 1980). It depends on the ability of the cell to withstand mechanical injury, the ability of the membranes to withstand degradation and the ability of the membranes and cytoplasm to withstand denaturation of proteins. Dehydration of sunflower leaves to -1.5 MPa caused injury to about 10% of the cells, but dehydration to below -2.0 MPa caused so much injury to organelles and membranes that recovery was impossible (Fellow and Boyer, 1978). However Gaff (1980) reported that some 60-70 species of ferns and seed plants, and many species of algae, lichens, and mosses can be dried in dry air and will recover fully after they have been rewatered.

2.8 MEASUREMENT OF WATER STRESS BY DIFFERENT METHODS

Plant water stress can be measured either from measurements of soil water content or from measurements of plant water status. The water content of plant tissue varies with species, organs, tissues and age. It also varies with the time of day, and with the season of the year. Leaf water status and transpiration are often better correlated with atmospheric conditions than with the soil moisture

content (Barrs, 1968; Boyer, 1969; Slavik, 1974; Turner, 1981). Young tissue generally has a high water content, but as cells mature the wall thickens and the proportion of dry matter increases, causing a decrease in percentage of water. Ackley (1954) determined that the water content of pear leaves decreased from 73 to 59% of their fresh weight from May to August, although water content per leaf increased somewhat. Leaves and stem tissues are most often sampled for measurement of plant water status. Measurement of water potential of roots is also necessary, because they play a role is absorbing the moisture from soil and in transfer of moisture to other parts of the plants (Kaufmann and Kramer, 1967; Slavikova, 1967; Wiebe et al., 1970; Fiscus, 1972; Hellkvist et al., 1974; Adeoye and Rawlins, 1981). Different areas of large leaves can differ in water status because of unequal exposure to the sun (Slavik, 1963; Rawlins, 1963).

One disadvantage of determining plant water stress is that it often involves harvesting entire plants or parts of plants. In the experiments reported in this thesis, use of these types of measurement was not possible, due to limited number of plants and pots available. Therefore, attention was focussed on measuring changes in soil water content, and using this as a guide to changes in root activity. Soil water content was determined using gypsum blocks.

2.8.1 Electrical resistance blocks or gypsum resistance blocks

The Gypsum block soil moisture meter was introduced by Bouyoucos and Hick (1940) as a simple and practical method of assessing the water content of soils under field conditions.

The blocks are buried in the soil and are connected by well-insulated leads to a resistance bridge. The water content of the blocks changes with that of the soil, producing measurable changes in the electrical conductivity of the solution between the electrodes. The blocks can be left in the soil for months or possibly for a year. Gypsum blocks are sensitive over a wide range of matrix potentials (-0.05 to -1.5 MPa). They are satisfactory in dry as well as in moist soil (Cummings and Chandler, 1940). With different types of soil 'field capacity' can be counted to a resistance of 400-600 ohms while 'wilting point' would occur at a resistance of 60,000-75,000 ohms. Resistance blocks are better in dry soil where tensiometers are not able to give a reliable reading. Resistance blocks can be calibrated against soil directly, by allowing them to equilibrate with a soil of a known water content and measuring resistance. They can also be calibrated against soil water tension if the relationship between soil water content and tension is known (Kelley, 1944; Kelley, et al., 1946; Haise and Kelley, 1946; Aitchison et al., 1951; Knapp et al., 1952; Slatyer and McIlroy, 1961). Gypsum resistance blocks are less sensitive to salt than nylon resistance blocks because of the dissolved calcium sulphate. Resistance readings from Gypsum blocks are unaffected by addition of up to about 2.2 metric tonnes of fertilizer per hectare (Bouyoucos, 1951). They are cheaper than other soil water content measurement equipment. They are very useful in monitoring gross changes in soil water content between irrigations. Also the progress of a wetting and drying front through the soil can be followed by the sudden reduction in

block resistance using a series of blocks buried at various depths in the soil.

2.9 GENERAL EFFECTS OF WATER STRESS

The general effects of water stress are reduction in plant size, vegetative growth and crop yield. Leaf expansion or leaf area, in particular, is severely inhibited by water stress (Slatyer, 1969). Decrease in leaf area results in lower light interception and hence lower yield. Studies of the effects of water stress have been concentrated either on development processes or on metabolic processes such as photosynthesis. Some workers believe that research would be more productive if physiological processes were studied at various stages of development. This is because some stages are very sensitive and even short periods of water stress at these times can have a large effect. Water stress affects every aspect of plant growth including anatomy, morphology, physiology and biochemistry, and nearly every process in plants involving turgor. Turgor pressure is high in enlarging cells, but some minimum level of turgor is necessary for cell expansion. Turgor is also important in relation to the opening of stomata and hence in photosynthesis, expansion of leaves and flowers and various movements in parts of the plants (Gale et al., 1966; Slatyer, 1969; Hsiao, 1973; Turner and Begg, 1978, 1981; Kozlowski, 1981; Taylor et al., 1982).

2.10 EFFECTS OF WATER STRESS ON CROP YIELD AND YIELD COMPONENTS, PARTICULARLY IN CEREALS SUCH AS WHEAT

There are many reports in the literature showing that low soil water availability limits yield and/or that irrigation increases yield. The degree of yield reduction by a water stress or enhancement through irrigation will depend on the degree, duration and timing of the stress and on the proportion of the total yield that comprises the economic yield of the crop. Because of the greater sensitivity of leaf development than photosynthesis and translocation to a water deficit crops such as pasture, tobacco and green vegetables (and cereals such as wheat, peas or fruit during reproductive growth) are often most sensitive to stress.

Total yield and economic yield may be affected differently by water stress. For example, in green peas, lack of irrigation decreased total yield by 47% but yield of peas by only 36% (Anderson and White, 1974). On the other hand, a water deficit at a critical stage of development in a determinate crop can markedly decrease the economic yield with a smaller effect on total above ground dry matter yield. For example, Turner (1966) observed a 70% decrease in grain yield of wheat from a water deficit imposed 5 weeks prior to ear emergence, but only a 52% decrease in total dry matter by the same treatment.

Downey (1971) reported that when water stress was imposed before anthesis the total above ground dry matter at harvest was decreased by 29% but grain yield was unaffected. However when water stress was allowed to develop during male meiosis in maize, the decrease in total dry matter was only 30% but grain yield was decreased by 47%. Water stress can influence the quality of small grain such as wheat and barley and can be

beneficial (Konovalov, 1959; Storrier, 1965; Turner, 1966; Campbell et al., 1969). When water deficit was imposed on wheat 5 weeks before ear emergence, the result in nitrogen percentage of the grain was increased by 53% over that in the well watered controls (Turner, 1966). An increase in nitrogen percentage would increase the quality of feeding and baking wheat and barley, but decrease the quality of malting barley. Cotton quality is reduced by drought stress (Marani and Amirav, 1971). Talha and Osman (1975) showed that water stress at all stages of development reduced the quality of sunflower oil, as indicated by the linoleic:oleic ratio, although both the percentage and quality of the oil was very low in this particular study.

Soil nutrient status can also markedly influence water use by crops and hence the time of onset of drought stress where water supply is limited. In situations of limited water supply, heavy nitrogen fertilizer use, or growth of wheat after a legume has been shown to produce vigorous vegetative growth that depletes soil water and can lead to a lower yield than with lower fertilizer application (Barley and Naidu, 1964; Fischer and Kohn, 1966a, 1966b, 1966c; Bond et al., 1971). For example Barley and Naidu (1964) showed that in a dry season with soil of medium fertility, wheat yields were 15 to 33% lower after the application of 130 kg/ha nitrogen than when no additional nitrogen was applied. Fischer and Kohn (1966a, 1966b) showed that application of nitrogen increased leaf area and evapo-transpiration in the vegetative phase and reduced the available soil water in the root zone at ear emergence and leaf relative water content

during grain filling.

2.10.1 Sensitivity of crops to water stress at different stages of development

The sensitivity of crops to moisture stress at different stages in their life cycle depends on the type of crop, growth stage, period of water stress, soil moisture conditions and climatic conditions. Different workers have distinguished growth stages in the same crop in different ways. Feekes (1941) divided the life cycle of wheat into 23 stages. Zadoks et al. (1974) identified 10 main stages. where as Zabluda (1939, 1940) defined six stages of development of the wheat plant. He suggested that the variable and often conflicting results obtained in drought resistance studies may be due to varietal differences in the time of formation of the reproductive organs relative to the external appearance of the plant. Salter and Goode (1967) have described different responses to water stress at various stages of growth of many crops. There is considerable evidence that most determinate cereal crops are very sensitive to water deficits from the time of floral initiation, during the booting stage, flowering, and to a lesser extent, during fruit and seed development. In indeterminate crops where these stages develop the situation is less clear. Perennial crops are sensitive to water deficits at the same stages, but it is doubtful whether the sensitivity during fruit development is more pronounced than it is during vegetative development. This is particularly the case when fruit development and vegetative growth are concurrent or when the rate of growth during a particular period largely determines the yielding

capacity of the crop in the following period, as is the case with apricot (Uriu, 1964; Fischer and Hagan, 1965).

The reproductive stages of plant growth are particularly sensitive to water stress. Generally water stress during initiation of flowering primordia and anthesis is especially injurious to wheat (Fischer, 1973; Siont et al., 1980). Legg et al. (1979) found that in barley, greater drought sensitivity at early drought was partly caused by reduction in number of grains per unit ground area, and partly by leaf area reduction which caused a reduction in light interception compared with treatments that had no or late drought. Salter and Goode (1967) reported the effects of drought stress at various stages of growth of different crops. It was found that wheat was specially sensitive to moisture stress during the shooting and earing stages of growth. According to Day and Intalap (1970), moisture stress during the jointing stage and later accelerated tiller senescence and reduced grain yield. Jensen and Mogensen (1984) found that when moisture stress was applied on the crop at any stage of development, the grain yield was reduced. Moisture stress prior to heading resulted in an increased percentage of nitrogen in the grain. A number of researchers (Azzi, 1922; Moliboga, 1928; Kezer et al., 1931; Robertson et al., 1934 Robins and Domingo, 1962; Kramer, 1963; Salim, Todd and Schlehuber, 1965; Fischer, 1973; Morgan, 1977) have found that booting to maturity and anthesis were more sensitive growth stages in comparison to other growth stages. At these stages flowers are injured and the number and the size of seeds are reduced. Apex and stem elongation and spikelet formation of wheat are inhibited by

water stress at early growth stages. Lodging was reduced by witholding irrigation water during the vegetative stage, but this decreased yield and yield components. Slavik (1966) reported that moisture stress reduced grain yield at all growth stages. During tillering moisture stress reduced fertile tiller number; during spikelet formation it decreased spikelet number; during anthesis it reduced the number of grains and during grain growth it reduced the grain weight. Singh and Malik (1983) worked out that when severe stress (-15 bars) was imposed during the planting to jointing stage grain yield was reduced about 34%. Straw yield and 1000 grain weight were also both reduced by various levels of moisture stress. Moisture stress of -25 bars at all growth stages decreased grain yield (Teare, Sionit and Kramer, 1982). Laing and Fischer (1977) found that semi-dwarf varieties selected under adequate soil moisture yielded well under reduced moisture supply. Monayeri et al. (1983) found that grain number per ear, average grain weight and grain yield per plant of wheat were decreased with increased soil moisture stress. A number of researchers (Passioura, 1977; Hodges, 1978; Rasmussen, 1979; Deloughery and Crookston, 1979) reported that moisture stress decreased harvest index. Day and Intalap (1970) have studied the effects of soil moisture stress at three stages of development, jointing, flowering formation and dough on the growth and grain yield of spring wheat planted in December. A critical period in the growth of wheat for moisture stress was the jointing stage. Water stress at jointing resulted in fewer days from planting to flowering, shorter plants, more lodging, lower grain yield,

lower grain volume weight, fewer heads per unit area and fewer seeds per head. Soil moisture stress at any stage of growth decreased grain yield. Hutchecon and Rennie (1960) determined that a single stress at any stage of growth significantly decreased grain yield of wheat especially when stress was applied at the dough stage. Day and Barmore (1971) have observed that flour yield was significantly reduced when water was withheld at jointing followed by the dough stage. The effect of drought on spike formation in wheat was studied in detail by Lobove (1939). The results of his work showed that drought during the earliest stages of spike initiation reduced the number of spikelets. Drought at a later stage when the florets began to differentiate in the spikelets, reduced the number of florets in the spike, though the number of spikelets remained unaffected. Drought at a still later stage, when the reproductive organs, stamens and pistils, began to differentiate in the florets, resulted in defective formation of the ovary and in partial and sometimes total sterility of the florets. Skazkin (1961) suggested that the drought resistance of plants was reduced after the appearance of the staminate tubercles in the spikelets of the central part of the spike. A high sensitivity to water shortage extended to the stage of pollen formation and ended after ear formation, flowering and fertilization had occurred. An analysis of the main stem of the wheat variety Lutescens 62 indicated that water shortage in the period prior to flowering resulted in most of the flowers in the spike being sterile, thus causing the reduction in grain number. Similar results to those of Skazkin were reported earlier by Nosatovskij

(1934) who suggested that the effect of soil drought during ear formation was on the androecia.

According to these workers (Skazkin, 1961; Slavik, 1966; Gebeyehou and Knott, 1983) moisture stress during anthesis time, caused damage to the flower organs and disturbance of the sexual processes. It reduced the number of grains and significantly reduced grain yield, 1000 grain weight and length of growing period. Singh and Narang (1971) found that delaying the first irrigation beyond 21 days after sowing caused a reduction in tiller number. Clarke Townley Smith, McCaig and Green (1984) determined that the biological yield was greater under irrigated than under unirrigated conditions. One of the most important consequences of the sensitivity of cell enlargement to small water deficits is marked reduction in leaf area. Leaf growth is generally more sensitive to water stress than stomatal resistance and CO_2 assimilation. Lower leaf area index can maintain leaf water potential at a higher level during the growth of the crops, thus reducing water stress (Woolhouse, 1967; Addicott, 1969). Water stress accelerates leaf senescence, because it increases the rate of leaf death (Mothes, 1928; Gates, 1964, 1968; Slatyer, 1967) and because the effects of water stress on many metabolic processes (such as protein and nucleic acid synthesis) are similar to those associated with senescence (Brady, 1973; Hsaio, 1973). Early maturity allows the plant to avoid the drought during later growth stages (Derera *et al.*, 1969; McKay, 1966, 1970) and contributes in reducing direct evaporation from the soil, promoting a rapid development of leaf area. According to the literature, wheat

cultivars with earlier vegetative growth and reduced LAI are more suitable where the amount of available water is limiting.

2.11 IMPORTANCE OF PHOTOSYNTHESIS UNDER DROUGHT STRESS

Photosynthesis is progressively decreased by water stress and negative values may develop when stress is severe (El Sharkawy and Hesketh, 1964; Slatyer, 1967). It is assumed that this response is mediated partly by way of impeded CO_2 supply following stomatal closure and partly by a direct effect of dehydration on the photosynthetic system. The rate of photosynthesis and size of photosynthetic surface after anthesis are considered important in determining yield in cereals. Photosynthesis of ears, stems and leaves during the grain filling period is generally recognized as the major contributor to grain yield in cereals (Allison and Watson, 1966; Thorne, 1966; Evans et al., 1975). A reduction in rate of photosynthesis or size of the photosynthetic surface by water stress should lead to a reduction in yield. For example, Fischer and Kohan (1966c) showed that the yield of field grown wheat was inversely correlated with the rate of senescence of photosynthetic tissue after anthesis when soil moisture deficits induced senescence. In later studies also in wheat, Fischer (1973) showed little reduction in yield arising from short but severe deficits. The potential for compensation for short periods of stress in the grain filling period is therefore high.

Wardlaw (1967) showed that under water stress, wheat translocated assimilates from the stem and lower leaves to the grain to compensate for the loss of flag leaf photosynthesis.

The importance of this is high lighted by Passioura (1976). He showed that about two thirds of the final grain weight came from redistribution of assimilates after anthesis and only one third from current assimilation in the period after anthesis in severely stressed wheat plants grown on a limited amount of stored water. The assimilates which are translocated are mainly soluble carbohydrate. These accumulate in wheat stems during a period when carbohydrate production in the leaves exceeds that required for development of the ear. Accumulation follows a pronounced drift, reaching a maximum during the early stages of grain formation, followed by a rapid decline towards maturity (Barnell, 1938; Lopatecki et al., 1957).

2.12 QUALITATIVE ESTIMATES OF WATER STRESS OR VISIBLE METHODS

The development of plant water stress can be visually assessed from the appearance of leaves. In some species such as apple, orange, pear, leaves wilt with a small decrease in water content. Some crop plants or trees show decreased stem length, e.g. sugar cane. This can be measured simply and quickly using a tape and comparing with unstressed control plants. Leaf colour changes because of change in leaf orientation with decreasing turgor. It can be seen in a variety of plants either by the eye or by the photography with infrared film. For example the leaves of beans, cotton, alfalfa, peanuts and wheat change to bluish or dark green as moisture stress, or salt stresses increase. Some varieties show this more than others. According to O'Toole and Maya (1978), leaf rolling and death of leaf tips is said to be reliable indicator of differences in water stress among rice

cultivars. Similarly the leaves of water stressed maize crops are indicated by perceptible loss of sheen and development of dull pale colour long before leaf rolling beings. Changes in turgor pressure can also cause changes in some leaves. For instance sugar cane straightens its leaves, usually the size of the leaves depends on the turgor pressure.

2.13 SALINITY

2.13.1 WHAT IS SALINITY?

The term saline soil is normally used in soil science to indicate a soil with an electrolyte concentration which is inhibitory to the growth of crop plants. The electrolytes which are particularly important are NaCl and Na_2SO_4. They are more dominant in soil than other salts such as $MgSO_4$, $CaSO_4$, $MgCl_2$, KCl and Na_2CO_3 (Flowers et al., 1977). These salts are mainly found in the soil solution and are linked with the clay particles. There is a continuous interchange or exchange of salts as ions between these two sites, to establish an equilibrium situation. The salts found in the soil solution, the soluble salts, can be extracted by drainage or suction and those held by the clay, the exchangeable salts, can be exchanged. There are three major classes of salt affected soil, saline soils, alkaline soils, and sodic soils.

2.13.2 Saline soil: By definition a saline soil contains in excess of 0.1% soluble salts (0.1% equals 2000 lb of salts in the 0 to 6 inch layer of soil) (Magistad, 1945; Chapman, 1966b). This concentration of salt is sufficient to

appreciably reduce the growth and yield of most crops. However, the growth inhibitory effect of this concentration can be altered by various factors. If a fairly high moisture level is maintained in the soil most of the time, e.g. by irrigation, the concentration of salts will be reduced and growth not as seriously affected as if the soil were permitted to become quite dry (Ayers et al., 1943). According to Richards (1954) in a saline soil, the electrical conductivity of the saturation extract (ECe) is greater than 4 millimhos per cm at 25°C, the exchangeable sodium percentage is less than 15 and the pH reading of the saturated soil usually less than 8.5. In saline soils the main problem is therefore one of a high soluble salt concentration which reduces water availability and causes toxicity. The salts present in saline soils consist mainly of natural salts, such as the chlorides and sulphates of sodium, calcium and magnesium. Sodium seldom comprises more than half of the soluble cations and therefore it is not adsorbed to any significant extent in the soil exchange complex. Saline soils can be recognized by the presence of a white efflorescence on the surface or by an oily looking surface devoid of vegetation.

2.13.3 Alkali soil: An alkali soil is one 'that contains sufficient exchangeable sodium to interfere with the growth of most plants, either with or without appreciable quantities of soluble salts. Whereas a calcium saturated soil, for example, tends to be well aggregated, well aerated and be readily permeable to water, a sodium-saturated soil has the opposite characteristics and is of very poor physical structure. There are two types of alkali soils, saline alkali soils and

non-saline alkali soils.

2.13.4 Saline alkali soils: Saline alkali soils contain sufficient exchangeable sodium to interfere with the growth of most crop plants and also contain appreciable quantities of soluble salts. The exchangeable sodium percentage is greater than 15, and the electrical conductivity of the saturation extract is greater than 4 millimhos per cm at 25°C. The pH value of the saturated soil is usually less than 8.5. Soils of the so-called black alkali type would come under this classification (Richards, 1954).

2.13.5 Non-saline alkali soil: Non-saline alkali soils contain sufficient exchangeable sodium to interfere with the growth of most crop plants but do not contain appreciable quantities of soluble salts. The exchangeable sodium percentage is greater than 15, and the electrical conductivity of the saturation extract is less than 4 millimhos per cm at 25°C. The pH reading of the saturated soil extract is usually greater than 8.5.

2.13.6 Saline sodic soils: Saline sodic soils contain sufficient quantities of both soluble salts and adsorbed sodium to reduce the yield of most plants. By definition the exchangeable sodium percentage is greater than 15, and the electrical conductivity of the saturation extract soil is usually more than 4 but less than 8.5. If Gypsum is present in appreciable quantities, the pH may be as low as 8.2. The soil solution of sodic soils is relatively low in soluble salts and the ionic composition differs considerably from that of saline soils. The predominant cation is sodium because at high pH and in the presence of the carbonate ion, calcium and

magnesium are largely precipitated as calcium and magnesium carbonate. The anions present consist mostly of chloride, sulphate, and bicarbonate, with small to moderate amounts of carbonate, depending on the pH of the soil. If carbonates are present in detectable amounts in the saturation extract, then the pH must be above 9. The exchangeable sodium present has a marked influence on the chemical and physical properties of sodic soils. As the portion of exchangeable sodium increases, the soil tends to become dispersed, less permeable to water and exhibits poor tilth. Sodic soils are usually plastic and sticky when wet and form large clods or crusts on drying. Their crusting tendency is a serious hazard to seedling emergence, and it often accounts for a poor stand of crops, causing reduced yield.

2.14 CAUSES OF SALINITY

The main causes of salinity in arid and semi-arid regions are rainfall, mineral weathering, 'fossil salts' and various surface waters and ground waters which redistribute accumulated salts, often as a result of man's activities. The soil contains soluble salts and rivers and well waters also contain salts. When water evaporates, the salts it carries are left behind. When there is limited rainfall and insufficient application of irrigation water to leach accumulated salts away, the soil becomes more saline with time (Meinzer, 1942; Eriksson, 1958). When the water table gets too high for applied irrigation water to do an effective job of leaching away the salts no matter how much water is applied salinity increases. In other cases the percolation rate of

water through the soil may be too slow to achieve an adequate leaching effect. Good soil drainage is generally the key to alleviating soil salinity. Unless good drainage can be provided, the salinity condition can only become increasingly worse. Chapman (1966b) reported that saline soils owe their origin to one or a combination of the following: (1) capillary rise of water (carrying dissolved salts), particularly when sub soil leaching is insufficient to remove the salts; (2) prevailing winds from the ocean which carry fine spray a short distance inland; (3) evaporation of inland seas and lakes; (4) inundation of land by seawater; and (5) inland basins lacking a drainage outlet and subject to periodic flooding and evaporation. The Mancos shales in Utah are examples of saline marine deposits. The ocean may be a direct source of so-called cycle salt along the sea shore through wind by sprays (Teakle, 1937). However, the main sources of salts affecting irrigated agriculture are surface and ground waters. When snow melts in the mountains and rain falls, the streams become rivers and move down to the sea. Rivers become loaded with increasing quantities of dissolved salts as they pass through the land, and thus the ocean is salty. For example, the Colorado River has a salinity level of around 0.87 mM (50 ppm) in the Rocky Mountains and around 17 mM (100 ppm) as the river nears the Gulf of California. The salinity of rivers is increased beyond natural salt loading by municipal sewage and sewage treatment plants and by irrigation, which leaches additional ground salts as well as applied fertilizer salts into the ground water and ultimately the rivers. In the case of the Colorado

River basin, approximately 50 percent of the river's salts comes from these human sources. In regions of high rainfall, dissolved CO_2 in the form of carbonic acid enters the soil and ionizes into bicarbonate and H^+. Thus the negative charged clay particles become acidic and the aluminium in them, which is precipitated at normal soil pH, comes into solution and also binds to the clay. Both Al^{3+} and H^+ are near the top of the lyotropic series, so they displace other cations from negatively charged soil particles. These cations as well as bicarbonate and other less strongly bound anions stay in the soil solution and drain into the ground water. Thus acidic soil not only contains toxic aluminium, which itself makes the soil nutrient poor, soluble aluminium enters plant cells where it lowers cell pH and disturbs normal metabolism. Approximately 25 percent of the worlds arable land suffers from excess acidity and its accompanying problems.

2.15 IONS CAUSING SALINITY OR DIRECT TOXICITY EFFECTS

There are many different ions associated with soil salinity by different ways but five are the most important: sodium, chloride, calcium, carbonate and bicarbonate.

2.15.1 Sodium: Na^+ is generally the dominant cationic component of the soil solution in saline soils (Lunt, 1966). One of the major effects of Na^+ is on soil structure - the effect being primarily a dispersion of soil colloids. Associated with this change in the aggregation of soil particles is a decrease in soil aeration. Incidentally, poor aeration appears to be associated with increased translocation of Na^+ to the tops of plants, since Na^+ exclusion (to the top)

is dependent on adequate aeration around the roots (Lunt, 1966). Sodium becomes absorbed by clay colloids and at high concentration causes displacement of potassium and calcium, leading to deterioration of soil structure. Soluble and exchangeable sodium and chloride are readily leached from soils and land can be reclaimed from the sea, e.g. in Holland, in 3-5 years. Sodium is an activator of transport ATP-ases in animals and possibly also in plants. There is evidence that sodium can replace potassium partly in some of its functions, e.g. it can substitute for potassium as an osmotic regulator in the guard cells of some plants, and also halophytes. Because sodium and chloride are so ubiquitous in nature and such small amounts are evidently required by most plants, deficiency symptoms have hardly ever been observed although the growth of many plants is reduced in soils low in common salts. Sodium and chloride toxicity effects include reduced growth and some wilting which is followed by chlorosis, bronzing and necrosis. Root growth is also markedly affected; the roots become stunted and development of laterals is suppressed. Addition of sodium salts, especially sodium chloride, to soil stimulates the growth of some plants, notably sugar beet, red beet, celery and turnips and cereals, and sometimes induces 'succulence' but it severely inhibits the growth of others.

2.15.2 Chloride: Cl^- salts are frequently involved, either partly or almost wholly, in salinity conditions. Cl^- salts can be, and often are, associated with accumulations of SO_4^{2-}, HCO_3^- and CO_3^{2-} ions in plants and soil (Eaton, 1966). According to Eaton (1966) symptoms of Cl^- excess include

burning and firing of leaf tips and margins, bronzing, premature yellowing and abscission of leaves and, less frequently, chlorosis. He describes Cl^- toxicity symptoms for various crops and indicates the concentrations of Cl^- in plants associated with toxicity. For most plants the internal concentration of Cl^- closely reflects the external concentration. Beets, barley, flax, cotton, wheat, and tomatoes are in the high tolerance group with regard to Cl^-. Functionally, the role of these elements(Cl^- in plant metabolism is still uncertain. The observation that chloride is essential for production of oxygen by isolated chloroplasts has led to the view that chlorides act as an electron transporting agent in photophosphorylation. A few chlorinated organic compounds have been identified in plants but there is no indication that they have an essential role in metabolic processes. Growth of lettuce, tomatoes, cabbage, and carrots (Daucus carota) is reduced by more than 50% in chloride deficient media. Chloride deficiency symptoms have been induced in tomato plants.

2.15.3 Calcium: When Ca^{2+} is associated with SO_4^{2-} in a salinity situation, the concentration of Ca^{2+} may not be very high owing to the relatively low solubility of $CaSO_4$, that is approximately 25-30 meq/litre. However, when Ca^{2+} is associated with Cl^-, its concentration can be very high. There are few if any specific symptoms associated with excesses of Ca^{2+} (Chapman, 1966a) symptoms are generally caused by the associated anion, for example, Cl^-or SO_4^{2-}. High levels of Ca^{2+} in a nutrient solution were lethal to orchard grass when the associated anions were either Cl^- or

NO_3^-(Wadleigh et al., 1951). Ca^{2+} excess in soils is usually associated with excesses of soluble salts (e.g. $CaCl_2$ or $CaCO_3$) as observed by Chapman (1966a). He noted that excess lime can be eliminated by $(NH_4)_2SO_4$ or other acidifying agents only when it is present in relatively low concentration in the soils. When excess soluble salts of Ca^{2+} are present, correction consists of leaching the salt out of the soil. Calcium deficiency results in early death of meristematic regions of stem and root. Malformation of young leaves causing the tips to be hooked back, is also a characteristic symptom. Later, the leaves may show marginal chlorosis and these areas eventually become necrotic. Once it is deposited in leaves, calcium, like sulphur, is immobilized, and symptoms of deficiencies tend to develop in young leaves as soon as supply is depleted. In the absence of calcium, roots do not grow well and often appear brown in colour and stunted. The presence of magnesium appears to enhance this effect. Degeneration at the apex of young fruits ('blossom end rot') is a common symptom of calcium deficiency in tomatoes.

2.15.4 Carbonate and Bicarbonate : Depending on pH, only HCO_3^- may be present, only CO_3^{2-} may be present, or there may be various proportions of these anions (Pratt, 1966). When CO_3^{2-} alone is present pH is high, organic matter is brought into solution, some seeps down in the soil and the rest accumulates in the surface of the soil and a condition known as 'black alkali' results. Absence of CO_3^{2-} or HCO_3^- in the soil has no adverse effect on plants. Phytotoxicity results when either of these ions is present in a high concentration (Pratt, 1966). Except for highly acid soils, HCO_3^- is

present in soil, but CO_3^{2-} is present in measurable concentrations only in soils with a pH of approximately 8.5 or higher. HCO_3^- has been associated with Fe chlorosis in many plants. High lime Fe chlorosis is associated with calcareous soils, but some of these soils do not produce high lime Fe chlorosis. Thus, lime concentration per se is not a clear-cut diagnostic index, according to Pratt (1966). He stated that sodium (Na) soils containing high lime, that is, containing $CaCO_3$, can be improved only by acidification to dissolve the $CaCO_3$, so that Ca^{2+} can replace Na^+ on the exchange complex. He added further that the HCO_3^- ion may not readily enter root cells, but that it would not need to enter in order to produce a high HCO_3^- concentration inside cells. In as much as HCO_3^- is produced by respiration, high external concentrations of HCO_3^- could cause an accumulation of metabolically produced HCO_3^- inside cells. Growth of beets was reduced less by HCO_3^- than was bean growth (Brown and Wadleigh, 1955). Comparison of cation accumulation in bean and beet leaves showed that treatment and chlorosis were not correlated with any particular cations or with the K/Ca ratio in both species, but rather with monovalent cations or the (Na + K)/(Ca + Mg) ratio. When given to bean plants, $NaHCO_3$ resulted in lowered Fe activity and Ca^{2+} concentration in leaves and enhanced K^+ concentration (Wadleigh and Brown, 1952). Along with accumulation of K^+, citric acid accumulates in leaves showing HCO_3^- induced chlorosis. It was concluded that the primary effect of the HCO_3^- ion is brought about through its effect on protoplasmic consistency of the absorbing cells of roots, so that bean plants accumulate relatively more monovalent cations and

relatively less divalent cations.

2.16 CLASSIFICATION OF SALT STRESS

On the basis of their tolerance to salinity plants can be divided into: (1) Glycophytes which tolerate only relatively low salt concentrations; (2) Halophytes which are adapted to live in saline environments, some of them are salt resistant and are able to grow and maintain normal metabolic functions in saline conditions (Yeo, 1983). Most crop plants are glycophtes.

2.16.1 Halophytes: The word halophyte literally means salt plant or salt lover, but it is used specifically for plants that can grow in the presence of high concentrations of all salts and tolerate relatively high concentrations of salts. They also tend to have relatively high values for the osmotic pressure of the tissue fluids. Some halophytes survive extremely high salt concentrations compared to the low concentrations that injure glycophytes. This difference is found both under natural and artificial conditions. Halophytes can grow on soils containing up to 20% salt although most grow on soil with 2-6% salt (Strogonov, 1964). They can grow in solution culture with very high salt concentration. They can accumulate large amounts of salts, e.g. a 10.1% solution in tissues of Salicornia.

2.16.2 Glycophytes: Glycophytes are defined as 'sugar lovers'. They tolerate only relatively low concentrations of salts. Most commonly grown crop plants are glycophytes. In general glycophytes grow well only under non-saline conditions. Yet even though most crop plants are glycophytes,

there is a rather wide range of salt resistance among them, from a maximum in beetroots to a minimum in carrots (Strogonov, 1964). Among grains, barley is more resistant than oat, which is more resistant than wheat (Ballantyne, 1962). Among a large number of crop plants that have been tested the most salt resistant are date palm, cotton, lucerne, sweet clover, asparagus, beets, citrus, strawberry and beans, but the order of resistance is not the same in all soils.

2.17 SALT RESISTANCE

Plants differ widely in salt resistance, from sensitive ones that are prevented from normal growth by low concentrations of NaCl to the most resistant halophytes from saline habitats. Among the most resistant are Rhizophora mangle which survives only at salinities that approximate to sea water, and Avicennia germinans which thrives in salinities in excess of sea water (Morrow and Nickerson, 1973). Among plants from saline habitats at least some, such as the above Rhizophora, are obligate halophytes, growing only in the presence of sufficient salt. The obligate halophytes include, both lower and higher plants, for instance, a blue green alga (Aphamothece halophytica., Tindall et al., 1977), diatoms (Paasche, 1975), marine yeast (Rhodotorula glutinis var salinaria., Ito and Takada, 1976), and the higher plants Suaeda maritima and Salicornia europaea. Even tissue cultures from the calli of these two plants must be supplied with NaCl (Von hedenstroem and Breckle, 1974) and this requirment can not be met by organic solutes of the same osmolarity.

Salt resistance depends on the age and stage of develop-

ment of the crop. For example salt resistance is low in young tomato and cotton plants. It becomes much higher by the bud stage, and decreases during flowering (Kovalskaia, 1958; Penskoy, 1956). Rice shows a similar increase in resistance with the plant bud age (Pearson and Bernstein, 1959). Salinity at tillering has been found to be twice as inhibitory as at heading. In barley plants, varietal differences in salt resistance increased during plant development (Greenway, 1965b). There was no direct relationship between the salt tolerance of some halophytes during germination (in salt solution up to 1.0M) and the salinity of their respective habitats (Waisel, 1958). All the other species tested did show a correlation. In the case of soyabeans, there is also no apparent relationship between the salt resistance of a variety during germination and during later growth (Abel and Mackenzie, 1964). Two sugar cane varieties differed in salt resistance, again only at the stage of germination and during early growth (El Gibaly and Goumah, 1969). After three months no negative effect on yield, growth and sugar content was found following watering with salinized water (6000 mmhos/cm). All species of crop tested by Choudhuri (1968) were less salt resistant at the seedling stage. The mechanism of salt resistance can be different in seedlings and mature plants (Hunt, 1965). In the case of fruit trees, salt resistance increases during initial growth but decreases as the plant grows older, dropping abruptly during the period of fruiting (Devyatov, 1962). The Cl^- and Na^+ contents of a more halophytic species Agropyron elongatum were considerably lower than those of a very resistant variety

of Hordeum vulgare, and were lower even when grown on highly saline sites (Greenway and Rogers, 1963). Similar results have been obtained with other plants when the salinity of their medium was increased progressively. Less resistant varieties of soyabean accumulated larger amounts of Cl^- (Abel and Mackenzie, 1964). Among cultivars of Glycine wightii, one group in particular was more resistant to salinity stress than the others (Gates et al., 1977) excluding Na and, to a lesser degree Cl, from the plant tops to a greater degree than the more sensitive cultivars. Following the early definitions of drought resistance, then salt resistance can be divided up in to salt avoidance and salt tolerance.

2.18 SALT AVOIDANCE

There are three different methods a plant can adopt to avoid the salt stress of its environment. (1) Salt avoidance due to salt excusion and, therefore, to low salt permeability. (2) Salt avoidance due to salt excretion by an active ion extrusion pump. This would confer resistance to both the primary stress and the secondary salt induced deficiency stress (avoidance of nutrient deiciency). (3) Salt avoidance due to dilution, perhaps depending on a high plastic extensibility of cell walls (Levitt, 1980)

2.18.1 Salt avoidance due to exclusion: When varieties of barley (Greenway, 1962a; 1962b) were treated with 125 or 250 meq NaCl/litre, the less resistant variety accumulated a higher content of Cl^- and Na^+ and a lower K^+ content than the two resistant varieties. The differences were particularly large in the inflorescences (Greenway, 1965b). Both the

passive and the active uptake of Cl^- were higher in the less resistant variety.

Even at high transpiration rates, the ascending sap attained only 1.5-4% of the concentration in the medium showing that most of the water flowed through regions of low salt permeability (Greenway, 1965a).

In the case of plants possessing the exclusion mechanism, the roots may show an impermeability to salt up to a point, followed by a 'burst' of salt causing poisoning and sometimes death (Strogonov, 1964). The salt resistance of such plants depends on maintenance of impermeability to the salt in the presence of high external concentrations. That maintenance of the normal differential permeability of the cell depends on a balance (about 10:1) between monovalent (K^+, Na^+) and divalent (mainly Ca^{2+}) cations. When this balance is disturbed by too high a concentration of monovalent cations, the permeability increases, leading to injury. Therefore a plant with salt avoidance due to exclusion must possess a low permeability to Na salts even in the presence of relatively high salt concentrations. The avoidance mechanism may be achieved by salt excretion as well as by salt exclusion, and the two mechanisms may exist in two closely related plants.

Avoidance of salt injury by salt exclusion is also dependent on temperature, thus the optimum temperature for growth of Chrysanthemum dropped with an increase in salinity (Lunt *et al.*, 1960). This was explained by the increase in accumulation of Na^+, Ca^{2+}, Cl^- with increase in temperature. Sodium ions tended to be excluded from the upper leaves unless temperature was high. Similarly, rice suffered more salt

injury at 30.7°C and 63.5% R.H. than at 27.2°C and 73.4% R.H (Ota and Yasue, 1959). This was explained by the greater intake of salt at high temperature and low humidity. The effect of temperature is persumably due mainly to the increased transpiration rate rather than the increased absorption rate, for such small changes in temperature (and relative humidity) can affect large changes only in the former processes.

2.18.2 Salt avoidance due to salt excretion by an active ion extrusion pump

It is difficult to distinguish between such a passive exclusion and an active extrusion (or excretion) of the salt due to a salt extruding pump. Both must be involved in salt resistant plants. The impermeability must be reasonably high, otherwise the salt would leak in more rapidly than the cell could pump it out. Similarly, complete impermeability is unlikely, and therfore even a slow leak into the cell would eventually lead to an injurious concentration in the absence of an extrusion pump.

In some highly adapted halophytes, the extrusion mechanism is localized in salt glands, which, consist of both collecting and excreting cells, and attempts have been made to locate extrusion pumps in the glands (Shimony et al., 1973).

2.18.3 Salt avoidance, due to dilution: It is dependent on the succulent mechanism. The cells (especially the parenchyma) enlarge due to an increase in water content, which prevents an excessive concentration of salts in the cell sap (Repp, 1958). The mechanism is well developed in Atriplex species (Greenway et al., 1966). Marine algae such as sea

weeds and the submerged angiosperm eel-grass (Zstera marina) are also adapted to withstand high salinity. Until this mechanism is understood, the dilution avoidance cannot be explained. Perhaps it depends on the maintenance of thin, plastically extensible cell walls, permitting continuous cell expansion by water uptake sufficient to balance every salt increment in the cell.

The "dilution" of the cell sap due to growth has also been found in some moderatily salt resistant nonhalophytes. Barley rapidly increases its NaCl concentration during early tillering, but shows little further change until grain formation due to the rapid growth (Greenway et al., 1965). During senescence, when growth decelerates, there is a marked increase in Cl^- and Na^+ concentration, and at any one time the ion concentrations are higher at low than at high growth rates (Greenway and Thomas, 1965). Even the varietal salt resistance of twenty accessions of Glycine javanica seemed to be directly related to growth rate (Gates et al., 1966b). This is also true of gram and wheat. The slow growing varieties suffered more concentrations of Nacl (0.8%) during early seedling growth (Sarin, 1961).

2.19 SALT TOLERANCE

Tolerant plants are those which can tolerate toxic ions in thier cells. Hayward and Wadleigh (1949) and Hayward and Bernstein (1958) have discussed salt tolerance of crops. The mechanisms whereby Cl^-or Na^+ ions are specifically toxic to sensitive species remain unknown. They added that identifying the mechanism of salt toxicity and distinguishing features

of salt tolerance appear to be major tasks for research on salt tolerance of plants. Levitt (1972) has observed that the term salt tolerance has been used in the literature for any plant possessing salt resistance, simply on the basis of its ability to tolerate the salinity in the external medium. This would, of course, include avoidance. Crop salt tolerance can be defined as the ability of plants to survive and produce economic yield under the adverse conditions caused by soil salinity. Salt tolerance of agricultural crops is typically expressed in terms of the yield decreases associated with soil salinity increases, or as relative crop yield on saline versus non-saline soil (Maas and Hoffman, 1977). The salt tolerance of ornamental plants on the other hand, is better expressed on the basis of survival and appearance, because yield is not generally important for such species. Sodium tolerance data has been reported by Pearson (1960) for several important agricultural crops. He has divided tolerant crops into three main groups on the basis of the exchangeable sodium percentage (ESP) they will tolerate in the soil.

(1) Moderately tolerant crops such as clover, oats, tall fescue, rice and Dallis grass can be grown from 20 to 40 ESP.

(2) Tolerant crops, for example wheat, cotton, alfalfa, barley, tomatoes, beets can be grown up to 40 to 60 ESP.

(3) Tolerant crops can be grown at ESP greater than 60. These crops include crested wheat grass, fairy way wheat grass, tall wheat grass, Rhodes grass.

2.20 METHODS OF MEASURING SALINITY

One of the most simple and most useful ways of assessing the soluble salt concentration in a soil is to measure the electrical conductivity of the saturation extract (units, mhos/cm at 25°C). Different crops respond in different ways to a given soluble salt concentration and the responses can be quantified in terms of the electrical conductivity value. On the basis of electrical conductivity (EC) measurements soils can be grouped as follows: (U.S.A. Department of Agriculture).

Electrical conductivity mmhos/cm (at 25°C)	Crop response
0-2	Salinity effects on yield are negligible
2-4	Yields of very sensitive crops are reduced
4-8	Yields of many crops are reduced
8-16	Only tolerant crops yield satisfactory
>16	Only very tolerant crops yield satisfactorily

Irrigation water is divided into four classes: low salinity, medium salinity, high salinity and very high salinity. The dividing points between these classes are being <150, 250-750, 750-2250 and >2250 umhos/cm. This range includes water that can be used for irrigation of most crops on most soils, to waters that are not suitable for irrigation under ordinary conditions.

2.21 GENERAL EFFECTS OF SALTS ON CROP GROWTH AND CROP YIELD

The general effects of salinity on crop growth depend on the crop, type of salts, quantity of salts, growth stage of crop and climatic conditions. Hayward and Wadleigh (1949),

Grillot (1956), Bernstein and Hayward (1958) and Bernstein (1962) all report that salinity affects plant growth by three major ways: (1) by increasing the osmotic pressure of the soil solution; (2) by causing the accumulation of certain ions at toxic concentrations in plant tissues; (3) by altering the plants mineral nutrition. Hayward and Spurr (1943, 1944) reported that the growth reduction with increasing osmotic pressure of the rooting medium, has been attributed to decreased water entry or availability. However, Bernstein (1961) reported that water absorption capacity is relatively unaffected by salinity. The reduced growth associated with osmotic stress is attributed to the processes of building up the osmotic pressure of developing cells (which is contingent upon accumulation of solutes), to meet the increasing osmotic pressure of the rooting medium and still maintain turgor. This theory suggests that salt tolerance may be defined as the degree to which osmotic adjustment can be made without sacrificing growth. There were some examples about the effects of salts on crop growth. Salt exclusion is generally accomplished through a preferential accumulation of ions in the root or in certain relatively insensitive tissues of the shoot of the plants exposed to moderate concentration in the rooting medium. The ability of salt stressed grasses to partition ions in their leaves was first recognised by Greenway (1962).

Exclusion of sodium and chloride from salt sensitive, metabolically active tissues in the shoot is a salt resistance mechanism found in a variety of crop plants (Greenway and Munns, 1980; Wyn Jones, 1981; Lauchli, 1984).

2.22 PLANT AND STAGES OF PLANT SENSITIVITY UNDER THE SALINE CONDITIONS

Plant sensitivity to salinity mostly depends on the stage of plant growth, period of exposure to salt, weather conditions and salt concentrations. Plant sensitivity to salinity often varies with plant growth stage (Maas and Hoffman, 1977). Some cereals are more sensitive during the emergence and early seedling growth stages than during either germination or the later growth stages, including grain development. Sugarbeet and safflower, on the other hand, are more sensitive during germination. To avoid a crop failure, the grower must know the salt sensitivity of his crops at each of their growth stages, and adopt appropriate management practices to minimize salinity damage.

The classification of crops according to salt tolerance fails to reveal certain specific problems because some plants are especially sensitive to salinity during certain stages (Bernstein and Hayward, 1958; Bernstein, 1961). For example, rice is quite tolerant during germination but becomes very sensitive during the seedling stage, and again somewhat so during the fertilization of the florets (Pearson and Bernstein, 1958). Rice can germinate at salinities up to 10 or 15 mmhos/cm, but the plants usually die if the salinity is in excess of 5 or 6 mmhos/cm during the seedling stage (Pearson and Ayers, 1958). Corn appears to be appreciably more tolerant during germination than the later stage of growth. Sugarbeet, on the other hand, can tolerate salinity levels of only about 4 mmhos/cm in the saturation extract during germination

but can easily tolerate three times this salt level once the young seedlings are well established. Barley is like rice in being more sensitive to salinity during the seedling stage than at earlier or later growth stages.

Occasionally, special practices may be required to permit a crop to survive during phases of minimum salt tolerance. For example, the paddy field is sometimes drained and refilled with fresh water to lower the salinity during the critical, sensitive flowering stage of rice. Special bedding practices have been developed to minimize salt accumulation around germinating seeds and for poor stands of furrow-irrigated row crops. Pearson (1960) reported that the deciduous fruits, nuts, citrus and avocado are extremely sensitive at the range of ESP values 2 to 10. Beans are sensitive at the ESP value 10-20. Kingsbury et al. (1984) reported that wheat is more sensitive during germination. (Francois et al., 1986), they presented the grain yield parameters of two Triticum wheat species. In 1982, bread wheat grain yield, as well as all parameters associated with grain yield, showed no significant reduction with soil salinity up to 10.8 ds/m. However in 1984, with higher soil salinities, grain yield was significantly reduced. The decreased yield resulted from decreased seed weight per spike and individual seed weight (expressed as the weight of 100 seeds). The number of spikes harvested per unit area was not affected by salinity. Straw yield of both species was more sensitive to salinity than grain yield, with thresholds of 4.5 ds/m for bread wheat and 3.2 ds/m for the durum cultivars, the reduction in each unit increase in salinity above these thresholds was less than that for grain

yield at 2.6 and 2.5% for the bread and durum cultivars, respectively. Corn (Kaddah and Ghowail, 1964), rice (Pearson, 1959) and sorghum (Francois et al., 1984) show a greater reduction in grain yield than straw yield under saline conditions. Abdul-Halim et al. (1988) did an experiment on Mexipak wheat (Triticum aestivum L). Mexipak proved to have high yield, good quality (Adary, 1973; Hassan and Al-Sabti, 1973) and was relatively salt tolerant (Abdul Halim et al., 1985). Results showed that increasing the soil salinity from 1.7 to 11.0 ds/m, and decreasing the available soil water from 75 to 25% resulted in independent and significant decreases in Maxipak wheat growth and yield components at different stages of plant development. Root growth showed more sensitivity to both available soil water and soil salinity level than other components. It has been concluded that at soil salinity levels of more than 8.0 ds/m available soil water became a limiting factor on wheat growth and the maintenance of 75% of available soil water during the growth period is recommended to obtain satisfactory grain yield.

Bernal et al. (1974), found differences in germination due to variety and these were clearly evident after seven days exposure to salinity. In these experiments some wheat varieties (Nadadores, Potan, Sonora, and Nuri) germinated at moderately high salinity levels (-20 atm) whereas seed from other varieies (Ciano and Cajeme) were some what less tolerant showing a 50% germination decrement at -16 atm. These findings indicate strong varietal effects at the germination stage as well as a relatively high tolerance to salinity. In the experiments, of Francois et al., (1988), salinity reduced

vegetative growth less than grain yield in Cananea 79 but more in Beaguelita `s'. Both cultivars were slightly less salt tolerant at germination than they were after the three leaf stage of growth. Chipa and Lal (1985), grew Kharachia 65, HD 2009, Kalyan Sona, Raj 1114, Raj 911 and Raj 821 in the soil with salinity ranging Ece from 4.2 to 18.1 mmhos/cm. Plant height, effective tiller number and grain and straw yield decreased with increasing salinity above Ece 8.1 mmhos/cm. Karachia 65 was the most salt tollerant with HD 2009 > Kalyan Sona > Raj 1114 > Raj 821 > Raj 911. Mass and Hoffman, (1976), reported that barley, corn, rice, and wheat are more sensitive during emergence and early seedling growth than during germination and later stages of growth and grain development. (Abdel halim et al., 1976; Abdul halim et al., 1985) reported for wheat, that shoot dry matter at tillering stage and root dry weight at maturity were depressed more than other wheat yield components at the higher soil salinity levels of 9.4 and 11.0 dsm^{-1}. Mass et al., (1986), found that total grain yield per plant was decreased most by salination during the vegetative stage and least during the grain maturation stage. The effect of salinity on yield at the reproductive stage was intermediate. Although moderate salinity levels increased grain yield in some cases. Larik and Saheal (1986), found percentage germination of all cv. of wheat decreased with increasing salt concentration. NaCl was more deleterious than Na_2SO_4. Tritcale was most salt tolerant at germination and also most salt sensitive at the seedling stage under Nacl salinization. Adverse effects of both salts were more pronounced on root than on shoot.

2.23 VISUAL SYMPTOMS OF PLANTS AFFECTED BY SALINITY

Visual salt toxicity symptoms usually do not appear until significant yield depression has already occurred. Therefore little can usually be done to increase crop yields after such symptoms appear. Measuring the EC of soil saturation extracts is a much better 'early warning' criterion for predicting crop yield depression as a consequence of root zone salinity than is the appearance of toxicity symptoms in plants. Plants affected by salinity are generally stunted. Leaves are smaller, though they may be thicker than those of normal plants. Leaves of salt affected plants are often a darker green than leaves of normal plants. In some grass species and crucifers, thickened layers of surface wax may cause a bluish green cast. Stunting of fruit development may also be evident (Hayward and Magistad, 1946). Unless the salt concentration is high enough to result in a burning or firing of leaves, there may be no symptoms other than stunting. Osmotically stressed plants may not show distinctive symptoms, however a comparison with normal plants growing in the same environment reveals the extent of salt inhibition (Bernstein, 1975). Soil salinity measurements, together with careful established salt tolerance data, aid in the diagnosis of suspected salt problems, salinity usually varies greatly across a salt affected field. The variation may extend from barren ears to ears of near-normal plant growth. Trees, vines, shrubs and vegetables such as beans exhibit leaf injury manifested by characteristic tip and marginal burning and in some cases, necrotic leaf damage. Such symptoms are often

associated with elevated concentration of specific ions in the leaves. Bronzing is also a characteristic symptom in some species. The frequency and length of root hairs of citrus were reduced by high concentration of Cl^- salts and there were numerous anatomical alterations (Hayward and Blair, 1942).

2.24 EFFECTS OF STRESS AT DIFFERENT STAGES AND ITS RELATIONSHIP WITH PLANT DEVELOPMENT

This section describes the development of a cereal plant during the stages in which stress was imposed in these experiments. It is presented as a framework for discussing the effects of the treatments.

All the organs of the shoot arise as primordia which are initiated by changes in patterns of cell division and growth at the shoot apex. The physiological and morphological changes at the apex presage changes in the external form of the plant. It is important to know how the environmental stresses (water stress and salinity stress) affect plant development and final yield in different crops. In some cases the plant response to a treatment is related to the activity of cells in the shoot apex or another meristem. When a treatment is applied at certain stages of development it may produce changes which lead to reduction in yield. For that purpose it is important to know the critical stage and to be able to assess it.

2.24.1 Development during the period start of tillering to stem extension

The apex forms in the seed during embryo development. When the seed is mature the embryo has already initiated three

or four leaf primordia. After germination more leaves are initiated on the dome shaped apex. During this period the dome initiates between eight and fifteen leaves, depending on variety, time of sowing and type of environment. After a full complement of leaves for that shoot has been initiated a phase of spikelet initiation follows and an embryo ear is formed. The transition from vegetative to floral phase is marked by elongation of the apex, which becomes cylindrical in form. The wheat plant at this stage is a seedling and the apex will remain at the vegetative stage from germination until between four and eight leaves have emerged on the main shoot. Generally winter wheat produces more leaves at this stage, compared to mid-duration and spring wheat varieties. Spikelet primordia are first recognised at the double ridges stage. After the double ridges stage, spikelet development proceeds and the primordia of florets and of floral organs are laid down in sequence. At about the time when spikelet initiation is complete stem elongation and rapid ear growth occur. During this stage further development of spikelets occurs. Each spikelet primordium in the embryo ear will eventually initiate eight to ten floret primordia. After the initiation of glume primordia the florets start to form. The lemma primordia are initiated first and then the axillary meristems differentiate to form the other floral structures. At the same time as the development of the spikelets proceeds the meristematic dome of the shoot apex continues to initiate more spikelets.

Leaf emergence and tillering also occur during the period TL-SE. Tiller buds arise from meristems in the axils of

leaves. A ridge of tissue is initiated and a swelling develops around its flanks to form the prophyll primordium. The growth and emergence of leaves and the growth and emergence of tillers are closely in phase with each other. The initiation of a tiller can be seen when the subtending leaf is fully expanded (Kirby and Fairs, 1970, 1972; Kirby and Riggs, 1978; Masle Meynard and Sebilotle, 1981). A tiller emerges when the third leaf following it has emerged so that tiller 2 emerges when leaf 5 emerges. Because of this ordered sequence of emergence of tillers, which is related to the number of leaves on the main shoot, a plant has a tillering potential which can be assessed and which under ideal conditions it will reach.

Usually all leaves will have been initiated by the start of tillering so that stress should have only a small effect on leaf number. The plant is producing spikelets and at the start of stem extension spikelet initiation ceases, so that stress should have a larger effect on total spikelet number. During TL-SE tillers are being produced so that stress at this time should also have a big effect on tiller production. Although leaf number is fixed, leaf area is increasing and that will also be affected by stresses.

2.24.2 Development during the period stem extension to booting

Stem extension starts from when the first node is detectable and when the ear is at the stamen initiation phase. The apex at this time is about 1.2 to 4 mm long. At this stage winter wheat has 11 to 13 leaves appeared, mid-winter wheat varieties 9 to 11 leaves and spring wheat varieties 8 to

10 leaves. During this period the florets mature in preparation for the final phase of the life cycle, grain filling and ripening. The embryo ears grow from about 3 mm long at the beginning of the phase to 80 mm long at anthesis. At the beginning of the phase the plant normally has produced its full complement of tillers, and the main shoot and each tiller has the potential to produce an ear. Therefore, at this point in the cycle of the plant the potential number of ears and spikelets per ear has been determined. In addition to the increase in the growth rate of the ear, stem growth starts at about the anther primordium stage, and occurs concurrently with ear growth. During this phase some of the developing ears die, and florets die in wheat. This may be due to the increase in the growth rate of the ears and stem, leaving insufficient resources (e.g. carbohydrate from photosynthesis or nitrogen compounds) to support the growth of all potential ears and florets. It is the smallest spikelets or florets with the lowest growth rate which are least able to compete for resources and it is these which die. Although a proportion of florets die in all cereal plants, stress due to such factors as drought, salinity, disease or excessive plant population will exacerbate the loss. Of central importance during this phase of growth and development is the role of certain cells in the anther and carpel which synchronously undergo meiosis and give rise to pollen in the anthers, and ovules in the embryo sac in the carpel. At meiosis the florets appear to be particularly vulnerable to stress. Experiments have shown that drought at this stage may lead to impaired development, floret sterility and reduction in grain

(Tottman and Makepeace, 1979; Kirby and Appleyard, 1981). Total number of spikelets is now fixed. Stress at this time influences the proportion of fertile and infertile spikelet - that is a decreased number of fertile and increased number of infertile spikelets. SE-BG is also normally a phase of tiller death and stress at this time may result in more tiller death. SE-BG is also a phase of rapid crop growth. Stress at this time can result in a large decrease in leaf area and dry matter production especially soluble carbohydrates in the stem and area of flag leaf, both of which are important for grain filling.

2.24.3 Development during booting to maturity

By this time most of the yield components are fixed, stress at this time should mainly affect yield by affecting grain growth. It should have relatively small effects on number of leaves and spikelets. At booting the rapidly growing ear is enclosed by the flag leaf sheath. It is easy to split open the leaf sheath and remove the ear. The meristematic dome has initiated nine floret primordia, the last of which is present only as a bump. The dome probably would not produce any more primordia. The glumes partially enclose the florets and the lemmas of florets 1 and 2 completely enclose the stamens and other structures. Small awns are present on lemmas 2 and 3. Stamen primordia are visible in the upper florets. Meiosis occurs during the green anther stage, when the anthers are about 1 mm long. Meiosis in the carpel and the anthers takes place at almost the same time. After completing this process anthers will turn a yellow colour. Anthesis occurs in all ears in the crop

within a few days. This can be clearly seen in open-flowering types where the crop has a mass of anthers hanging from the ears, and gaping florets. Following fertilization there is a period of very rapid cell division during which most of the cells of the endosperm are formed. Following this phase and overlapping it is a phase of cell growth and differentiation and deposition of starch in the endosperm. In parallel with the growth of the endosperm the fertilized egg cell gives rise by cell division to the embryo. At maturity this will already have formed the shoot apex and leaves and will comprise about 15% of the grain dry weight. During grain growth dry weight increases, slowly at first and then with a long period of almost constant growth rate. During the period of uniform growth the grain will be increasing in dry weight by about 1.5 mg per day. Finally the growth rate slows down to zero as the grain reaches maximum dry weight. Fresh weight also increases steadily at first but attains a maximum before the dry weight and then declines. During the period anthesis to harvest the leaves on the ear bearing shoots slowly senesce (Sofield et al., 1977; Vos, 1981).

CHAPTER 3

WATER STRESS EXPERIMENTS

3.1 INTRODUCTION

The experiments were conducted at Aber Farm, University College of North Wales, Bangor, U.K. There were two experiments. The first started in October 1987 and the second in October 1988. The main purpose of the experiments was to see the effect of water stress at three different stages on three different wheat varieties. Wheat varieties selected were of long, medium and short duration.

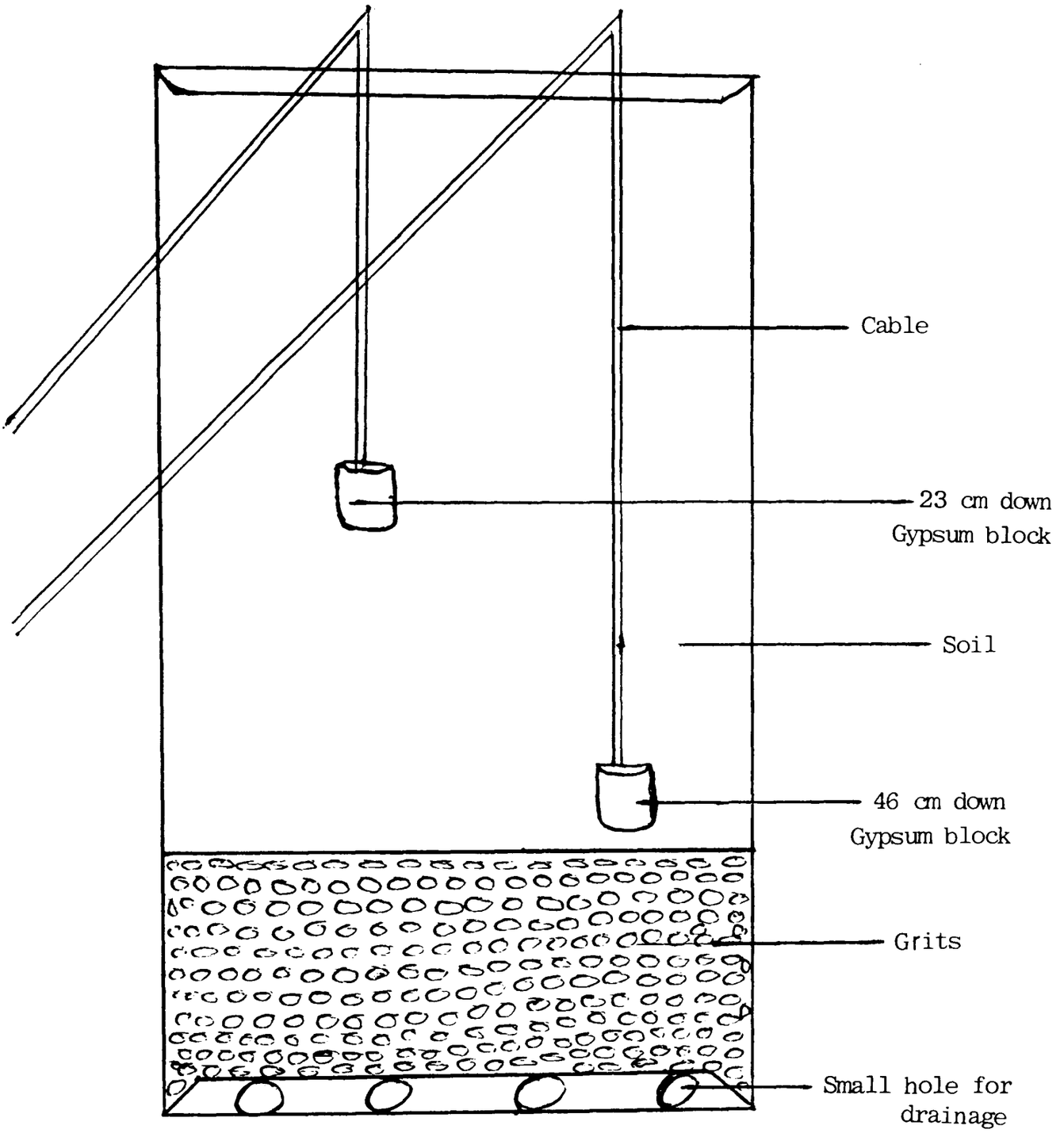
3.2 MATERIALS AND METHODS

Both experiments were conducted in an unheated glasshouse and did not use supplementary light.

3.2.1 Cultural conditions: The experiments were done in pots. Due to the limited number of pots available two sizes were used. Twenty four pots 40 cm x 40 cm square surface and 76 cm deep and 24 round pots 38 cm diameter and 56 cm deep were used. Pots of different sizes were allocated to the different blocks of the experiments. Large, deep pots were used in an attempt to create conditions suitable for root growth (Hurd, 1964, 1968).

In the bottom of the pots grit was placed to a depth of soil approximately 12 to 15 cm to clear a drainage system, as shown in Figure 1. In the first year field soil was used. Soil was collected from a field that had a previously grown spring barley and grass for silage and grazing. The soil type was the Denbigh series, which is a dark brown slightly stoney clay loam (Soil Survey of England and Wales 1984). In the second year peat was mixed in with the soil by proportion 2:3 by volume to improve the fertility and structure of the soil.

Figure 1. Large plastic pots used in water stress experiments



Plants were regularly watered when required, except during the water stress periods, when no water was applied. Three varieties were tested. They were: Norman, a winter wheat; Fenman, a winter wheat with a low vernalisation requirement; Wembley, a spring wheat. The seeds of Norman and Fenman were supplied by the Plant Breeding Institute, Cambridge, U.K. and the seed of Wembley was supplied from a commercial seed supplier. Details of sowing and harvesting dates of all treatments and varieties are shown in Table 1. Four water stress periods were tested: (1) From the start of tillering to the start of stem extension (first node detectable) (TL-SE); (2) From the start of stem extension to the start of booting (SE-BG); (3) From the start of booting to maturity (BG-MT); (4) Control (water as required). Growth stages were identified using the Zadoks Decimal Growth Stage Key (Zadoks et al., 1974). Watering was stopped when the appropriate stage was shown clearly in 75% of all plants. Rewatering started when the following stage was shown in 75% of all plants. The details of the periods of withholding water in all varieties with starting dates and stopping dates and total days under water stress are presented in the results section 3.3.2 (Table 6). In the second experiment during the stress period between stem extension and booting stage stressed plants of Norman and Fenman showed symptoms of severe water stress. To avoid death of these plants, they were given a small amount of water on two occasions.

3.2.2 Experimental design: A randomized complete block design was used in both experiments. The pots of different varieties were placed in separate, but adjacent parts of the

Table 1 Dates of sowing and harvesting and total number of days from sowing to harvest (in parentheses) for the three varieties of wheat and four treatments tested in water stress Experiments 1 and 2.

	varieties		
Experiment 1	Norman	Fenman	Wembley
Date of sowing	16.11.87	22.2.88	7.4.88
Dates of harvesting Water stress period			
Tillering to stem extension Total days	23.6.88 (220)	6.7.88 (135)	1.8.88 (117)
Stem extension to booting Total days	23.6.88 (220)	6.7.88 (135)	1.8.88 (117)
Booting to maturity Total days	12.6.88 (209)	23.6.88 (122)	13.7.88 (98)
Control Total days	23.6.88 (220)	6.7.88 (135)	1.8.88 (117)
Experiment 2 Date of sowing	22.10.88	20.2.89	8.4.89
Dates of harvesting Water stress period			
Tillering to stem extension Total days	29.6.89 (250)	14.7.89 (144)	28.7.89 (111)
Stem extension to booting Total days	29.6.89 (250)	14.7.89 (144)	28.7.89 (111)
Booting to maturity Total days	6.6.89 (227)	30.6.89 (130)	14.7.89 (97)
Control Total days	29.6.89 (250)	14.7.89 (144)	28.7.89 (111)

glasshouse to avoid shading of late sown plants (e.g. of Wembley) by early sown plants (e.g. of Norman). Blocks were located in similar positions inside the glasshouse. Four replications were used. In a block all pots were the same size.

3.2.3 Sowing: All varieties were sown at the same planting density of 300 plants per m^2. Before seed was sown the germination percentage was checked, using a germination incubator. For each variety 800 seeds at random were taken out from the seed bag. 100 seeds were put in each of eight petri dishes on moist filter paper and placed in an incubator set at 25°C. The petri dishes were checked regularly until no further germination was recorded. The mean germination percentage and S.E of the mean values of each variety are shown in Table 2. All varieties had a germination % of between 80 and 90%. As a precaution some extra seeds were sown in a small pot to fill gaps where seed had not germinated. Phosphorus and potassium as 0-24-24 compound fertilizer was mixed into the surface of the pots before sowing at the rate of 80 kg P_2O_5/ha and 80 kg K_2O/ha. The quantities required were calculated for each pot separately. 5.33 gram were applied to the large pots and 3.78 gram were applied to the small pots. Nitrogen fertilizer was applied as ammonium nitrate (34.5% N) to all pots at the rate of 200 kg N/ha. Half of this was applied at the start of tillering stage and the other half at the start of booting stage. 4.63 gram ammonium nitrate was added to the large pots and 3.28 grams to small pots. This practice was followed for all varieties.

3.2.4 Soil water content: Soil water content was measured

Table 2 Germination percentage of seeds of the different wheat varieties (Norman, Fenman and Wembley) used in both water stress and salinity Experiments 1 and 2.

	Mean of germination percentage	S.E.of mean
Experiment 1		
Norman	85.75	1.39
Fenman	86.25	1.28
Wembley	88.12	2.12
Experiment 2		
Norman	89.63	1.22
Fenman	87.88	1.30
Wembley	88.88	1.73

using gypsum resistance blocks (Model 5201, Soil Moisture Equipment Corporation, U.S.A.). In the first experiment there was one resistance block placed at a depth of 46 cm in the centre of all the pots in two blocks of the experiment. In Experiment 2, there were two resistance blocks placed at depths 46 cm and 23 cm in all pots in two blocks of the experiment. The gypsum resistance blocks were installed before germination but after sowing by using an auger to take out the soil. Resistance was measured weekly with a resistance bridge meter (Cat. No. 5500, Soil Moisture Equipment Corporation, U.S.A.), during the water stress stages. The relationship between bridge reading and soil water content was determined by equilibrating the blocks with soil of known water content in a plastic bowl. In the first experiment the relationship between soil water content and tension was determined using a pressure membrane apparatus shown as in Figure 2. It was not possible to repeat this in Experiment 2 due to malfunction in the equipment. Some workers have done gypsum block calibration by placing than in the pressure membrane apparatus and measuring the resistance under various pressures (Haise and Kelley 1946). Such calibration permits estimation of the metric potential of the soil from the resistance readings of the blocks. Therefore in these experiments the resistance blocks were calibrated using the same soil that was used for the gypsum blocks calibration curve (Kelley, 1944; Kelley et al., 1946; Aitchison et al., 1951; Knapp et al., 1952; Slatyer and McIlroy, 1961). The calibration curves are shown in Figures 3 and 4. In both experiments when soil moisture content (%) decreased, the gypsum block resistance reading was

Fig.2. Relationship between soil moisture content (%) and tension determined using pressure membrane apparatus

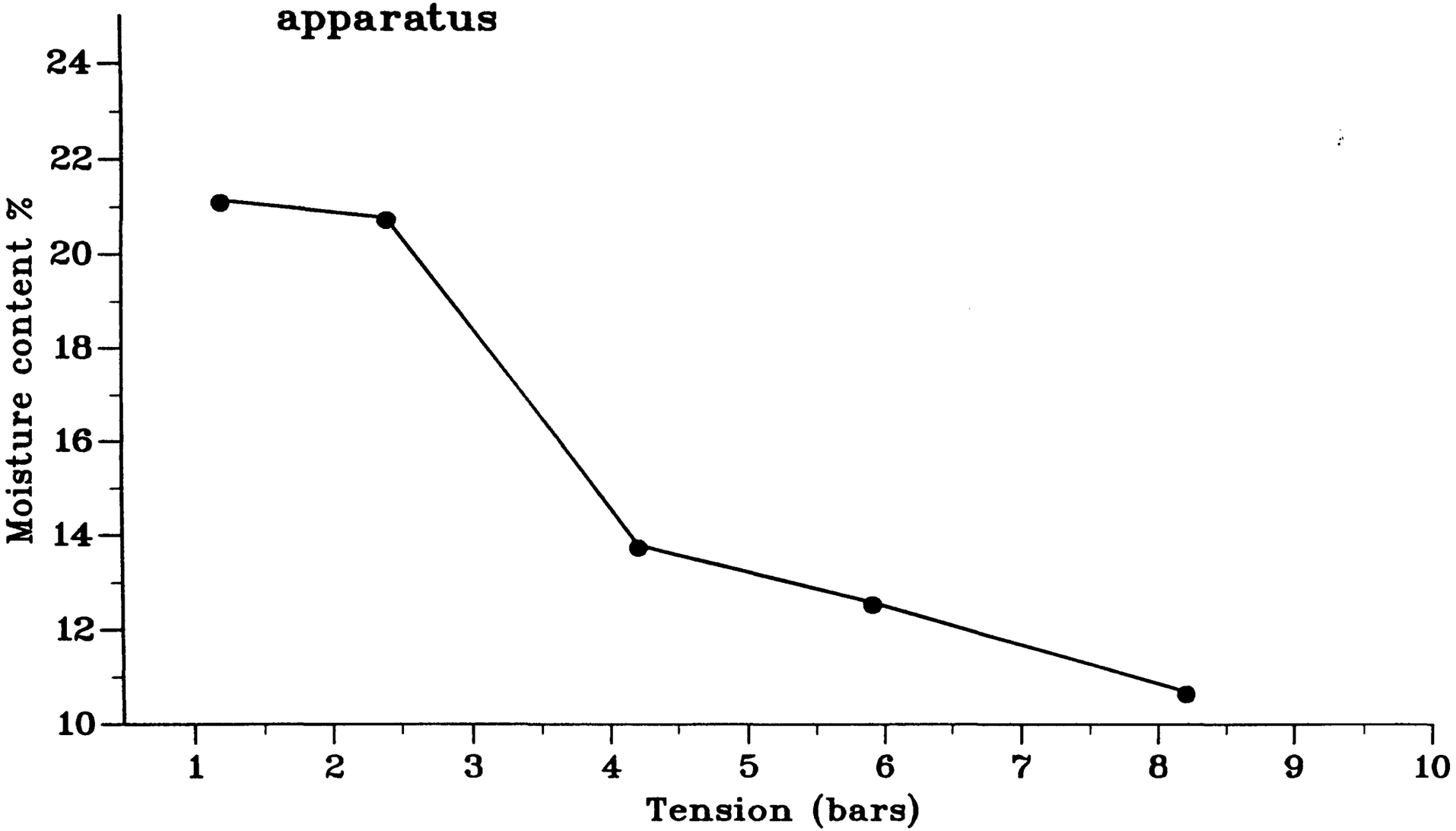


Fig.3: Relationship between soil moisture content % and resistance reading for field soil used in Experiment 1

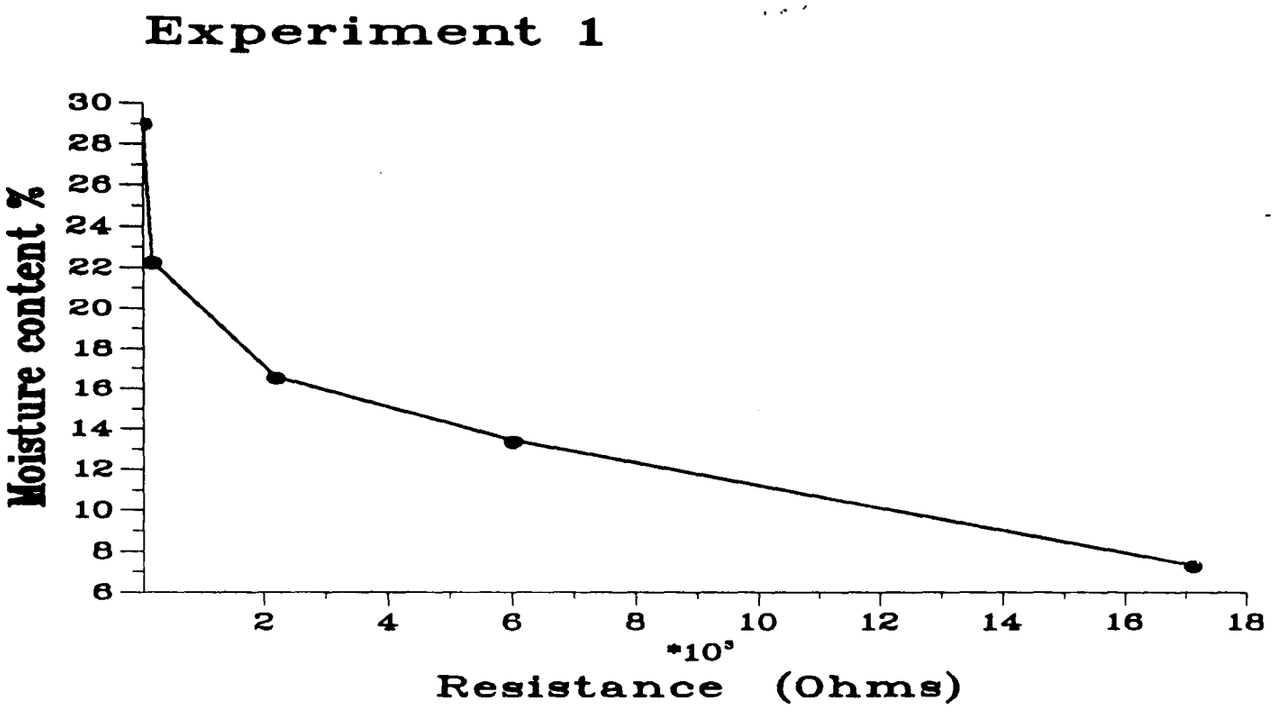
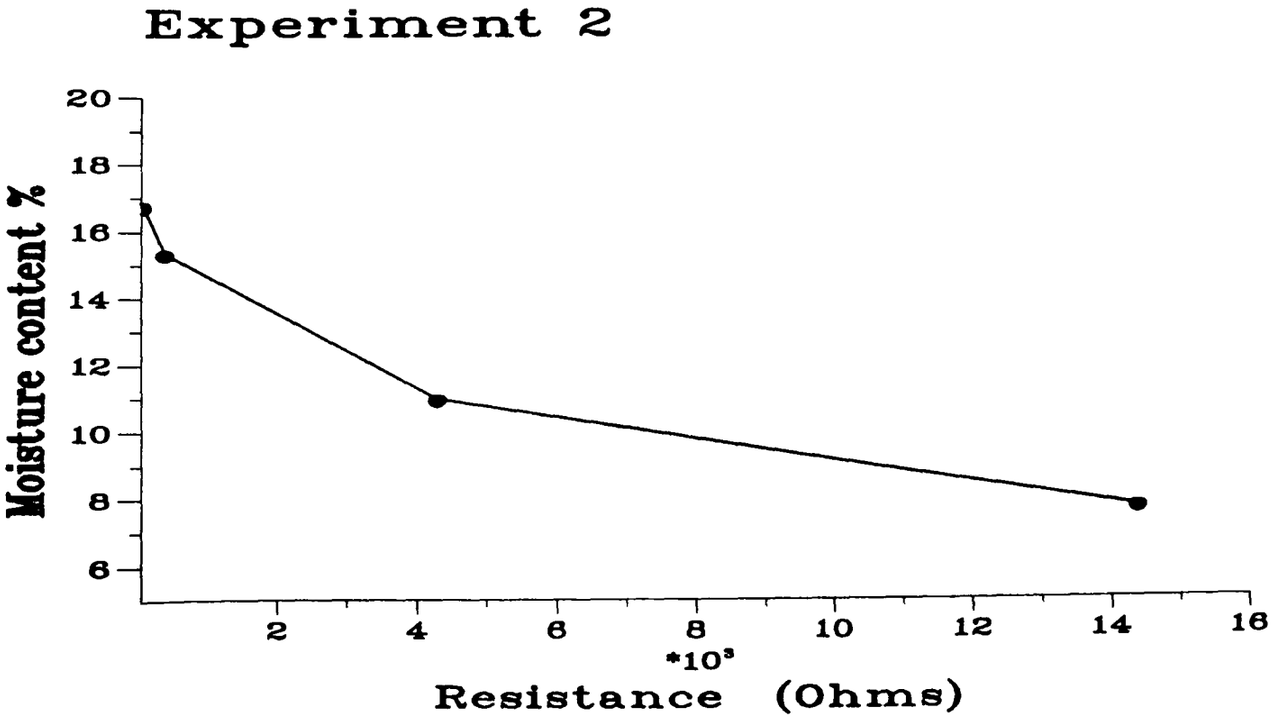


Fig.4: Relationship between soil moisture content % and resistance reading for mixed peat soil used in Experiment 2



increased. In Experiment 1 the maximum moisture % tested was 29% and the minimum resistance was 100 ohms. The lowest moisture % was 7% and the maximum gypsum block resistance reading was 1700 ohms. In Experiment 2, the trend was very similar, but soil moisture % was different because peat had been mixed with the soil. The maximum soil moisture tested was 17% and the minimum resistance was 100 ohms. The lowest moisture % tested was 7% and the maximum resistance reading was 1400 ohms. The curves were used to relate the gypsum block readings from the pots to soil moisture %.

3.2.5 Plant measurements

3.2.5.1 Leaf number: The total number of leaves appeared was counted on four fixed plants per pot at two week intervals. The third, fifth and seventh leaves were marked with white paint to help in recognizing leaf number.

3.2.5.2 Number of tillers: The total number of tillers was recorded on four fixed plants in each pot at two week intervals. One coloured plastic wire ring was placed on the main shoot to help in recognizing the plants. Plant height was measured on the same four plants at two week intervals.

3.2.5.3 Growth analysis: Destructive harvests for growth analysis were carried out at the end of each stress period and at anthesis. At each harvest four plants were removed from each pot. Plants were harvested systmatically starting from one side of the pot and working across the pot. Leaf area, stem area, ear area, dry weight and nitrogen % were recorded. Leaf area and stem area were measured in cm^2 using an automatic area meter (Model AAM-7, Hayashi Denkoh Co Ltd,

Tokyo, Japan). Ear area was determined from measurements of length and width multiplied by 2. It was assumed that only half of the ear would be lit at any one time, in the same way that calculation of leaf area includes only one leaf surface. To calculate total green leaf area per plant it was assumed that one surface of leaves, one surface of stems and two surfaces of ears intercepted light. To determine dry weight the plants were put in paper bags, and dried at 70 to 80°C for 2 to 3 days.

3.2.5.4 Soluble carbohydrate: After drying the material was ground to pass through a 2 mm sieve. Soluble carbohydrates were determined using the method of Deriaz (1961) and Thomas (1977).

3.2.5.5 Nitrogen analysis: The nitrogen % of dried ground plant material was determined using the Kjeldahl method (A.O.A.C., 1955).

3.2.5.6 Grain growth: Grain growth measurements started 14 days after anthesis and continued weekly until harvest. At each harvest two main shoot ears were removed from each pot of two replications. The ears were dried at 70 to 80°C in an oven for two to three days. The grains were threshed out, counted, then again dried and weighed to determine average grain weight. For each pot grain weight was plotted against time in days after anthesis. Rate of grain growth (mg/day) was determined as the slope of a linear regression ($y=mx+c$) fitted through the points of the linear phase of grain growth. Start of grain growth was determined by extrapolating the fitted regression back to zero grain weight. The end of grain growth was determined by extrapolating the fitted regression

line to grain weight at the final harvest. Rate and duration of grain growth were calculated separately for each sampled pot and effects of variety and water stress and variety and salinity were determined by putting these values into an analysis of variance. An example of the data from one pot of control treatment of Norman in the water stress Experiment 1, together with the fitted regression equation is shown in Figure 5. The calculation is shown below:

Days after anthesis	Average grain weight (mg)
14	16.37
21	29.30
28	40.18
35	44.50
42	55.89

From linear regression intercept (c)= -0.45. Slope (m) = +1.35

Start of grain growth = value of x at y = 0 = -c/m

= -(-0.45)/ 1.35 = 0.33 days after anthesis

End of grain growth = value of x at y = final weight

= y-c/m =55.89-(-0.45)/1.35 = 41.73 days after anthesis

Duration = End - start =41.73 -0.33 =41.40 days after anthesis

The values of the slope and intercept, for water stress experiment 1 together with their standard errors, are shown in Table 3. It can be seen that linear regression always gave a good fit to the data, and values of the linear correlation coefficient ranged between 0.97 and 1.00. A similar method has been used by other workers (Wright and Hughes, 1987a).

Fig.5. Relationship between average grain weight and time (days after anthesis) for one pot in water stress in Experiment 1

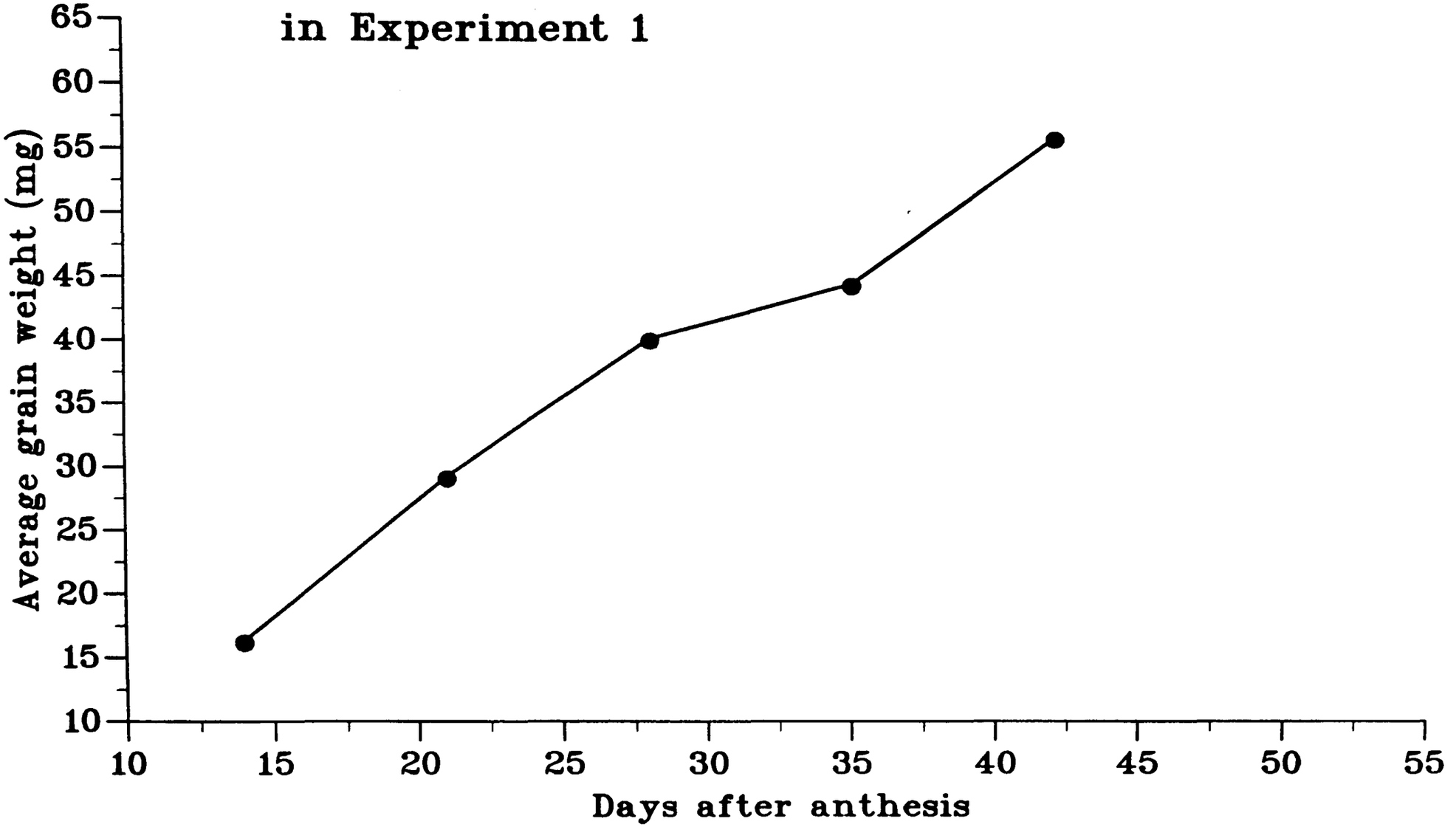


Table 3 Values of the slope, intercept and linear correlation coefficient in the relationship between average grain weight and time in days after anthesis.

Varieties and treatments	Slope	±S.E.	Intercept	±S.E.	R value
Replication 1					
Norman					
Tillering to stem extension	1.30	0.18	-1.62	5.43	0.97
Stem extension to booting	1.42	0.16	-2.63	4.76	0.98
Booting to maturity	1.00	0.21	+1.73	4.60	0.98
Control	1.37	0.11	-0.68	3.18	0.99
Fenman					
Tillering to stem extension	1.62	0.10	-12.00	2.59	0.99
Stem extension to booting	1.84	0.16	-13.70	4.03	0.99
Booting to maturity	1.56	0.02	-6.47	0.46	1.00
Control	1.95	0.01	-14.20	0.32	1.00
Wembley					
Tillering to stem extension	1.20	0.12	-1.40	3.15	0.99
Stem extension to booting	1.32	0.10	-2.45	2.35	0.99
Booting to maturity	1.20	0.03	+1.32	0.59	0.99
Control	1.25	0.03	+1.55	0.69	0.99
Replication 2					
Norman					
Tillering to stem extension	1.21	0.10	-1.60	2.86	0.99
Stem extension to booting	1.15	0.17	+2.98	4.99	0.97
Booting to maturity	1.17	0.15	-1.46	3.23	0.99
Control	1.35	0.12	-0.45	3.43	0.99
Fenman					
Tillering to stem extension	1.83	0.13	-12.40	3.22	0.99
Stem extension to booting	1.63	0.10	-9.24	2.59	0.99
Booting to maturity	1.30	0.97	-0.99	2.10	0.99
Control	1.78	0.24	-11.20	6.09	0.98
Wembley					
Tillering to stem extension	1.28	0.17	-2.46	4.40	0.98
Stem extension to booting	1.26	0.10	+0.35	2.58	0.99
Booting to maturity	1.40	0.26	-2.41	5.66	0.98
Control	1.35	0.15	-4.13	3.83	0.99

3.2.5.7 Yield and yield components

Approximately 30 plants were remaining in the large pots and 15 plants were remaining in small pots. These were harvested at maturity to determine yield and yield components. All ears were counted. The number of fertile and infertile spikelets were counted on a random sample of ten ears per pot. Straw length was measured on a random sample of 10 stems per pot. Ear and straw dry weight were recorded by drying in an oven at 70-80^{o}C for 2 to 3 days. The ears were threshed using a small scale threshing machine. Number of grains was determined using an electronic seed counter (Numigral Tecator Hogames, Sweden). The grains and straw were then ground, and the ground material was used to determine nitrogen % using the Kjeldahl method (A.O.A.C., 1955). Grain weight per plant, number of grains per plant, number of ears per plant, number of fertile and infertile spikelets per ear, number of grains per ear, number of grains per spikelet, harvest index, and average grain weight were calculated.

3.2.6 WEATHER RECORD

Daylength was obtained from tables of the Smithsonian Institute (Anon, 1966). Hours of bright sunshine were recorded at a field site, approximately 800 meter from the glasshouse. Maximum and minimum temperatures inside the glasshouse were recorded daily using a thermometer.

3.2.7 USE OF PESTICIDE AND INSECTICIDE

The plants were regularly checked. Powdery mildew and aphids were the main problems attacking the plants. It was

noticed that sometimes pests were first attacking the stressed plants. As soon as plants became affected, they were sprayed. The fungicide fenpropimorph (Mistral, Rhone and Poulenc) was used to control powdery mildew and dimethoate systemic insecticide (Murphy's insecticide, Rhone and Poulenc) was used to control aphids. Both chemicals were applied the recomendad rate and in the recommendad amount of water according to the manufactuer's recommendations.

3.3 RESULTS

3.3.1 WEATHER CONDITIONS EXPERIENCED DURING THE EXPERIMENTS

Daylength, hours of bright sunshine and mean temperature were calculated for each experiment from 20 October, just before the earliest sowing of Norman was made.

3.3.1.1 Daylength: Weekly average daylength is shown in Figure 6. Daylength decreased until 10 weeks. During this time daylength was only 8 hours and then it increased and the highest average daylength was 18 hours.

3.3.1.2 Average hours of bright sunshine:

Weekly averages of daily hours of bright sunshine are shown in Figure 7. In both years the trend was very similar. In the first year, 1987-88, hours of bright sunshine fluctuated between 0 to 4 hours up to 20 weeks. Then it increased and the highest recorded sunshine hours was 9 to 10 hours, which was after 25 weeks. In Experiment 2, 1988-89, the trend was very similar, sun hours fluctuated between 0 to 5 hours up to 20 weeks.

3.3.1.3 Weekly average of daily temperature during growing season

Both water stress and salinity experiments in 1987-88 were planted in the same glasshouse and experienced the same average weekly temperatures, which are shown in Figure 8. In these experiments, temperature was fluctuating between 5^{o}C and 10^{o}C up to 17 weeks. After 17 weeks it increased up to 25^{o}C.

Weekly averages of daily temperatures recorded in the glasshouse during 1988-89 water stress Experiment 2 are shown in Figure 9. The average temperature was fluctuating between 7 and 15^{o}C up to 25 weeks. It then increased up to a maximum

Fig.6. Average weekly day length (hours) for both water stress and salinity Experiments 1 and 2

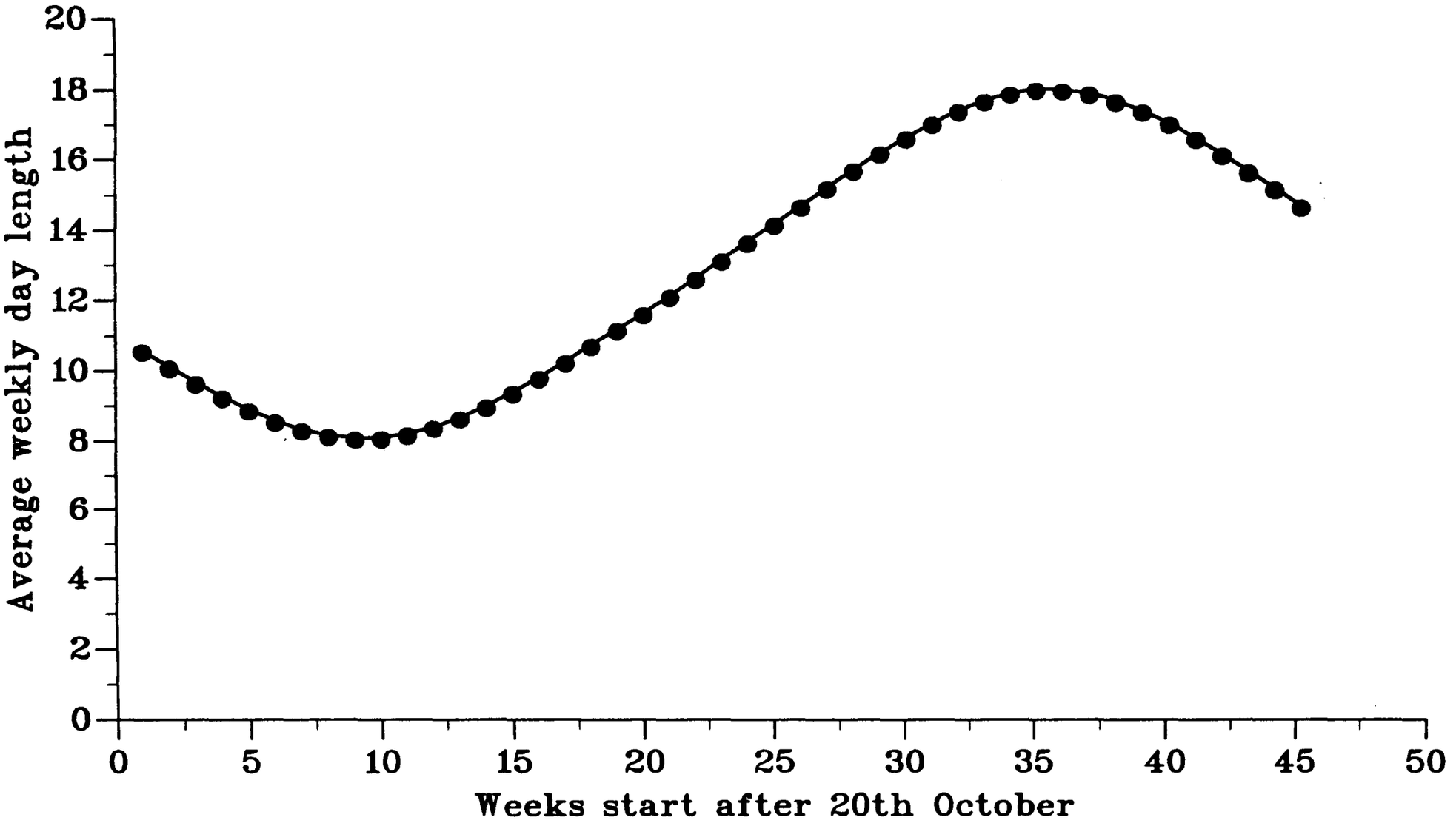
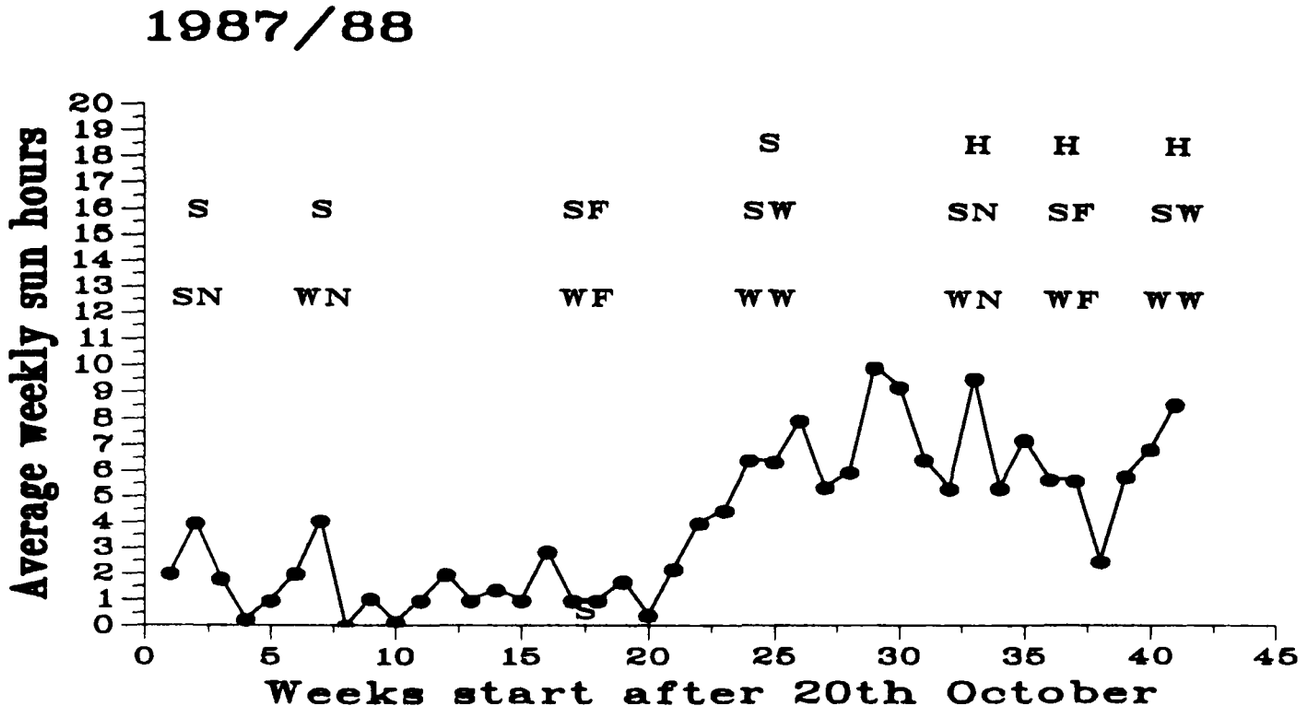
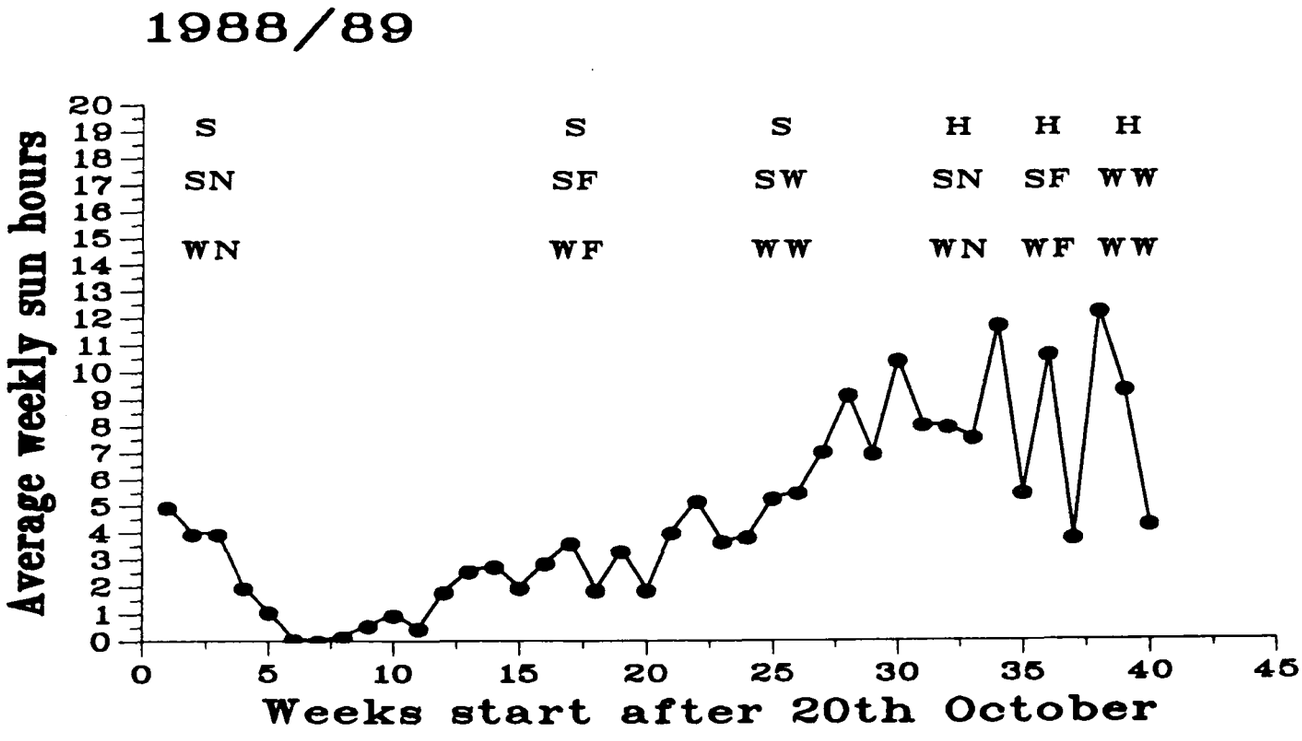


Fig.7: Average weekly hours of bright sunshine during growing of varietes in both water stress and salinity Experiments 1 and 2.





WN, WF, WW = Norman, Fenman and Wembley in water stress Experiment

SN, SF, SW = Norman, Fenman and Wembley in Salinity Experiment

S = Sowing; H = Harvesting

Fig.8. Average weekly temperature during growing varieties in both water stress and salinity Experiment 1

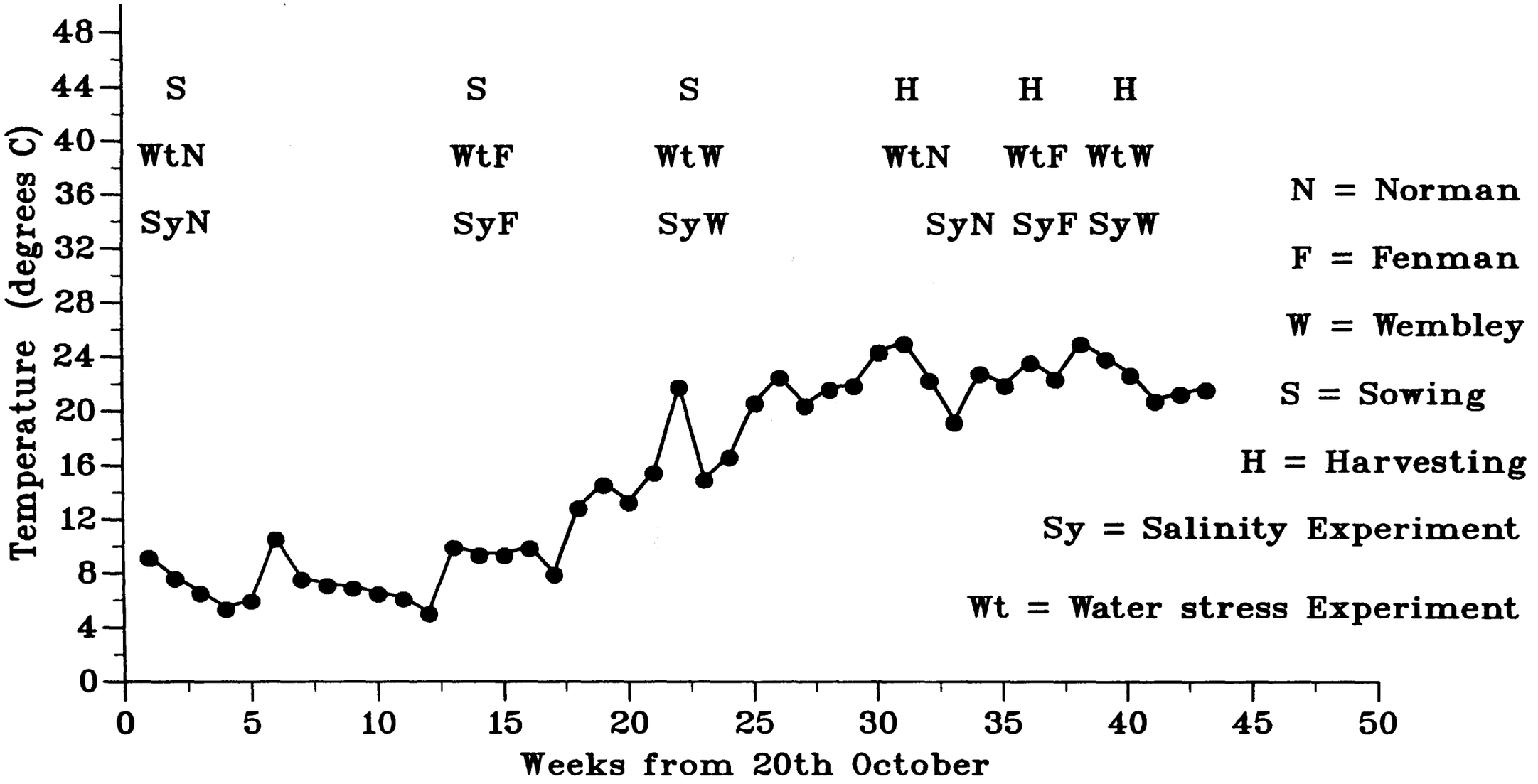
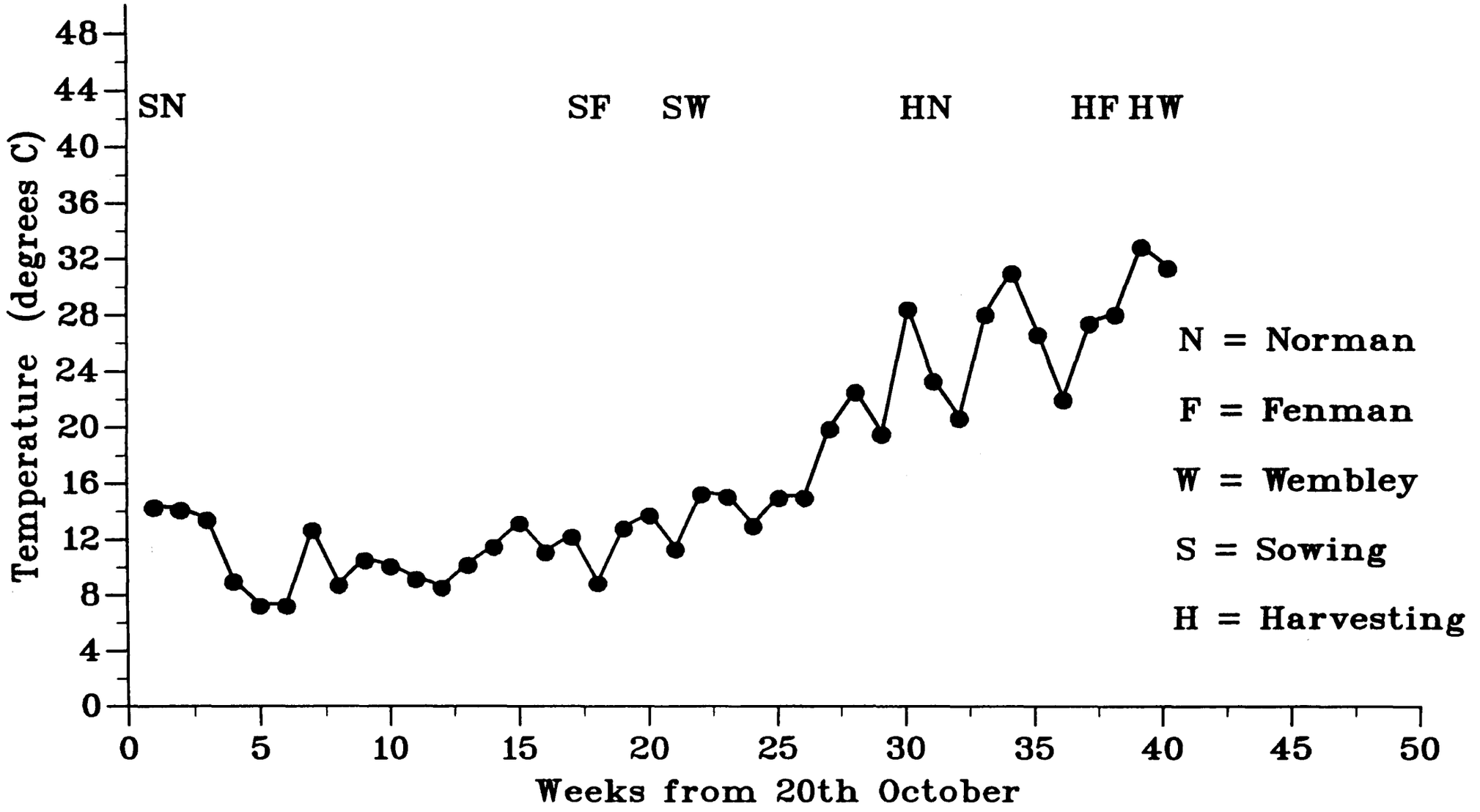


Fig.9. Average weekly temperature during growing varieties in water stress Experiment 2



of 34°C. After 30 weeks it was always above 22°C.

In both years in both experiments, the trend of temperature was very similar, for the water stress and for the salinity experiments. Norman variety was sown early and it experienced low temperatures during its early growth. Fenman also experienced low temperature but for a shorter period than Norman. Wembley variety was grown, when temperatures were higher and all the time above 20°C.

3.3.1.4 Average daily hours of bright sunshine at different stages

Average daily hours of bright sunshine during stress periods for the water stress and salinity Experiments 1 and 2, are shown in Table 4. In Experiments 1 and 2, in Norman, there were few bright sun hours during the stress period TL-SE. Average hours of bright sunshine were much higher in the later stress periods, and for the other varieties. Average hours of bright sunshine during the stress period BG-MT were similar for all varieties. The average hours of bright sunshine during the whole growth period were higher in Experiment 2 than in Experiment 1, and especially during the stress period BG-MT. The general trend was that the short duration varieties and later stress periods experienced longer hours of bright sunshine.

3.3.1.5 Average temperature at different stages

Table 5 shows the average temperatures experienced by each variety during the stress periods for water stress Experiments 1 and 2.

In both years the average temperatures experienced by Norman during TL-SE were approximately half those experienced

Table 4 Average hours of bright sunshine per day during stress periods in water stress and salinity Experiments 1 and 2.

	Varieties		
Stress period	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	1.45	6.34	7.13
Stem extension to booting	5.34	7.35	8.59
Booting to maturity	7.38	7.21	6.65
Control	3.61	5.33	6.73
Experiment 2			
Tillering to stem extension	1.75	4.92	8.44
Stem extension to booting	4.44	8.90	8.40
Booting to maturity	8.32	8.60	8.53
Control	4.08	6.43	7.65

Table 5 Average temperatures (^{o}C) experienced by each variety during stress periods in water stress Experiments 1 and 2.

	Varieties		
Stress period	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	11.05	18.86	20.25
Stem extension to booting	16.61	20.12	21.22
Booting to maturity	22.11	22.79	22.59
Control (whole growth period)	13.26	17.65	21.23
Experiment 2			
Tillering to stem extension	10.67	16.98	23.76
Stem extension to booting	14.97	23.76	22.25
Booting to maturity	23.16	25.54	26.52
Control (whole growth period)	15.35	19.36	24.06

by Wembley. The average temperatures experienced during SE-BG were also much lower for Norman than for Fenman and Wembley. Average temperatures experienced during BG-MT were similar for all varieties. Over the whole growth period the average temperature experienced increased as the duration of the variety decreased. Average temperatures were also higher in Experiment 2 than in Experiment 1.

3.3.2 DATES OF WATER STRESS STARTING AND STOPPING PERIOD

In these experiments comparing each variety at each stage the stress periods were longer in Norman than in the other varieties, except for BG-MT in Experiment 2 as shown in Table 6. This was because Norman was sown earlier and experienced cold temperatures and shorter days during its development. For the stages TL-SE and SE-BG Norman took a longer time in Experiment 2 than in Experiment 1, because of the earlier sowing, and plants reached the start of these stages earlier when temperature lower and days were shorter. For Fenman the period TL-SE was longer in Experiment 2 than in Experiment 1 due to lower temperature. In Wembley the period TL-SE was shorter in Experiment 2 than in Experiment 1 due to higher temperature. In both years in Fenman and Wembley the length of the periods SE-BG and BG-MT were similar. The period from SE-BG was shorter period than TL-SE and BG-MT, but not in Norman in Experiment 2. In both years in Fenman and Wembley the stress period SE-BG was very short and shorter than in Norman.

3.3.3 SOIL MOISTURE CONTENT

In Experiments 1 and 2 water stress at TL-SE had a much

Table 6 Dates of starting and stopping water stress and total days under stress at each stage for each variety in Experiments 1 and 2 *

	Stages		
	Tillering to stem extension	Stem extension to booting	Booting to maturity
Experiment 1			
Norman			
Date stress started	8.2.88	5.4.88	2.5.88
Date stress stopped	5.4.88	2.5.88	12.6.88
Total days under stress	57	27	41
Fenman			
Date stress started	5.4.88	30.4.88	15.5.88
Date stress stopped	30.4.88	15.6.88	23.6.88
Total days under stress	25	15	39
Wembley			
Date stress started	28.4.88	19.5.88	29.5.88
Date stress stopped	19.5.88	29.5.88	13.7.88
Total days under stress	21	11	39
Experiment 2			
Norman			
Date stress started	7.12.88	3.3.89	2.5.89
Date stress stopped	3.3.89	2.5.89	6.6.89
Total days under stress	86	60	34
Fenman			
Date stress started	3.4.89	9.5.89	22.5.89
Date stress stopped	9.5.89	22.5.89	30.6.89
Total days under stress	36	14	39
Wembley			
Date stress started	9.5.89	25.5.89	5.6.89
Date stress stopped	25.5.89	5.6.89	14.7.89
Total days under stress	17	12	39

* The control plants were not water stressed.

smaller effect on soil moisture % in Norman than in Fenman and Wembley as shown in Tables 7 to 9. As the soil dried out then the resistance readings became high and out of range of the original calibration (Figure 3 and 4). In these cases estimated values of soil moisture percentage were calculated assuming that moisture content decreased linearly with resistance reading. These values are shown in the table in parentheses. In Norman moisture % decreased slowly. In Fenman and Wembley it decreased much more quickly. The final moisture % reached was lower in Fenman than in Norman and Wembley in Experiment 1. In Experiment 2 the final % reached was much lower in Wembley than in Fenman and Norman. In Experiment 2 in Norman and Fenman water stress at TL-SE decreased moisture % more at 23 cm than at 46 cm. In Experiment 1 in Fenman water stress at TL-SE started to decrease soil moisture % after the first week and it reached a soil moisture content of 15.05%. In Experiment 2 the gypsum block at 46 cm started to show decreased soil moisture % after the fourth week and it reached a soil moisture content of 13.00%. The gypsum block at 23 cm gave a lower moisture content of 9.15% in the last week of the stress period. In Experiment 1, in Wembley water stress at TL-SE decreased soil moisture % only in the last week. In Experiment 2 the gypsum block placed at 46 cm started to give a lower soil moisture reading after the third week. In the fourth week it showed a moisture content of 1.68%. The gypsum block at 23 cm down showed a very rapid decrease in soil moisture % after the second week. In the control all varieties had a similar soil moisture % at all stages and there were no differences during

Table 7 Soil moisture % during stress periods in Experiment 1. (Gypsum block placed 46 cm down). Each value is the mean of two Gypsum blocks.

Varieties	Norman		Fenman		Wembley	
Stress period	TL-SE	Control	TL-SE	Control	TL-SE	Control
Weeks after start of stress period						
1	28.7	28.5	28.0	28.2	28.0	28.0
2	28.7	28.5	26.0	27.6	28.0	28.0
3	24.0	27.5	23.9	27.6	28.0	28.0
4	23.6	27.1	16.0	28.0	19.8	28.0
5	23.0	28.0	15.0	27.6	-	-
6	21.5	27.2	-	-	-	-

Varieties	Norman		Fenman		Wembley	
Stress period	SE-BG	Control	SE-BG	Control	SE-BG	Control
Weeks after start of stress period						
1	27.8	28.0	28.0	27.0	24.3	28.5
2	26.6	27.6	24.9	26.5	20.3	28.7
3	20.9	27.1	22.5	26.7	-	-
4	17.3	28.0	-	-	-	-
5	8.5	27.3	-	-	-	-
6	*	-	-	-	-	-

Varieties	Norman		Fenman		Wembley	
Stress period	BG-MT	Control	BG-MT	Control	BG-MT	Control
Weeks after start of stress period						
1	19.1	24.9	22.7	24.0	25.0	28.7
2	14.5	21.7	19.2	26.4	21.1	25.2
3	7.2	26.6	12.5	24.0	13.1	23.6
4	*	*				

* No resistance reading after this week due to extreme drying of soil.

Table 8 Soil moisture % during stress periods in Experiment 2. (Gypsum block placed 46 cm down) Each value is the mean of two Gypsum blocks.

Varieties	Norman		Fenman		Wembley	
Stress period	TL-SE	Control	TL-SE	Control	TL-SE	Control
Weeks after start of stress period						
1	16.4	16.4	16.4	16.5	16.4	16.4
2	16.4	16.4	16.4	16.4	16.4	16.4
3	16.4	16.4	16.4	16.4	10.2	16.4
4	16.4	16.4	16.4	16.4	(1.7)	16.4
5	16.4	16.4	15.9	16.4	-	-
6	16.4	16.5	13.0	16.4	-	-
7	16.4	16.4	-	-	-	-
8	16.4	16.4	-	-	-	-
9	16.1	16.4	-	-	-	-
10	16.1	16.4	-	-	-	-
11	15.0	16.4	-	-	-	-
12	13.3	16.4	-	-	-	-

Varieties	Norman		Fenman		Wembley	
Stress period	SE-BG	Control	SE-BG	Control	SE-BG	Control
Weeks after start of stress period						
1	16.4	16.4	15.1	16.4	15.4	16.4
2	16.4	16.4	12.2	16.4	10.2	16.4
3	16.4	16.4	*	16.4	(4.1)	16.4
4	14.0	16.4	-	-	-	-
5	(1.4)	16.4	-	-	-	-
6	(0.8)	16.4	-	-	-	-
7	*	16.4	-	-	-	-
8	*	16.4	-	-	-	-
9	*	16.4	-	-	-	-
10	*	16.4	-	-	-	-

Varieties	Norman		Fenman		Wembley	
Stress period	BG-MT	Control	BG-MT	Control	BG-MT	Control
Weeks after start of stress period						
1	16.4	16.4	15.2	16.00	16.0	16.4
2	14.2	16.4	(3.3)	16.00	14.3	16.4
3	(4.4)	16.4	*	16.00	9.3	16.5
4	*	16.4	*	16.00	8.3	16.4
5	*	16.4	-	-	(1.1)	16.5
6	*	16.4	-	-	*	16.3

* No resistance reading after this week due to extreme drying of soil

Table 9 Soil moisture % during stress periods in Experiment 2. (Gypsum block placed 23 cm down). Each value is the mean of two Gypsum blocks.

Varieties	Norman		Fenman		Wembley	
Stress period	TL-SE	Control	TL-SE	Control	TL-SE	Control
Weeks after start of stress period						
1	16.4	16.4	16.4	16.4	16.4	16.4
2	16.4	16.4	16.4	16.4	14.9	16.4
3	16.4	16.4	16.4	16.4	(0.8)	16.4
4	16.4	16.4	16.0	16.4	*	16.4
5	16.4	16.4	14.0	16.4	-	-
6	16.4	16.4	9.1	16.4	-	-
7	16.4	16.4	-	-	-	-
8	16.0	16.4	-	-	-	-
9	15.2	16.4	-	-	-	-
10	14.1	16.4	-	-	-	-
11	9.3	16.4	-	-	-	-
12	8.3	16.4	-	-	-	-

Varieties	Norman		Fenman		Wembley	
Stress period	SE-BG	Control	SE-BG	Control	SE-BG	Control
Weeks after start of stress period						
1	16.4	16.4	14.3	16.4	15.1	16.4
2	16.4	16.4	(1.0)	16.4	8.4	16.4
3	13.5	16.4	*	16.4	(1.1)	16.4
4	(1.0)	16.4	-	-	-	-
5	*	16.4	-	-	-	-
6	*	16.4	-	-	-	-
7	*	16.4	-	-	-	-
8	*	16.4	-	-	-	-
9	*	16.4	-	-	-	-
10	*	16.4	-	-	-	-

Varieties	Norman		Fenman		Wembley	
Stress period	BG-MT	Control	BG-MT	Control	BG-MT	Control
Weeks after start of stress period						
1	16.2	16.4	15.1	16.4	16.4	16.4
2	11.0	16.4	(3.2)	16.4	13.1	16.4
3	*	16.4	*	16.4	(1.0)	16.4
4	*	16.4	*	16.4	*	16.4
5	*	16.4	-	-	-	-
6	*	16.4	-	-	-	-

* No resistance reading after this week due to extreme drying of soil.

the growth periods.

In Experiment 1, in Norman water stress at SE-BG started to decrease soil moisture % after the second week and the readings were out of range after the sixth week. In Experiment 2 the gypsum block at 46 cm depth showed a decreased soil moisture % after the fourth week and the readings were out of range after the seventh week. In Experiment 2 at 23 cm soil moisture % decreased after the second week and the readings were out of range after the fifth week. In Experiment 1 in Fenman water stress at SE-BG, decreased soil moisture % after the first week. In the last week of the stress period soil moisture was 22.75%. In Experiment 2 in Fenman water stress at SE-BG decreased soil moisture % in the second week. In the third week the readings were out of range. In Fenman water stress at SE-BG rapidly decreased moisture content at 23 cm depth and after the second week the readings were out of range. In Experiment 1 in Wembley water stress at SE-BG slightly decreased soil moisture % in the second week. In Experiment 2 in Wembley water stress at SE-BG started to decrease moisture % after the second week. By the last week it had declined to 4.08%. In Wembley water stress at SE-BG in Experiment 2 decreased soil moisture content at 23 cm depth, in the second week. Moisture % was 1.11 in the third week. In both experiments in all varieties water stress at BG-MT, rapidly depleted soil moisture and the readings were out of range in the fourth week.

3.3.4 NUMBER OF LEAVES APPEARED ON THE MAIN STEM

The effects of variety on the number of leaves appeared on the main stem are shown in Figure 10.

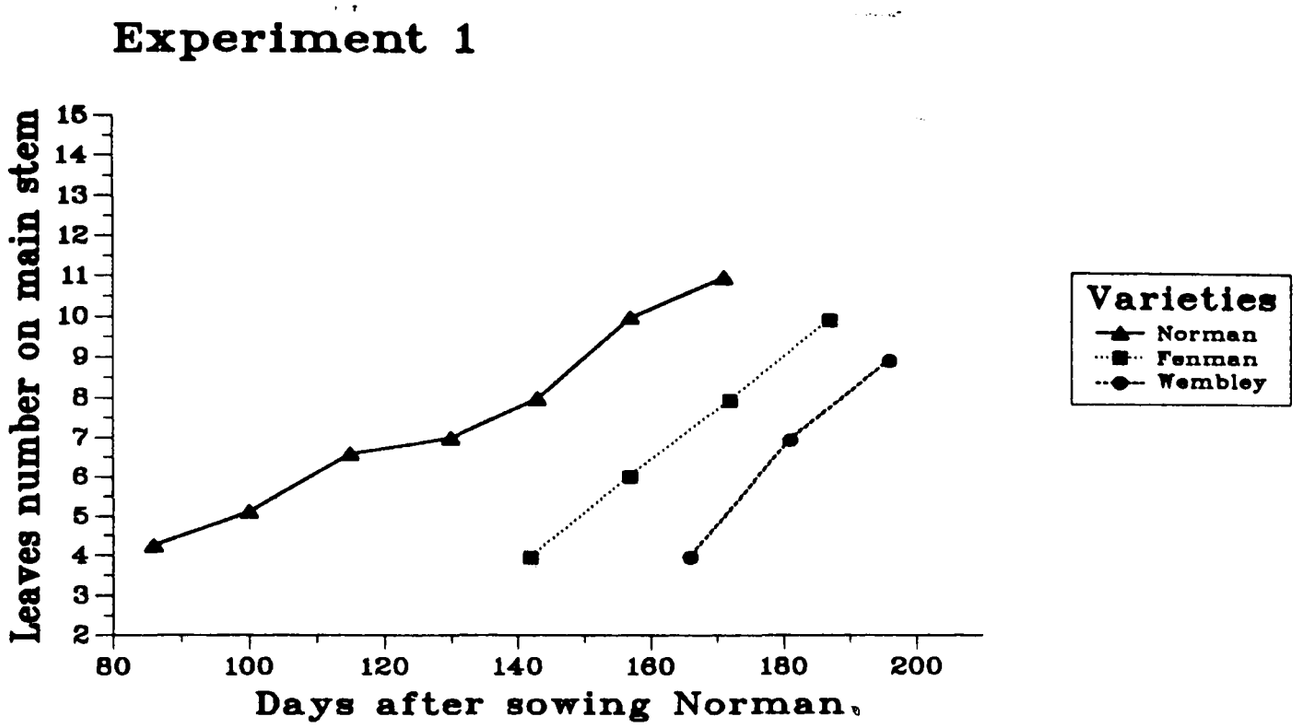
In Experiment 2 water stress at SE-BG resulted in a small but significant decrease in the number of leaves appeared on the main stem. Norman had a greater number of leaves on the main stem than Fenman and Wembley in the control. In both years in Norman, leaf appearance took 170-180 days. In Fenman it took 80 to 100 days and in Wembley 50 to 60 days. During growing of Norman, there was lower temperature from germination to stem extension, and it took a long time for leaves to appear. During growing of Fenman it was mid winter from germination to stem extension, and it was very cold up to time of tiller appearance. After that time temperature increased and the leaves appeared steadily in Fenman. In Wembley all leaves appeared very quickly due to higher temperature and short duration variety.

3.3.5 NUMBER OF SHOOTS PER PLANT

The general pattern of tillering was that plants produced between 2 and 5 shoots shown in Figure 11 to 13. After maximum number of shoots was reached some shoots died. However it was noted that fewer shoots died in the control treatments as shown in Figures 12 to 13.

Generally all stress treatments decreased the number of shoots in all varieties. In some cases shoot number were decreased by the end of the stress period and in some cases shoot number started to decrease at the start of the stress period. It was dependent on temperature, plant height and

Fig.10: Number of leaves appeared on main stem of control plants in water stress Experiments 1 and 2



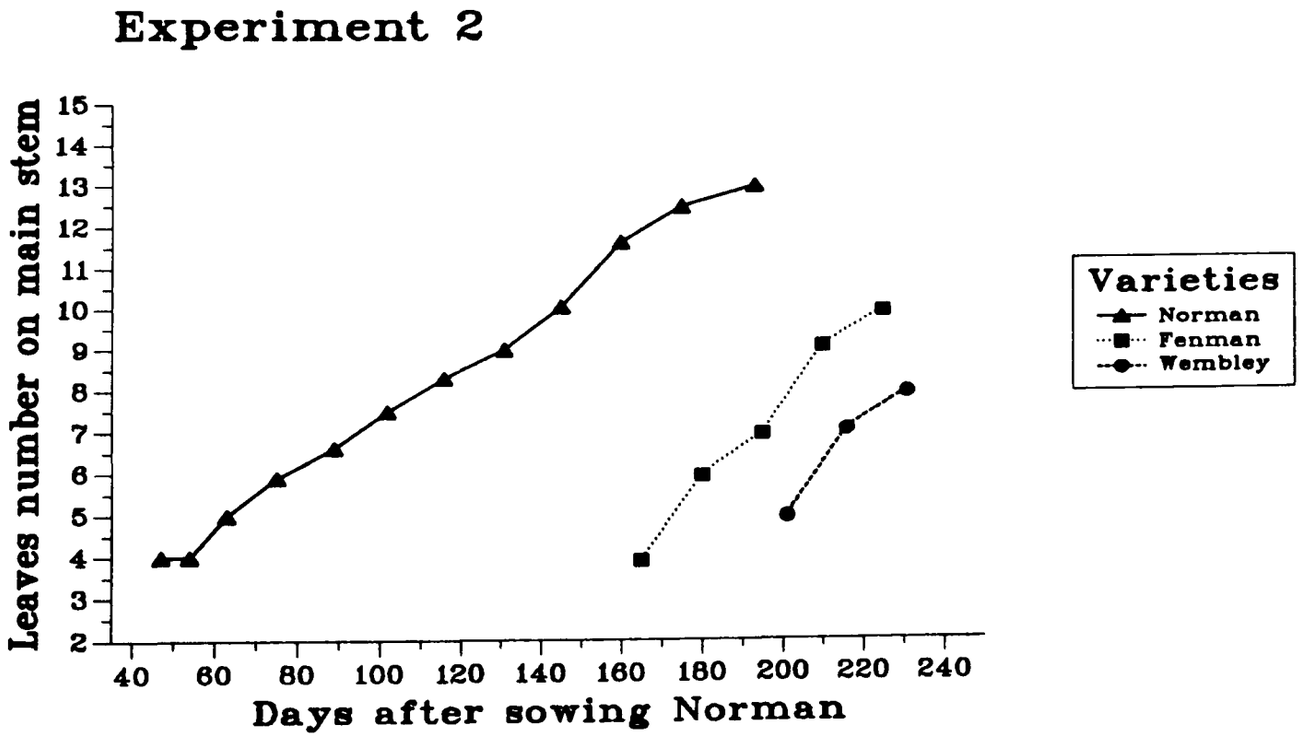
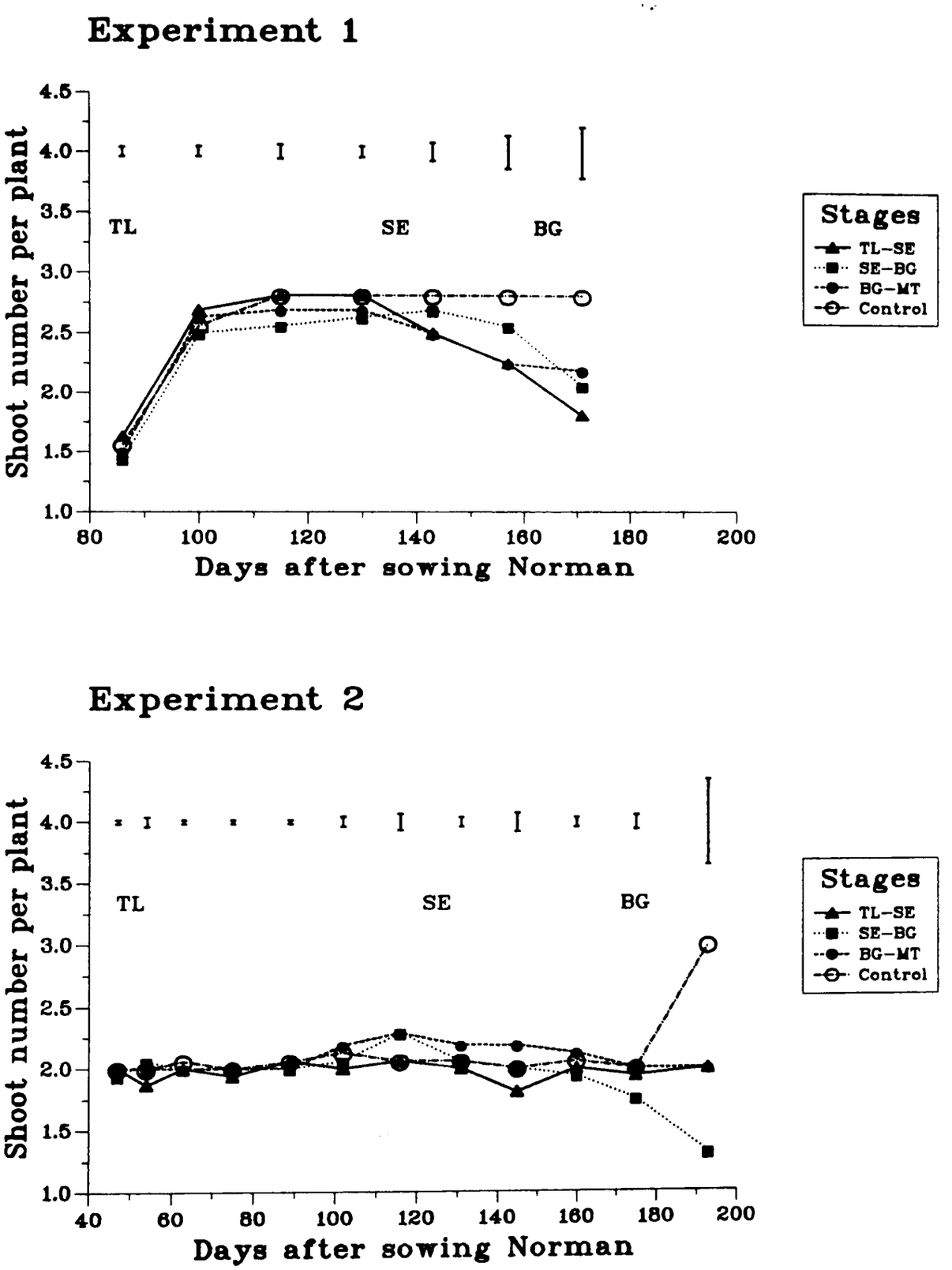


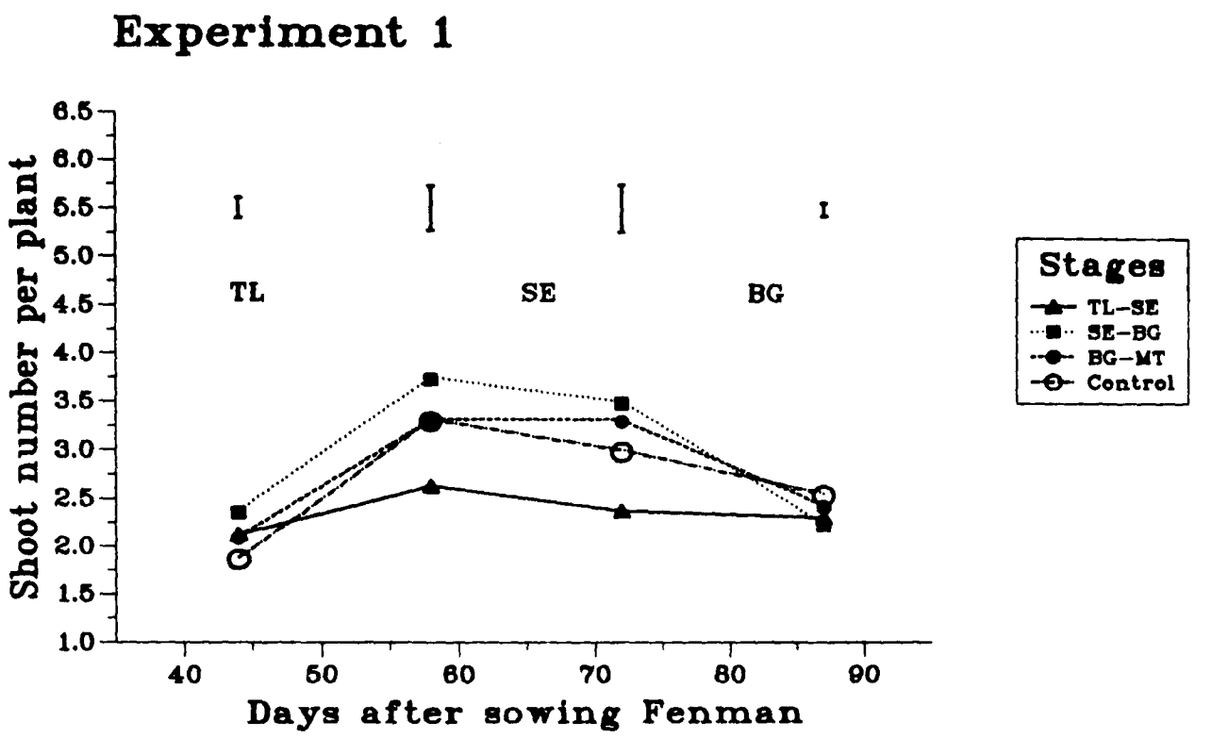
Fig.11: Effect of water stress on shoot number per plant in Norman variety in water stress Experiment 1 and 2.

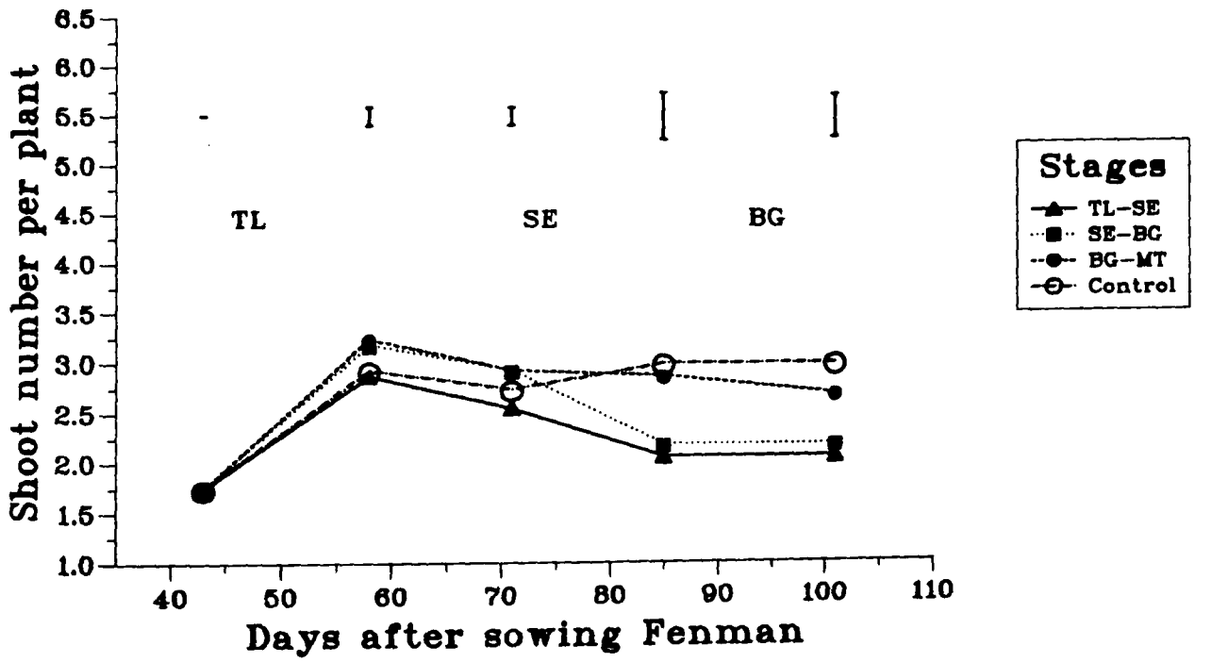


TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

Fig.12: Effect of water stress on shoot number per plant in Fenman variety in water stress Experiment 1 and 2.

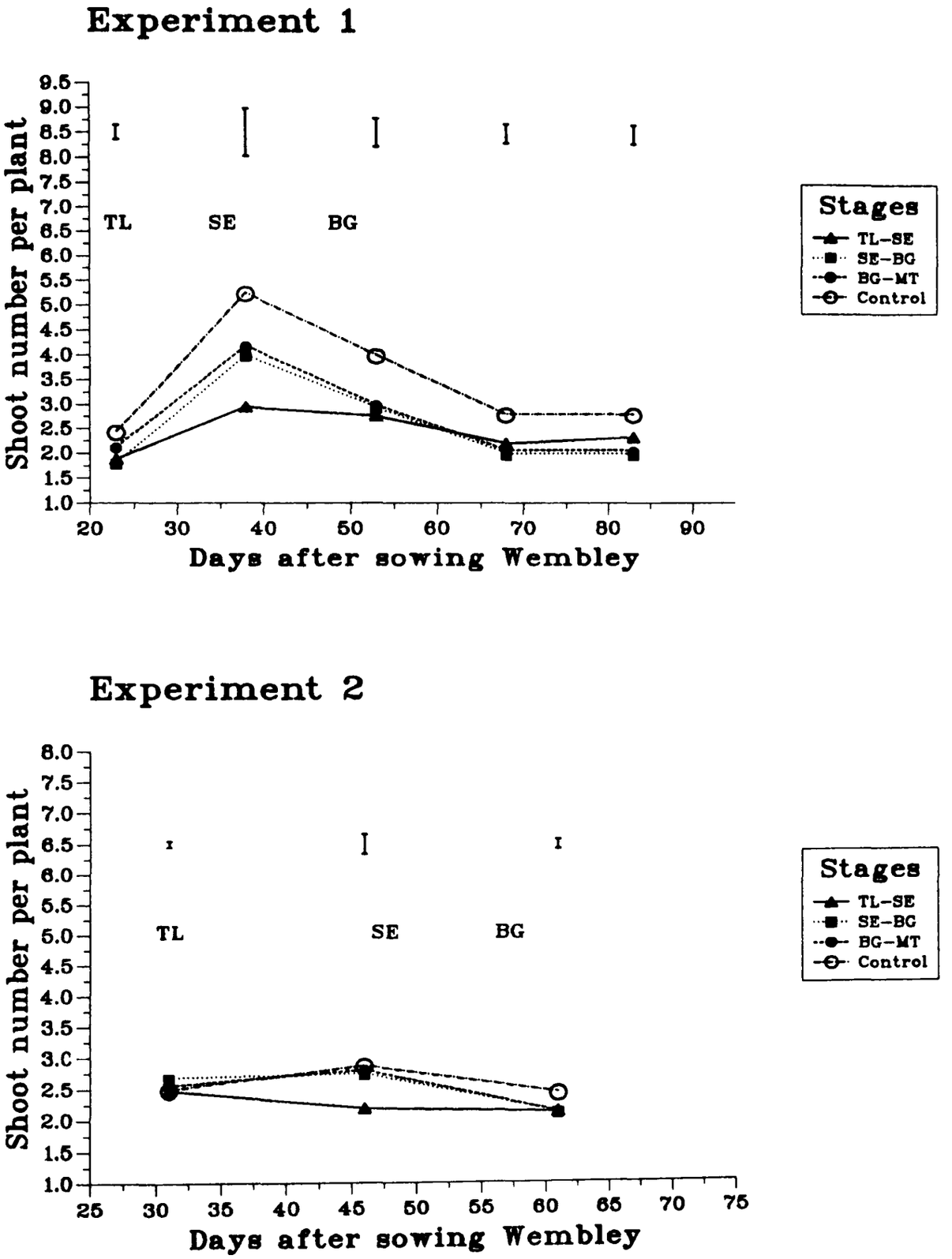




TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

Fig.13: Effect of water stress on shoot number per plant in Wembley variety in water stress Experiment 1 and 2.



TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

period of stress. For example, in Norman water stress at TL-SE, started to decrease shoot number at the end of the stress period (Figure 11). In Fenman and Wembley in Experiment 1 and 2, water stress started to decrease shoot number after the second week of the stress period (Figures 12 and 13). Water stress at SE-BG started to decrease number of shoots per plant at the start of the stress period in all varieties. The decrease was sometimes significant. At the start of booting the ears had emerged and shoot death was complete. However, during the period BG-MT in the water stress treatments, some death of shoots with ears occurred. These ears contained no grain at harvest, although they were counted as ears in the determination of yield components.

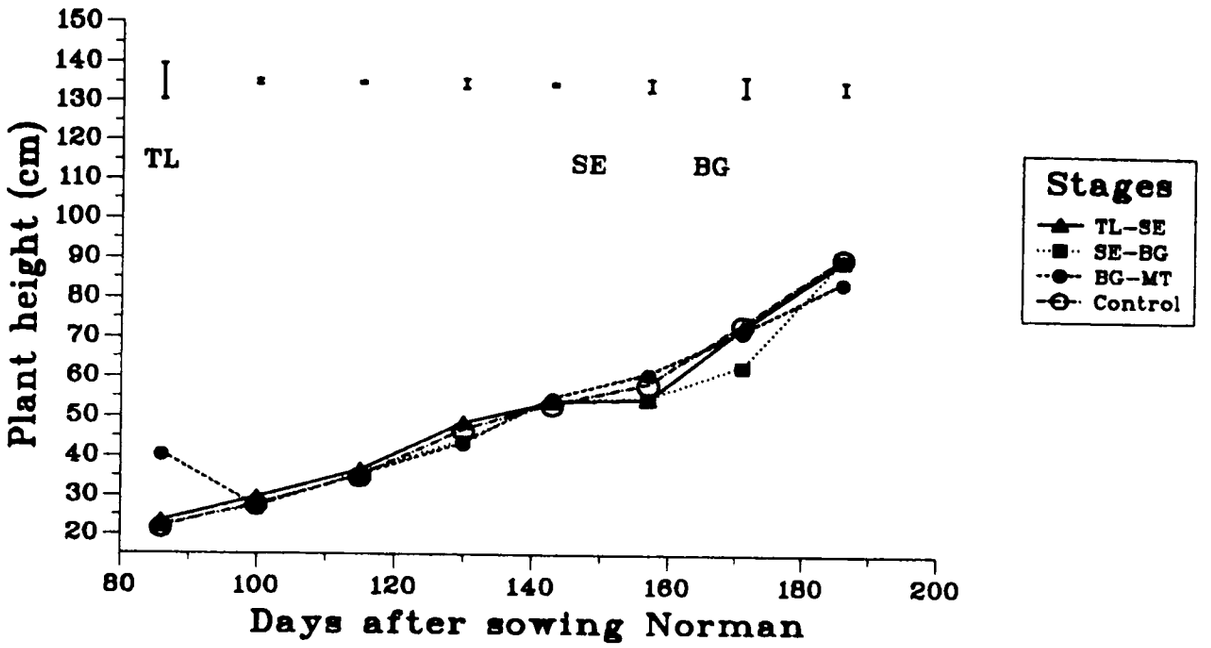
3.3.6 PLANT HEIGHT OF MAIN STEM

The results are described stage by stage for each variety and for Experiments 1 and 2 and are shown in Figures 14 to 16.

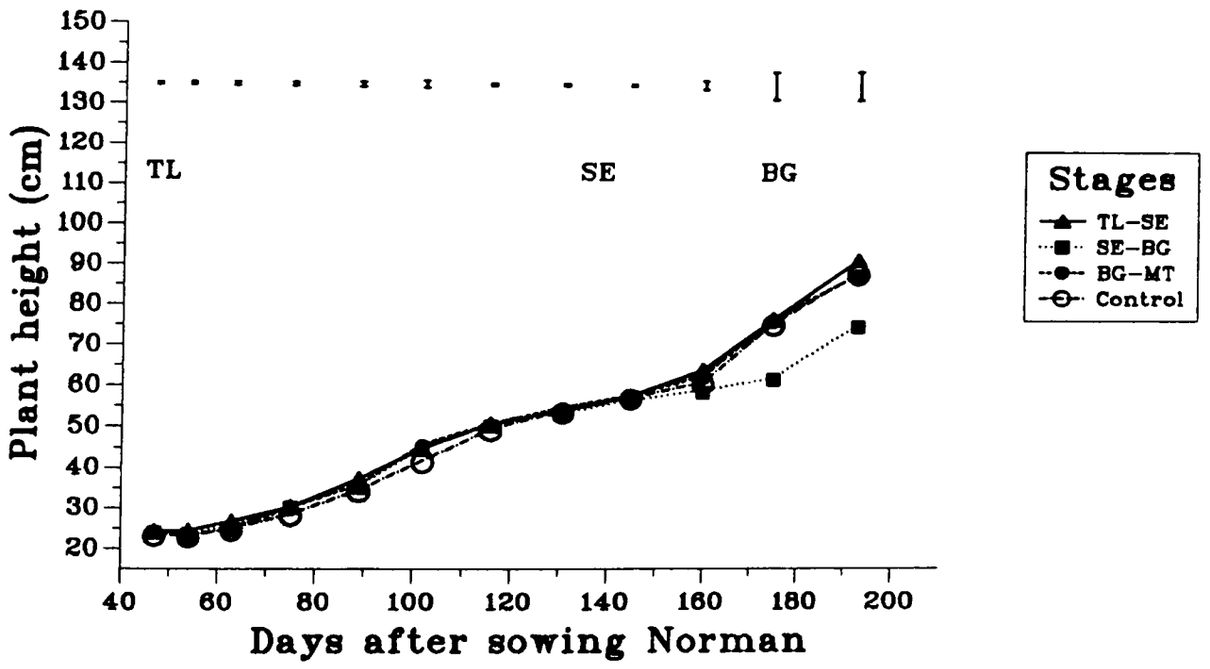
The effects of water stress on plant height were very similar in both years in all varieties. Generally plant height was decreased by all water stress treatments during stress periods and then recovery occurred. In some cases the effect of water stress was significant, but mostly it was not significant. Water stress at TL-SE had no significant effect on plant height in Norman (Figure 14). In both Experiments 1 and 2 in Fenman water stress at TL-SE decreased plant height but later the plants recovered (Figure 15). In Wembley in both years water stress at TL-SE decreased plant height during the stress period (Figure 16). Recovery took place in Experiment 1 but not in Experiment 2. In Norman, Fenman and

Fig.14: Effect of water stress on plant height of main stem of Norman variety in water stress Experiment 1 and 2.

Experiment 1



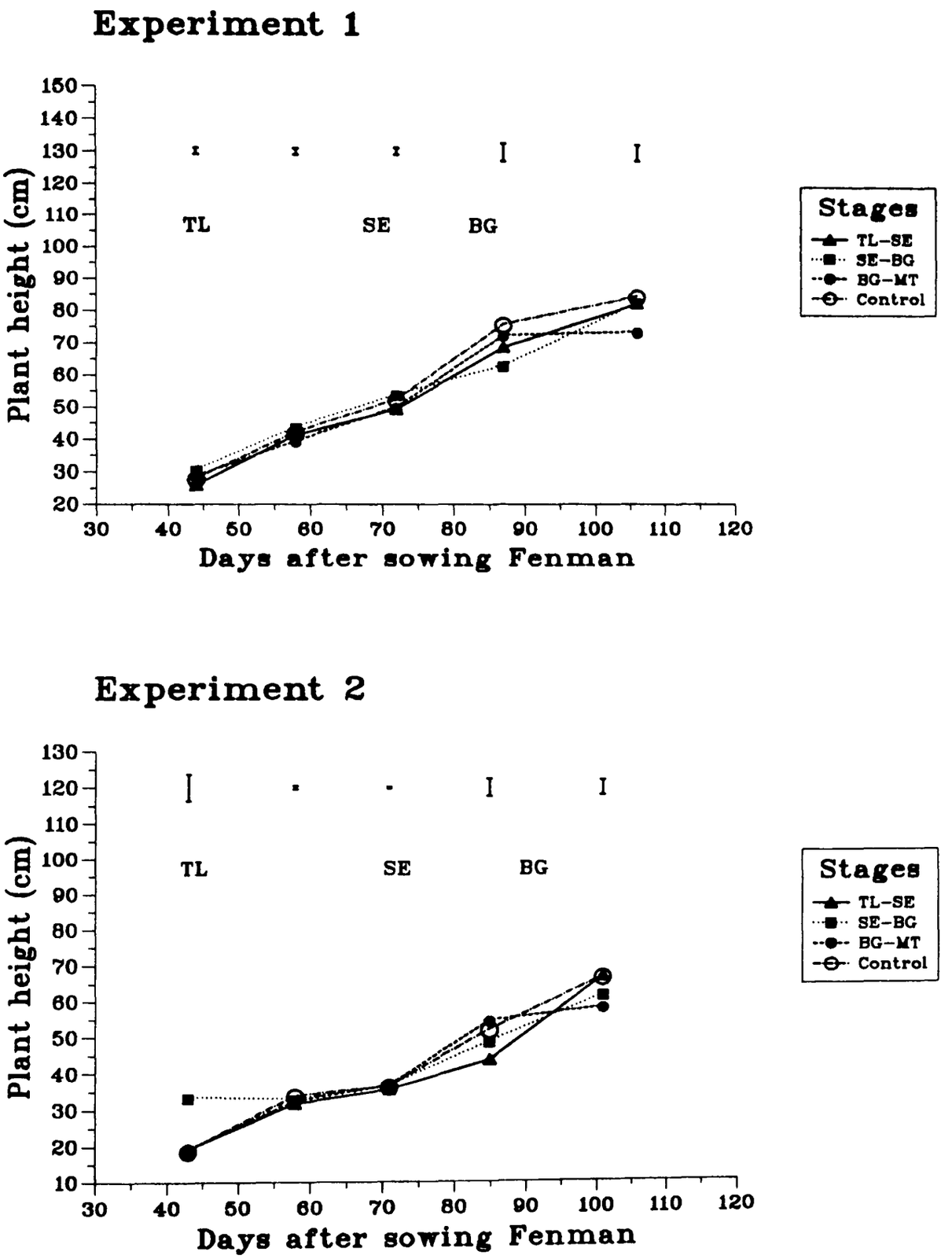
Experiment 2



TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

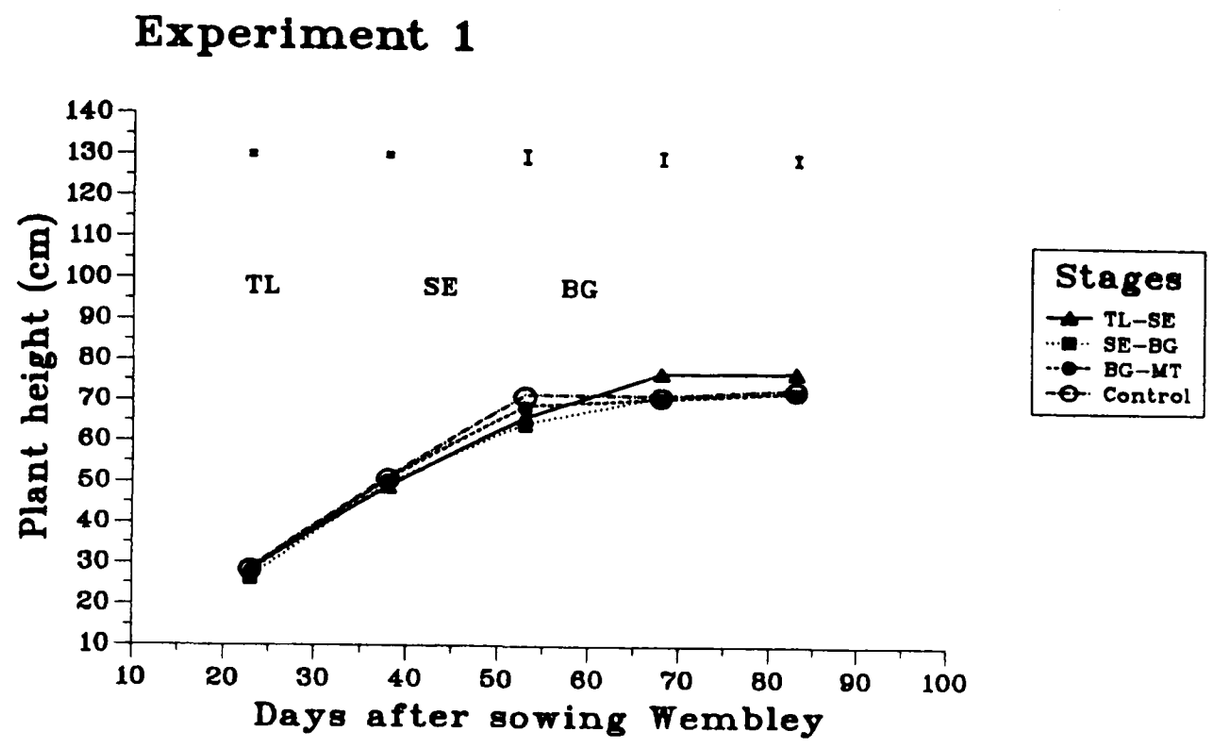
Fig.15: Effect of water stress on plant height of main stem of Fenman variety in water stress Experiment 1 and 2.

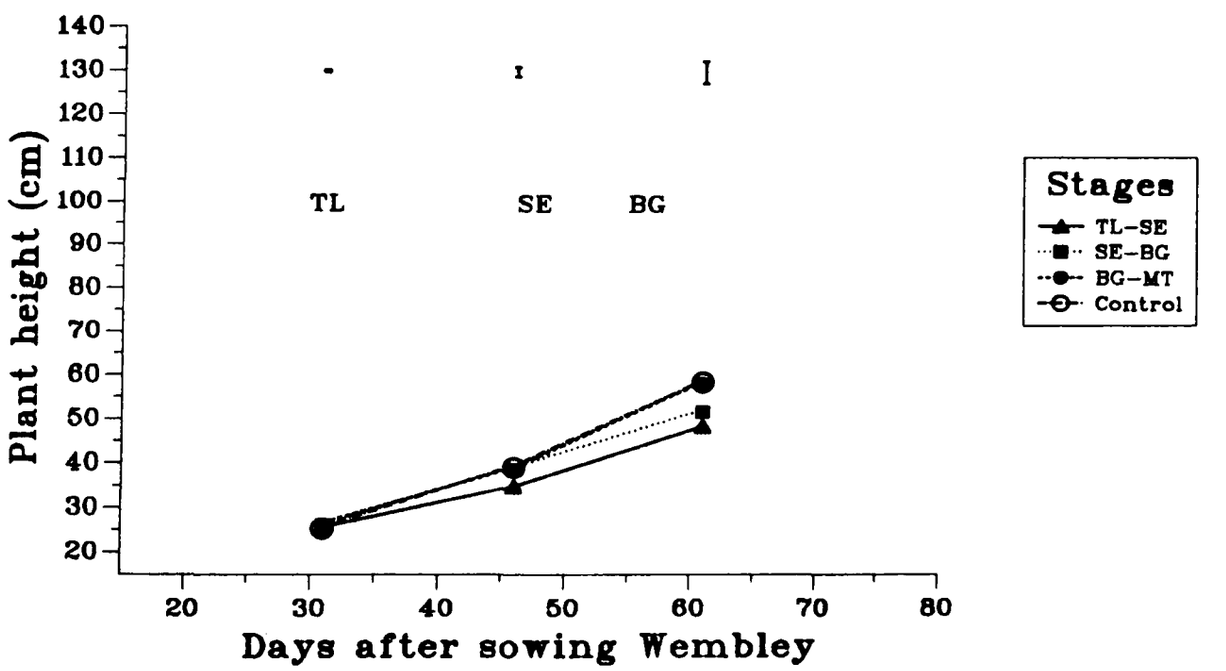


TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

Fig.16: Effect of water stress on plant height of main stem of Wembley variety in water stress Experiment 1 and 2.





TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

Wembley, water stress at SE-BG decreased plant height and then recovery occurred in Experiment 1 but not in Experiment 2. Water stress at BG-MT had little effect on Norman (Figure 14), but decreased plant height in Fenman in both years (Figure 15). Water stress at BG-MT had no significant effect on plant height in Wembley (Figure 16).

3.3.7 SIGNIFICANCE OF MAIN EFFECTS AND INTERACTIONS IN GROWTH ANALYSIS AND YIELD DATA

To determine the effects of water stress and variety on growth and yield the data for growth parameters recorded at the end of each stress period and for yield and yield components of each variety were pooled before analysis of variance was performed.

All tests of significance were made at the 5% probability level. Where treatment effects were found to be significant treatment means were then compared by calculating a least significant difference (LSD) using the values of the standard error of a treatment mean and of Q from tables of the Studentized Range. The test is referred to as Tukey's test (Zar, 1984).

L.S.D. = S.E. of means x Q (k, df)

k = number of means to be compared

df = residual degrees of freedom

S.E. = the standard error of the treatment means being compared.

In the results tables, N.S. indicates not significant.

All data were analysed on the DEC 20 or VAXA computing facilities available at U.C.N.W., Bangor, using GENSTAT or

MINITAB statistical packages.

In all water stress and salinity experiments in both years, generally the interactions were significant for grain yield and almost all yield components. For some results the interactions were not significant. These were for infertile spikelets per ear, plant height, leaf number, grain nitrogen %, straw nitrogen % and nitrogen uptake per plant. The main effects of variety and main effects of stress at different stages are presented in order to show the main trends in the data, and also because for some parameters the interaction was significant in one experiment but not both. In both water stress and salinity experiments in both years, generally there were no significant interactions for the growth characteristics recorded at different stages.

The varieties were sown at different times and therefore experienced different climatic conditions during growth and in particular during different stress periods. However, stress was imposed at the same stage of development in each variety, and therefore results for all varieties and stress treatments were combined for analysis of variance.

3.3.8 MAIN EFFECT OF WATER STRESS AT DIFFERENT STAGES ON GROWTH CHARACTERISTICS

3.3.8.1 Main effect of water stress at stem extension

In both Experiments 1 and 2, leaf area, stem area, dry weight per plant and nitrogen uptake per plant at stem extension were significantly decreased by water stress at TL-SE (Table 10). Nitrogen % was decreased significantly in Experiment 1, but not in Experiment 2.

Table 10 Main effect of water stress at stem extension on growth characters in Experiments 1 and 2.

	Stages			
	TL-SE	Control	S.E.M.	L.S.D. (P=0.05)
Experiment 1				
Leaf area per plant (cm^2)	120.50	181.00	7.79	23.15
Stem area per plant (cm^2)	10.95	17.41	0.71	2.12
Dry weight per plant (g)	0.71	1.10	0.03	0.08
Nitrogen %	2.65	3.50	0.13	0.38
Nitrogen uptake per plant (g)	0.02	0.04	0.0016	0.0047
Experiment 2				
Leaf area per plant (cm^2)	98.50	154.80	3.93	11.68
Stem area per plant (cm^2)	8.97	14.25	0.35	1.05
Dry weight per plant (g)	0.63	0.91	0.032	0.09
Nitrogen %	3.27	3.40	0.12	N.S.
Nitrogen uptake per plant (g)	0.02	0.031	0.0013	0.0037

3.3.8.2 Main effect of water stress at booting

In Experiment 1 water stress at SE-BG resulted in all growth characters measured at booting having significantly lower values than the control except nitrogen % (Table 11). In Experiment 2 water stress at SE-BG significantly decreased leaf area, stem area, dry weight, nitrogen % and nitrogen uptake per plant at booting. The data values for water stress at SE-BG were lower than those for water stress at TL-SE and the control, except nitrogen %, which was significantly lower than TL-SE only.

3.3.8.3 Main effect of water stress at anthesis

In Experiments 1 and 2, total leaf area (except flag leaf area which was measured separately), flag leaf area, stem area, ear area, dry weight per plant and nitrogen % at anthesis were significantly affected by water stress at different stages (Table 12). In both years nitrogen uptake per plant was not significantly different. In Experiment 1, generally all water stress treatments had a significantly lower value of all parameters compared to the control. In Experiment 1 the three stressed treatments showed no significant differences in leaf area, flag leaf area, stem area and dry weight per plant. Water stress at SE-BG has given significantly higher nitrogen % than the other treatments in Experiment 1. In Experiment 1, there were no significant differences in nitrogen uptake per plant between stress treatments and the control. Generally in Experiment 2, all water stress treatments decreased all measured parameters. Leaf area per plant was significantly lower in all water stress treatments compared to the control. Flag leaf area

Table 11 Main effect of water stress at different stages on different growth characters at booting in Experiments 1 and 2.

	Stages				
	TL-SE	SE-BG	Control	S.E.M.	L.S.D. (P=0.05)
Experiment 1					
Leaf area per plant (cm^2)	181.80	138.00	269.50	16.09	56.47
Stem area per plant (cm^2)	28.00	23.10	40.60	1.93	6.78
Dry weight per plant (g)	1.78	1.81	2.85	0.16	0.57
Nitrogen %	2.62	1.92	2.16	0.12	0.41
Nitrogen uptake per plant (g)	0.044	0.033	0.060	0.0035	0.12
Experiment 2					
Leaf area per plant (cm^2)	145.20	76.70	197.40	6.63	23.28
Stem area per plant (cm^2)	30.27	22.08	37.04	0.95	3.35
Dry weight per plant (g)	2.53	2.26	3.50	0.17	0.60
Nitrogen %	2.52	2.19	2.12	0.50	0.18
Nitrogen uptake per plant (g)	0.034	0.039	0.052	0.0022	0.0079

Table 12 Main effect of water stress at different stages on growth characters at anthesis in Experiments 1 and 2.

	Stages					
	TL-SE	SE-BG	BG-MT	Control	S.E.M.	L.S.D. (P=0.05)
Experiment 1						
Leaf area per plant (cm^2)	126.30	125.70	90.70	179.10	9.64	36.82
Flag leaf area per plant (cm^2)	39.50	28.00	38.00	52.90	2.55	9.93
Ear area per plant (cm^2)	34.40	32.70	33.90	44.80	2.09	7.97
Stem area per plant (cm^2)	45.70	41.70	43.30	61.70	2.45	9.37
Dry weight per plant (g)	3.59	3.11	3.43	4.77	0.19	0.71
Nitrogen %	1.41	1.63	1.44	1.36	0.047	0.18
Nitrogen uptake per plant (g)	0.051	0.050	0.049	0.065	0.0035	N.S.
Soluble carbohydrate %	0.55	0.56	0.60	0.60	0.026	N.S.
Soluble carbohydrate Content (mg) per plant	11.48	10.26	13.00	17.37	0.99	3.78
Experiment 2						
Leaf area per plant (cm^2)	129.80	88.50	42.00	181.60	6.63	25.31
Flag leaf area per plant (cm^2)	50.50	26.90	25.60	45.40	4.88	18.64
Ear area per plant (cm^2)	42.60	34.40	52.80	55.90	3.64	13.91
Stem area per plant (cm^2)	49.10	30.90	39.60	53.00	2.27	8.67
Dry weight per plant (g)	3.74	2.50	3.56	4.31	0.29	1.10
Nitrogen %	2.02	2.14	1.66	1.79	0.094	0.36
Nitrogen uptake per plant (g)	0.051	0.046	0.042	0.056	0.0048	N.S.
Soluble carbohydrate %	0.65	0.64	0.78	0.72	0.035	0.14
Soluble carbohydrate content (mg) per plant	16.79	9.52	17.01	19.76	1.50	5.73

and stem area per plant was significantly decreased by water stress at SE-BG and BG-MT. Ear area per plant were significantly decreased by water stress at SE-BG. Dry weight per plant was significantly decreased by water stress at SE-BG. Water stress at TL-SE and BG-MT gave dry weight per plant non-significantly lower than the control. Nitrogen % was significantly increased by water stress at SE-BG in both years. Water stress at TL-SE also increased nitrogen % but not significantly. There were no significant effects of time of water stress on nitrogen uptake per plant.

In Experiment 1 soluble carbohydrate % was not significantly affected by water stress but it was in Experiment 2. In Experiment 2 water stress at SE-BG gave soluble carbohydrate % significantly lower than water stress at BG-MT. The other treatments were not significantly different from each other. In Experiment 1 soluble carbohydrate content was significantly decreased by water stress at TL-SE, SE-BG and BG-MT. In Experiment 2 soluble carbohydrate content was significantly decreased with water stress at SE-BG.

3.3.9 MAIN EFFECT OF VARIETIES ON GROWTH CHARACTERISICS IN WATER STRESS EXPERIMENTS 1 AND 2

3.3.9.1 Main effect of varieties on growth characteristics at stem extension

In Experiment 1, there was no significant effect of variety on leaf area, stem area, nitrogen uptake per plant at stem extension (Table 13). However, dry weight per plant and nitrogen % showed significant differences between varieties. Dry weight per plant was significantly higher in Norman than

Table 13 Main effect of varieties on growth characters at stem extension in water stress Experiments 1 and 2.

	Varieties				
	Norman	Fenman	Wembley	S.E.M.	L.S.D. (P=0.05)
Experiment 1					
Leaf area per plant (cm^2)	165.40	134.50	152.20	9.54	N.S.
Stem area per plant (cm^2)	15.76	12.84	13.94	0.87	N.S.
Dry weight per plant (g)	1.18	0.81	0.71	0.04	0.12
Nitrogen %	2.17	3.02	4.05	0.16	0.56
Nitrogen uptake per plant (g)	0.027	0.025	0.029	0.0019	N.S.
Experiment 2					
Leaf area per plant (cm^2)	142.40	119.10	118.50	4.82	17.39
Stem area per plant (cm^2)	12.38	11.67	10.78	0.43	N.S.
Dry weight per plant (g)	1.03	0.83	0.45	0.039	0.14
Nitrogen %	3.20	3.37	3.44	0.14	N.S.
Nitrogen uptake per plant (g)	0.033	0.028	0.016	0.0015	0.0055

in Fenman and Wembley. Wembley had a significantly higher nitrogen % than Fenman. Fenman had significantly higher nitrogen % than Norman. In Experiment 2 Norman had a significantly higher leaf area, dry weight, and nitrogen uptake per plant than Fenman. These parameters were significantly higher in Fenman than in Wembley, except leaf area per plant. There were no significant differences between varieties in stem area and nitrogen %.

3.3.9.2 Main effect of varieties on growth characteristics at booting

In Experiment 1, there were no significant differences in leaf area and stem area between varieties at booting (Table 14). Dry weight per plant was significantly higher in Norman than in Wembley. Wembley had a significantly lower dry weight per plant than Fenman. Nitrogen % and nitrogen uptake per plant were lower in Norman compared to Fenman. In Experiment 2 Norman had a significantly higher leaf area, stem area, dry weight and nitrogen uptake per plant than Fenman and Wembley. Norman had a significantly lower nitrogen % than Fenman and Wembley.

3.3.9.3 Main effect of varieties on growth characteristics at anthesis

In Experiment 1, Norman had a significantly higher leaf area and dry weight per plant than Wembley (Table 15). Wembley had a significantly lower leaf area and dry weight per plant than Fenman. Wembley had significantly higher flag leaf area per plant than Norman. In Experiment 1, stem area, ear area, nitrogen % and nitrogen uptake per plant, showed no significant differences between varieties. In Experiment 2,

Table 14 Main effect of varieties on growth characters at booting in water stress Experiments 1 and 2

	Varieties				
	Norman	Fenman	Wembley	S.E.M	L.S.D. (P=0.05)
Experiment 1					
Leaf area per plant (cm^2)	176.90	209.40	203.00	16.09	N.S.
Stem area per plant (cm^2)	32.70	31.40	127.60	1.93	N.S.
Dry weight per plant (g)	2.56	2.29	1.59	0.16	0.57
Nitrogen %	1.50	2.35	2.85	0.12	0.41
Nitrogen uptake per plant (g)	0.039	0.053	0.044	0.0035	0.012
Experiment 2					
Leaf area per plant (cm^2)	216.00	92.10	111.10	6.63	23.28
Stem area per plant (cm^2)	52.88	22.59	13.93	0.95	3.35
Dry weight per plant (g)	6.02	1.44	0.82	0.17	0.60
Nitrogen %	1.10	2.55	3.17	0.05	0.18
Nitrogen uptake per plant (g)	0.065	0.036	0.025	0.0022	0.0079

Table 15 Main effect of varieties on growth characters at anthesis in water stress Experiment 1 and 2.

	Varieties				
	Norman	Fenman	Wembley	S.E.M.	L.S.D. (P=0.05)
Experiment 1					
leaf area per plant (cm^2)	158.50	134.90	98.00	8.35	28.87
Flag leaf area per plant (cm^2)	26.80	47.90	44.10	2.20	7.63
Ear area per plant (cm^2)	37.90	36.10	35.30	1.81	N.S.
Stem area per plant (cm^2)	47.90	47.10	49.30	2.13	N.S.
Dry weight per plant (g)	4.03	3.86	3.29	0.16	0.56
Nitrogen %	1.49	1.51	1.37	0.041	N.S.
Nitrogen uptake per plant (g)	0.069	0.069	0.05	0.0030	N.S.
Soluble carbohydrate %	0.54	0.64	0.56	0.022	0.078
Soluble carbohydrate content (mg) per plant	6.98	17.73	14.37	0.86	2.97
Experiment 2					
Leaf area per plant (cm^2)	131.30	117.80	82.40	5.74	21.62
Flag leaf area per plant (cm^2)	52.20	35.90	23.20	4.23	14.68
Ear area per plant (cm^2)	59.60	41.40	39.80	3.15	10.94
Stem area per plant (cm^2)	60.30	39.50	28.20	1.99	6.82
Dry weight per plant (g)	7.16	1.86	1.56	0.25	0.86
Nitrogen %	0.98	2.22	2.50	0.081	0.28
Nitrogen uptake per plant (g)	0.07	0.04	0.04	0.0042	0.015
Soluble carbohydrate %	1.20	0.50	0.39	0.031	0.11
Soluble carbohydrate content (mg) per plant	40.66	4.35	2.29	1.30	4.49

at anthesis Norman had a significantly higher leaf area, flag leaf area, stem area, ear area, dry weight and nitrogen uptake per plant compared to Wembley. However, Norman had a lower nitrogen % than Fenman and Wembley. The values for Fenman were generally in between those for Norman and Wembley. Wembley had a leaf area and stem area significantly lower than Fenman. For other parameters Wembley generally gave results which were not significantly lower than Fenman.

In Experiment 1, Fenman had a higher soluble carbohydrate % and content than Norman and Wembley. In Experiment 2, Norman had a significantly higher soluble carbohydrate % than Fenman and Fenman had a significantly higher value than Wembley. In Experiment 2, soluble carbohydrate content was significantly higher in Norman in comparison to Fenman and Wembley.

3.3.10 MAIN EFFECT OF WATER STRESS AT DIFFERENT STAGES ON GRAIN YIELD, YIELD COMPONENTS AND OTHER CHARACTERS IN EXPERIMENTS 1 AND 2

The results are presented in two sections, the variety x water stress interaction was significant for many, but not all, yield components in both years. Therefore, to show the main trends for varieties and water stress at different stages, the main effects of these factors are presented and discussed briefly.

The effects of water stress at different stages on yield and yield components and other characters recorded at harvest in Experiments 1 and 2 are shown in Tables 16 and 17 respectively. Generally grain yield and yield components are

Table 16 Main effects of water stress at different growth stages on yield and yield components and other characters recorded at harvest - Experiment 1.

	Stages					
	TL-SE	SE-BG	BG-MT	Control	S.E.M.	L.S.D. (p=0.05)
Grain weight per plant (g)	2.26	2.47	1.15	3.26	0.075	0.29
Average grain weight (mg)	43.30	44.64	29.14	46.57	0.83	3.16
Number of grains per plant	54.20	58.76	45.03	74.68	1.76	6.73
Number of ears per plant	1.42	1.44	1.42	1.74	0.038	0.14
Number of grains per ear	38.84	41.46	32.62	44.14	1.26	4.83
Fertile spikelets per ear	17.02	17.84	17.63	18.76	0.23	0.88
Number of grains per fertile spikelet	2.28	2.33	1.85	2.34	0.068	0.26
Infertile spikelet per ear	4.05	3.36	4.01	2.63	0.18	0.68
Harvest index %	45.38	47.46	36.44	48.43	1.00	3.81
Straw dry weight per plant (g)	2.70	2.81	1.96	3.58	0.12	0.45
Plant height of main stem (cm)	84.02	82.33	74.83	83.22	0.66	2.54
Number of leaves on main stem	10.00	10.00	10.00	10.00	-	N.S.
Nitrogen % in grain	1.86	1.90	1.90	1.78	0.098	N.S.
Nitrogen % in straw	0.51	0.62	0.60	0.39	0.036	0.14
Nitrogen uptake per plant (grain + straw) (g)	0.056	0.064	0.034	0.072	0.0027	0.010
Average grain weight of grain growth (mg)	44.05	46.08	34.11	48.42	0.89	3.74
Rate of grain growth (mg/day)	1.39	1.44	1.28	1.51	0.050	0.21
Duration of grain growth (days)	34.25	34.67	26.79	33.32	0.78	3.28

Table 17 Main effects of water stress at different growth stages on yield and yield components and other characters recorded at harvest - Experiment 2

	Stages					
	TL-SE	SE-BG	BG-MT	Control	S.E.M.	L.S.D. (P=0.05)
Grain weight per plant (g)	1.80	1.77	0.92	3.10	0.14	0.54
Average grain weight (mg)	32.03	34.14	22.23	34.67	1.22	4.67
Number of grains per plant	56.5	51.4	43.5	89.5	3.38	12.91
Number of ears per plant	1.52	1.53	1.41	1.94	0.051	0.20
Number grains per ear	38.70	35.19	30.50	47.37	1.51	5.77
Fertile spikelets per ear	16.86	16.42	16.38	18.90	0.28	1.067
Number of grains per fertile spikelet	2.22	2.12	1.83	2.45	0.085	0.33
Infertile spikelets per ear	3.03	4.12	4.52	2.40	0.20	0.76
Harvest index %	48.16	46.27	34.29	52.58	1.75	6.68
Straw dry weight per plant (g)	2.00	2.11	2.073	2.89	0.13	0.49
Plant height of main stem (cm)	71.81	69.40	63.21	74.69	1.043	3.98
Number of leaves on main stem	10.33	10.25	10.33	10.33	0.024	0.092
Nitrogen % in grain	2.01	2.20	2.97	1.97	0.050	0.19
Nitrogen % in straw	0.57	0.64	0.86	0.54	0.053	0.20
Nitrogen uptake per plant (grain + straw) (g)	0.043	0.049	0.042	0.070	0.0025	0.0096
Average grain weight of grain growth (mg)	35.50	36.75	24.20	38.83	0.99	4.14
Rate of grain growth (mg/day)	1.05	1.04	0.68	1.11	0.070	0.29
Duration of grain growth (days)	34.71	35.88	37.19	35.06	1.78	N.S.

described in detail in the interaction tables 20 to 28. Water stress at different stages significantly affected grain yield and yield components in both Experiments 1 and 2. Generally all water stress treatments decreased grain yield and yield components compared to the control. Particularly, water stress at BG-MT significantly decreased grain yield and yield components. However, the number of infertile spikelets per ear, grain nitrogen % and straw nitrogen % were increased by the water stress treatments.

In Experiment 1 water stress at TL-SE and BG-MT resulted in a significantly higher number of infertile spikelets per ear than the control. With water stress at SE-BG the number of infertile spikelets was not significantly higher than the control and not significantly lower than TL-SE and BG-MT. In Experiment 2 with water stress at SE-BG and BG-MT the number of infertile spikelets was significantly higher than the control. Water stress at TL-SE gave a significantly lower number of infertile spikelets than water stress at SE-BG and BG-MT, but not significantly higher than the control.

In both years water stress at BG-MT significantly decreased plant height. Plant height was relatively unaffected by water stress at other stages. Water stress had no significant effects on number of leaves on the main stem in Experiment 1. In Experiment 2 water stress at SE-BG resulted in a very small but significant decrease in the number of leaves on the main stem. This was because in Fenman and Wembley all replicates of each variety had the same number of leaves, whereas in Norman two of the four replicates had an average of 13 leaves and the other two replicates had an

average of 12.5 leaves. There were no significant effects of water stress on grain nitrogen % in Experiment 1. In Experiment 2 water stress at BG-MT resulted in a significantly higher grain nitrogen % compared to all other treatments. In Experiment 1, water stress at BG-MT and SE-BG has given straw nitrogen % significantly higher than the control but not significantly higher than TL-SE. Both stages SE-BG and BG-MT had no significant differences to each other. In Experiment 2, water stress at BG-MT significantly increased straw nitrogen % compared to TL-SE, SE-BG and control. In Experiment 1 water stress at BG-MT significantly decreased nitrogen uptake per plant in comparison to water stress at TL-SE, SE-BG and the control. In Experiment 2 all water stress treatments gave a nitrogen uptake per plant significantly lower than the control. In Experiment 1 average grain weight, rate, and duration of grain growth were significantly decreased by water stress at BG-MT. Water stress at TL-SE and SE-BG had no significant effects. Similar trends were present in Experiment 2, except that the duration of grain growth was not significantly affected.

3.3.11 MAIN EFFECT OF VARIETIES ON YIELD, YIELD COMPONENTS AND OTHER CHARACTERS IN EXPERIMENTS 1 AND 2

The main effects of varieties on yield, yield components and other characters recorded at harvest for water stress, Experiments 1 and 2 are shown in Tables 18 and 19 respectively.

The effects of variety on grain yield and yield components were generally significant except for grain number per

Table 18 Main effects of varieties on yield, yield components and other characters recorded at harvest in water stress - Experiment 1.

	Varieties				
	Norman	Fenman	Wembley	S.E.M.	L.S.D. (P=0.05)
Grain weight per plant (g)	2.16	2.53	2.16	0.065	0.22
Average grain weight (mg)	34.66	41.93	46.15	0.72	2.48
Number of grains per plant	59.65	59.05	55.80	1.53	N.S.
Number of ears per plant	1.27	1.49	1.76	0.033	0.11
Number of grains per ear	46.64	39.44	31.70	1.09	3.78
Fertile spikelets per ear	18.33	17.37	17.75	0.20	0.69
Number of grain per fertile spikelet	2.54	2.27	1.79	0.059	0.20
Infertile spikelets per ear	4.13	2.59	3.82	0.15	0.54
Harvest index %	37.42	49.71	46.15	0.86	2.99
Straw dry weight per plant (g)	3.45	2.46	2.39	0.102	0.36
Plant height of main stem (cm)	89.13	81.04	73.13	0.57	1.99
Number of leaves on main stem	11.00	10.00	9.00	-	-
Nitrogen % in grain	1.73	1.94	1.91	0.085	N.S.
Nitrogen % in straw	0.55	0.38	0.75	0.031	0.11
Nitrogen uptake per plant (grain + straw) (g)	0.053	0.057	0.059	0.0023	N.S.
Average grain weight of grain growth (mg)	40.80	47.50	42.04	0.77	2.90
Rate of grain growth (mg/day)	1.24	1.69	1.29	0.043	0.16
Duration of grain growth (days)	37.22	27.91	31.64	0.68	2.55

Table 19 Main effects of varieties on yield, yield components and other characters recorded at harvest in water stress Experiment 2.

	Varieties				
	Norman	Fenman	Wembley	S.E.M.	L.S.D. (P=0.05)
Grain weight per plant (g)	2.42	1.99	1.37	0.12	0.42
Average grain weight (mg)	30.74	31.32	30.25	1.058	N.S.
Number of grains per plant	77.4	58.7	44.3	2.93	10.16
Number of ears per plant	1.41	1.74	1.65	0.044	0.15
Number of grains per ear	54.37	32.91	26.55	1.31	4.54
Fertile spikelets per ear	20.02	16.48	14.92	0.24	0.84
Number of grains per fertile spikelet	2.71	1.99	1.77	0.074	0.26
Infertile spikelets per ear	4.48	2.75	3.33	0.17	0.59
Harvest index %	39.55	45.83	50.60	1.51	5.25
Straw dry weight per plant (g)	3.43	2.09	1.28	0.11	0.38
Plant height of main stem (cm)	85.19	65.62	58.55	0.90	3.13
Number of leaves on main stem	12.94	10.00	8.00	0.021	0.072
Nitrogen % in grain	1.82	2.29	2.76	0.043	0.15
Nitrogen % in straw	0.34	0.73	0.89	0.046	0.16
Nitrogen uptake per plant (grain + straw) (g)	0.051	0.055	0.048	0.0022	N.S.
Average grain weight of grain growth (mg)	34.10	33.68	33.67	0.86	N.S.
Rate of grain growth (mg/day)	1.01	0.98	0.92	0.060	N.S.
Duration of grain growth (days)	35.10	35.11	36.92	0.15	N.S.

plant in Experiment 1 and average grain weight (mg) in Experiment 2 which were not significant. In Experiment 1, Fenman had a significantly higher grain weight than the other varieties. In Experiment 2, Norman had a significantly higher grain weight than Fenman and Wembley.

In Experiment 1 Norman had the highest grain number per ear and per fertile spikelet, and the highest number of fertile spikelets per ear. However, it had the lowest number of ears per plant and average grain weight. Similar trends were present in Experiment 2, except that there was no significant difference between varieties in average grain weight.

The number of infertile spikelets per ear has given significant differences in varieties in both years. Both years' results were similar. Norman had significantly more infertile spikelets per ear than Fenman, but not significantly more than Wembley. There were significant differences in both years in plant height between varieties. In both years Wembley had shorter plant height than Fenman which was shorter than Norman. The interaction between water stress and varieties for number of leaves per plant was not significant in Experiment 1, but it was in Experiment 2. In Experiment 1 Norman had 11 Fenman 10 and Wembley had 9 leaves. In Experiment 2, results, Norman had 12.94, Fenman had 10 and Wembley had 8 leaves. In both years Norman had more leaves than Fenman, which had more leaves than Wembley. Grain nitrogen % was higher in Wembley and Fenman than in Norman, but this was significant in Experiment 2 only. In both years Wembley had a significantly higher straw nitrogen % than

Norman. In Experiment 1, Fenman had a significantly higher average grain weight and rate of grain growth than Norman and Wembley. Norman had a significantly longer duration of grain growth than Fenman and Wembley, Fenman had a significantly shorter duration of grain growth than Wembley. In Experiment 2 average grain weight, rate and duration of grain growth were not significantly affected by variety.

In these experiments, at final harvest there were no significant effects of water stress in Experiments 1 and 2 on the number of detectable stem nodes on the main stem as shown in Table 20. The values of this character were similar in both experiments, but were different between varieties. In both experiments Norman had more dectable stem nodes than Fenman and Fenman had more than Wembley, as found by Kirby et al. (1985b).

The numbers of detectable stem nodes were similar for each variety in the water stress experiments.

3.3.12 EFFECTS OF VARIETIES AND WATER STRESS ON YIELD, YIELD COMPONENTS AND OTHER CHARACTERS RECORDED AT HARVEST

3.3.12.1 Grain weight per plant (g)

In both years all water stress treatments decreased grain weight per plant, but for individual varieties the decrease was not always significant (Table 21). Water stress at BG-MT significantly decreased grain weight per plant in all varieties in Experiment 1.

In Experiment 1, in Norman with water stress at TL-SE grain weight per plant was significantly lower than with water stress at SE-BG, and applied water stress at SE-BG resulted in

Table 20 Detectable stem nodes on the main stem of plants of different wheat varieties, Norman, Fenman and Wembley in water stress Experiments 1 and 2.

Variety	Water stress Experiments Mean	S.E.of mean
Experiment 1		
Norman	5.7	o.153
Fenman	4.6	o.163
Wembley	3.6	0.163
Experiment 2		
Norman	5.7	0.153
Fenman	4.6	0.163
Wembley	3.6	0.163

Table 21 Effect of varieties and water stress on grain weight per plant (g) in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	1.59	2.72	2.45
Stem extension to booting	2.38	2.60	2.43
Booting to maturity	1.07	1.41	0.96
Control	3.61	3.39	2.78
S.E. of means = 0.13; L.S.D. (P = 0.05) = 0.64			
Experiment 2			
Tillering to stem extension	2.37	1.67	1.36
Stem extension to booting	2.23	1.77	1.30
Booting to maturity	1.16	0.84	0.77
Control	3.93	3.33	2.04
S.E. of means = 0.24; L.S.D. (P = 0.05) = N.S.			

a significantly lower grain weight per plant than the control. In Fenman and Wembley water stress at TL-SE non-significantly decreased the grain weight per plant compared to the control. Water stress at SE-BG resulted in significantly lower grain weight per plant compared to the control in Fenman but not significantly less compared to the control in Wembley. In the controls Wembley had a significantly lower grain weight per plant than Norman and Fenman. The Norman control gave a grain weight per plant not significantly higher than the Fenman control.

The interaction between water stress and variety was not significant in Experiment 2. The main effects of water stress at different stages (Table 16 and 17) showed that all water stress treatments significantly decreased grain weight per plant compared to the control. In particular water stress at BG-MT gave significantly much lower than TL-SE, SE-BG. The main effect of variety was also significant. Norman gave significantly higher grain weight per plant than Fenman and Fenman gave significantly higher than Wembley.

3.3.12.2 Average grain weight (mg)

In Experiment 1 owing to water stress average grain weight was significantly less at BG-MT compared to the control in all varieties (Table 22). In Norman average grain weight was lower with water stress at TL-SE than with water stress at SE-BG but this was not significant. With water stress at SE-BG average grain weight was lower compared to the control but not significantly. In Fenman with water stress at TL-SE average grain weight was not significantly lower than with water stress at SE-BG and the control. In Wembley water stress at

Table 22 Effect of varieties and water stress on average grain weight (mg) in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	34.12	44.82	50.97
Stem extension to booting	37.94	47.15	48.84
Booting to maturity	23.19	28.94	35.27
Control	43.38	46.82	49.50
S.E. of means = 1.43; L.S.D. (P = 0.05) = 7.085			
Experiment 2			
Tillering to stem extension	29.89	36.22	29.97
Stem extension to booting	39.86	32.49	30.09
Booting to maturity	18.60	21.18	26.91
Control	34.60	35.40	34.02
S.E. of means = 2.12; L.S.D. (P = 0.05) = 10.48			

TL-SE and SE-BG had no significant effects on average grain weight. In both Experiments 1 and 2 in the controls the varieties showed no significant differences in average grain weight. In Experiment 2 with water stress at BG-MT average grain weight was significantly lower compared to the control in Norman and Fenman but not significantly in Wembley. With water stress at BG-MT average grain weight was lower than in the other treatments in all varieties, in some cases this was significant and in some non-significant. In Norman with water stress at TL-SE average grain weight was significantly lower than with water stress at SE-BG. Water stress at TL-SE non-significantly decreased average grain weight compared to the control. In Norman water stress at SE-BG has given average grain weight higher than the control but not significantly. In Fenman with water stress at TL-SE average grain weight was not significantly higher than SE-BG and the control. Water stress at SE-BG resulted in a non-significantly less average grain weight compared to the control. In Wembley water stress at TL-SE and SE-BG resulted in similar average grain weight. At these stages average grain weight was not significantly less than the control.

3.3.12.3 Number of grains per plant

In Experiment 1, the results show that water stress at BG-MT gave a significantly lower number of grains per plant than the control in all varieties (Table 23). In Norman water stress at TL-SE gave significantly fewer grains per plant in comparison to water stress at SE-BG, water stress at SE-BG gave significantly fewer grain per plant than the control. In Fenman water stress at TL-SE decreased numbers

Table 23 Effect of varieties and water stress on number of grains per plant in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	46.3	60.7	55.6
Stem extension to booting	63.0	55.3	58.0
Booting to maturity	45.9	47.9	41.3
Control	83.3	72.4	68.3
S.E. of means = 3.053; L.S.D. (P = 0.05) = 15.11			
Experiment 2			
Tillering to stem extension	78.7	45.7	45.1
Stem extension to booting	55.9	54.3	44.1
Booting to maturity	61.9	40.2	28.4
Control	113.3	94.5	59.7
S.E. of means = 5.85; L.S.D. (P = 0.05) = 28.95			

of grain per plant but this was not significant in comparison to the control. Water stress at SE-BG resulted in significantly fewer number of grains per plant compared to the control in Fenman. In Wembley with water stress at TL-SE and SE-BG numbers of grains per plant were non-significantly less, compared to the control, and non-significantly higher than water stress at BG-MT. Norman had more grains per plant than Fenman. Fenman had more grains per plant than Wembley, but the differences between the varieties were not significant.

In Experiment 2 the trends were very similar to Experiment 1. Water stress at BG-MT gave significantly lower number of grains per plant compared to the control in all varieties. In Norman and Fenman all water stress treatments significantly decreased number of grain per plant. In Norman water stress at TL-SE gave non-significantly higher number of grain per plant than SE-BG, but significantly less compared to the control. In Fenman water stress at SE-BG decrease number of grain per plant significantly compared to the control. In Wembley water stress at TL-SE and SE-BG has given non-significantly fewer grains per plant than the control. In the control Wembley had significantly fewer grains per plant than Norman but not Fenman.

3.3.12.4 Number of ears per plant

The interaction between water stress and variety for number of ears per plant (Table 24), was not significant in Experiment 1, but it was in Experiment 2. However , in Experiment 1 the main effects of water stress and variety were significant. All water stress treatments significantly decreased number of ears per plant but there were no signifi-

Table 24 Effect of varieties and water stress on number of ears per plant in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	1.09	1.47	1.69
Stem extension to booting	1.32	1.36	1.64
Booting to maturity	1.15	1.42	1.71
Control	1.50	1.72	2.01
S.E. of means = 0.065; L.S.D. (P = 0.05) = N.S.			
Experiment 2			
Tillering to stem extension	1.36	1.43	1.76
Stem extension to booting	1.15	1.91	1.55
Booting to maturity	1.52	1.34	1.37
Control	1.62	2.26	1.94
S.E. of means = 0.089; L.S.D. (P = 0.05)= 0.44			

cant differences between them. Norman gave significantly lower number of ears per plant than Fenman and Fenman gave lower than Wembley. In Experiment 2 in all varieties, all water stress treatments decreased number of ears per plant. In Norman water stress at SE-BG significantly decreased number of ears per plant. Water stress at TL-SE gave non significantly similar to BG-MT in Norman, both stages had a lower number of ears per plant than the control but not significantly. In Fenman water stress at TL-SE and BG-MT has given significantly lower number of ears per plant than SE-BG and the control. In Wembley water stress at BG-MT resulted in significantly fewer number of ears per plant compared to the control but not significantly less than water stress at TL-SE and SE-BG. Water stress at TL-SE and SE-BG has given non-significantly lower number of ears per plant than the control. In the controls Fenman had significantly more ears per plant than Norman but not significantly more than the Wembley control.

3.3.12.5 Number of grains per ear

For number of grains per ear (Table 25) the interaction between variety and water stress was not significant in Experiment 1 but it was in Experiment 2. In Experiment 1, the main effects of water stress and the main effects of variety were significant. Water stress at BG-MT gave a significantly lower number of grains per ear than TL-SE and the control. Water stress at TL-SE gave a significantly lower number of grains per ear than the control but not significantly less than SE-BG. Norman gave a significantly higher number of grains per ear than Fenman and Fenman

Table 25 Effect of varieties and water stress on number of grains per ear in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	42.3	41.3	32.9
Stem extension to booting	48.0	40.8	35.6
Booting to maturity	40.1	33.5	24.3
Control	56.2	42.2	34.0
S.E. of means = 2.19; L.S.D. (P = 0.05) = N.S.			
Experiment 2			
Tillering to stem extension	58.8	31.7	25.6
Stem extension to booting	48.8	28.3	28.5
Booting to maturity	40.5	29.8	21.2
Control	69.4	41.8	30.9
S.E. of means = 2.61; L.S.D. (P = 0.05) = 12.94			

significantly higher than Wembley.

In Experiment 2 water stress at all stages decreased number of grains per ear compared to the control, but the decrease was not significant for all varieties and stages. In all varieties water stress at TL-SE resulted in fewer grains per ear than the control, but this was not statistically significant. In Norman water stress at SE-BG and BG-MT significantly decreased number of grains per ear compared to the control. In Fenman water stress at SE-BG gave significantly lower number of grains per ear compared to the control. In Fenman and Wembley water stress at BG-MT gave a non-significantly lower number of grains per ear than the control. In the controls Norman had significantly more grains per ear than Fenman and Wembley.

3.3.12.6 Fertile spikelets per ear

In comparison to other yield components the number of fertile spikelets per ear was relatively less affected by water stress (Table 26). In Experiment 1, water stress at SE-BG and BG-MT had no significant effects on the number of fertile spikelets per ear in all varieties. Water stress at TL-SE, resulted in a significant decrease in Norman compared to the control, but not in Fenman and Wembley. In the controls Norman had significantly more fertile spikelets per ear than Fenman. Fenman had fewer fertile spikelets per ear than Wembley, but this was not significant. In Experiment 2, in Norman water stress at TL-SE decreased the number of fertile spikelets per ear but this was not significant. Water stress at SE-BG resulted in a significantly lower number of fertile spikelets per ear compared to the control but not

Table 26 Effect of varieties and water stress on number of fertile spikelets per ear in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	16.65	17.52	16.89
Stem extension to booting	18.45	17.02	18.05
Booting to maturity	18.23	16.95	17.73
Control	19.98	17.98	18.33
S.E. of means = 0.40; L.S.D. (P = 0.05) = 1.97			
Experiment 2			
Tillering to stem extension	19.82	16.17	14.58
Stem extension to booting	18.33	15.85	15.07
Booting to maturity	20.20	15.93	13.00
Control	21.73	17.95	17.02
S.E. of means = 0.48; L.S.D. (P = 0.05) = 2.39			

significantly lower than water stress at TL-SE and BG-MT. In Fenman water stress at TL-SE resulted in slightly more fertile spikelets per ear than water stress at SE-BG and BG-MT, but slightly lower compared to the control. These differences were not significant. In Fenman with water stress at SE-BG the number of fertile spikelets per ear was not significantly lower than the control. In Wembley water stress at TL-SE and BG-MT gave significantly less fertile spikelets per ear than the control. In the controls Norman had significantly more fertile spikelets per ear than Fenman and Wembley.

3.3.12.7 Number of grains per fertile spikelet

The interaction between variety and water stress (Table 27) for number of grains per fertile spikelet was not significant in Experiment 1, but it was significant in Experiment 2. In Experiment 1 the main effects of water stress and the main effects of variety were significant. Water stress at BG-MT significantly decreased number of grains per fertile spikelet lower than TL-SE, SE-BG and control. Water stress at TL-SE, SE-BG were not significantly different to each other and the control. Norman had significantly more grains per fertile spikelet than Fenman and Fenman had significantly more than Wembley.

In Experiment 2, generally all water stress treatments had a lower grain number per fertile spikelet compared to the control but some were not significant. Water stress at BG-MT significantly decreased number of grains per fertile spikelet in Norman, but not in Fenman and Wembley. Water stress at TL-SE and SE-BG decreased number of grains per fertile spikelet but this was not significant. In the controls Norman

Table 27 Effect of varieties and water stress on number of grains per fertile spikelet in Experiments 1 and 2.

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	2.5	2.4	2.0
Stem extension to booting	2.6	2.4	2.0
Booting to maturity	2.2	2.0	1.4
Control	2.8	2.4	1.9
S.E. of means = 0.12; L.S.D. (P = 0.05) = N.S.			
Experiment 2			
Tillering to stem extension	3.0	2.0	1.8
Stem extension to booting	2.7	1.8	1.9
Booting to maturity	2.0	1.9	1.6
Control	3.2	2.3	1.8
S.E. of means = 0.15; L.S.D. (P = 0.05) = 0.73			

had significantly more number of grains per fertile spikelet than Wembley.

3.3.12.8 Harvest index %

In Experiment 1, water stress at BG-MT significantly decreased harvest index in all varieties (Table 28). In Norman with water stress at TL-SE harvest index was not significantly decreased compared to water stress at SE-BG. Water stress at TL-SE resulted in a significantly lower harvest index compared to the control in Norman. In Wembley and Fenman water stress at TL-SE and SE-BG had no significant effects on harvest index. In the controls Norman had a significantly lower harvest index than Fenman.

In Experiment 2 the interaction of variety and stages was not significant. The main effects of water stress at stages and varieties were significant. Water stress at BG-MT significantly decreased harvest index lower than water stress at TL-SE, SE-BG and the control. Harvest index was not significantly different between water stress at TL-SE, SE-BG and control. In varieties Wembley had a non significantly higher harvest index than Fenman and Fenman had significantly higher than Norman.

3.3.12.9 Straw dry weight per plant (g)

In Experiment 1 (Table 29), straw dry weight per plant was significantly decreased by water stress at TL-SE, SE-BG and BG-MT in Norman. Water stress at TL-SE and SE-BG gave significantly higher straw weight per plant than water stress at BG-MT in Norman. In Fenman and Wembley water stress at all stages decreased straw weight per plant but the effects were not statistically significant except with BG-MT in

Table 28 Effect of varieties and water stress on harvest index (%) in Experiments 1 and 2.

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	32.75	52.42	50.97
Stem extension to booting	40.22	53.32	48.84
Booting to maturity	34.08	39.96	35.27
Control	42.63	53.14	49.50
S.E. of means = 1.73; L.S.D. (P = 0.05) = 7.77			
Experiment 2			
Tillering to stem extension	41.09	52.44	50.95
Stem extension to booting	42.59	46.07	50.16
Booting to maturity	25.04	32.82	45.02
Control	49.50	51.98	56.27
S.E. of means = 3.028; L.S.D. (P = 0.05) = N.S.			

Table 29 Effect of varieties and water stress on straw dry weight per plant (g) in Experiments 1 and 2.

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	3.24	2.48	2.39
Stem extension to booting	3.59	2.28	2.55
Booting to maturity	2.07	2.06	1.75
Control	4.88	2.99	2.86
S.E. of means = 0.20; L.S.D. (P = 0.05) = 1.01			
Experiment 2			
Tillering to stem extension	3.22	1.48	1.30
Stem extension to booting	3.01	2.02	1.30
Booting to maturity	3.57	1.71	0.94
Control	3.94	3.15	1.58
S.E. of mean = 0.22; l.S.D. (P = 0.05) = 1.10			

Wembley. In the control Norman had a significantly higher straw weight per plant than Fenman and Wembley which were not significantly different. The results of Experiment 2 show that straw weight per plant was decreased by all water stress treatments. In Fenman water stress at all stages significantly decreased straw weight per plant compared to the control. In Norman and Wembley water stress at all stages had no significant effects on straw weight per plant. However, in both varieties water stress treatments resulted in less straw weight per plant than the control. In the controls Norman and Fenman had significantly higher straw weight per plant than Wembley.

3.4 DISCUSSION

3.4.1 DIFFERENCES IN RESPONSE BETWEEN WATER STRESS EXPERIMENTS 1 AND 2

Many workers have reported decreasing of yield and yield components by water stress. It depends upon crop, crop stages, period of water stress, type of soil, climatic conditions as shown in the literature review (Kramer, 1959, 1963; Vaadia et al., 1961). In both water stress experiments, generally all water stress treatments in all varieties decreased the yield and yield components and all growth characters either less or more by different processes as found by other workers (Salter and Goode, 1967; Jensen and Mogensen, 1984). There was greater reduction in yield, yield components and in growth characters in Experiment 2 in comparison to Experiment 1, as shown in Tables 30 and 31. This could be due to differences in climate or soil type. Over the whole growth period, both temperature and the number of hours of bright sunshine were higher in Experiment 2 than in Experiment 1. Therefore rates of evapotranspiration were probably higher in Experiment 2 than in Experiment 1.

There was a clear difference between the normal field soil, used in Experiment 1 and the mixed peat soil used in Experiment 2. These are shown in mixed peat soil Figures 2 and 3, and also in Tables 7 to 9. The results of the calibration of the resistance blocks suggested that the soil used in Experiment 1 had a higher moisture holding capacity than the soil used in Experiment 2. At the lowest resistance readings the soil used in Experiment 1 had a moisture content of 28%

Table 30 Percentage reduction in yield and yield components due to water stress in Experiment 1

Yield and Yield Components	Stages TL-SE %	SE-BG %	BG-MT %
Experiment 1			
Grain weight per plant (g)	30.67	24.23	64.70
Average grain weight (mg)	7.02	4.14	37.40
Grain number per plant	27.42	21.32	39.70
Ear number per plant	18.39	17.24	18.40
Grain number per ear	12.00	6.07	26.10
Fertile spikelet per ear	9.28	4.90	6.00
Grain number per fertile spikelet	2.56	0.42	20.90
Infertile spikelet per ear	-53.99	-27.76	-52.40
Harvest index %	6.30	2.00	24.80
Straw dry weight per plant (g)	24.58	21.51	45.30
Plant height of main stem (cm)	-0.96	1.07	10.10
Leaf number on main stem	0.00	0.00	0.00
Nitrogen % in grain	-4.50	-6.74	-6.70
Nitrogen % in straw	-30.77	56.41	84.60
Nitrogen uptake per plant (g)	22.22	11.11	52.80
Final average grain weight of grain growth (mg)	9.03	4.83	29.60
Rate of grain growth (mg/day)	7.95	4.64	15.20
Duration of grain growth (days)	-2.79	-4.05	19.60

Table 31 Percentage reduction in yield and yield components due to water stress in Experiment 2

Yield and Yield Components	Stages TL-SE %	SE-BG %	BG-MT %
Experiment 2			
Grain weight per plant (g)	41.90	44.80	70.30
Average grain weight (mg)	7.61	1.53	35.88
Grain number per plant	36.87	42.57	51.39
Ears number per plant	21.65	21.13	27.32
Grain number per ear	18.30	25.71	35.61
Fertile spikelet per ear	10.79	13.12	13.33
Grain number per fertile spikelet	9.39	13.47	25.31
Infertile spikelet per ear	-26.38	-71.66	-88.33
Harvest index %	8.41	12.00	34.79
Straw dry weight per plant (g)	30.79	26.99	28.27
Plant height of main stem (cm)	3.86	7.08	15.37
Leaf number on main stem	0.00	0.77	0.00
Nitrogen % in grain	-2.18	-11.68	-55.76
Nitrogen % in straw	-5.55	-18.52	-59.26
Nitrogen uptake per plant (g)	38.57	30.00	40.00
Final average grain weight of grain growth (mg)	8.58	5.36	37.68
Rate of grain growth (mg/day)	5.14	6.49	38.74
Duration of grain growth (days)	0.99	-2.33	-6.08

where as the soil used in Experiment 2 had moisture content of 17%. At the highest resistance readings both soils had a moisture content of 8%. Although the resistance readings do not corresspond with field capacity and permanent wilting point, the results suggest that the soil used in Experiment 1 may have had a higher available water capacity.

The following sections discuss in more detail the effects of water stress at different stages on the different varieties in Experiment 1 and 2. The final section discusses differences between varieties in the water stress experiments

3.4.2 EFFECT OF WATER STRESS AT DIFFERENT STAGES

3.4.2.1 Effect of water stress during tillering to stem extension.

During this stage after the final leaf has been initiated, spikelets start to appear (Kirby and Faris, 1970, 1972; Kirby and Riggs, 1978; Kirby et al., 1982, 1985b). Water stress at TL-SE decreased leaf area, stem area and dry weight per plant at stem extension similarly in both years. Reduction in leaf area index in response to drought has been found by other workers (Boyer, 1970). In research work carried out in India (Choudhury and Kumar, 1980), moisture stress from sowing to maximum tillering stage resulted in a reduction in leaf area. Water stress decreased nitrogen % in Experiment 1 but not in Experiment 2, although the reasons for this are not clear. At later stages water stress usually increases nitrogen %. Slavik (1966) and Singh and Narang (1971) also found that the nitrogen % increased as the dry weight per plant decreased due to water stress. In both experiments nitrogen uptake was

similar due to similar dry weight per plant. Richards and Wadleigh (1952) reported that nitrogen concentrations are generally higher in stress treatments. Leaf number is determined before tillering, so it was assumed that none of the treatments had any affect on leaf number. Water stress at SE-BG resulted in a small decrease in number of leaves due to severe water stress as reported by (Kirby and Faris, 1970, 1972; Kirby and Riggs, 1978; Kirby et al., 1982, 1985b). Water stress at TL-SE decreased number of tillers as shown in figures 11 to 13. Other workers (Slavik, 1966; Singh and Narang, 1971; Innes et al., 1981; Chaturvedi at al., 1981) have also found that water stress at tillering to stem extension decreased growth measurements and tiller number as well as yield and yield components. In these experiments during TL-SE in Norman temperature was low and there were few bright sunshine hours so that this stage was longer than in other varieties. Kirby et al. (1982, 1985b), Biryukov and Lyashok (1983) and Schofield et al. (1988) found that winter wheat varieties took a long time during growing from tillering to stem extension. During TL-SE in Norman, due to low temperature and fewer sun hours the stress had its major effect at the end of the stress period. During the early part of the stress period there was little evapotranspiration from the plant and soil, and the gypsum block readings started to decrease only at the end of the stress period. In Fenman and Wembley, during TL-SE, temperature was higher so that growth was rapidly decreased, due to rapid soil drying and greater loss of water from leaves. In these varieties the gypsum readings started to decrease earlier and the soil reached a

lower moisture content at the end of the stress period, particularly in Wembley, although the stress period was shorter. With these varieties at this stage number of tillers was decreased at the start of the water stress period. Biryukov and Lyashok (1983) found that water stress at TL-SE decreased shoot number and growth measurements faster in spring wheat varieties because of high temperature. The upper surface of the soil dried before and quicker than the lower surface of the soil. A water stress during TL-SE decreased the growth measurements of all varieties. This suggests that the stressed plants were not able to get sufficient water from the lower portion of the soil or other hand at this stage roots are not able reach lower than below 9" (Salter and Goode, 1967). Plant height was unaffected by water stress during TL-SE, except in Wembley in Experiment 2, where soil moisture content was rapidly decreased. Salter and Goode (1967) found that with moisture stress at any stage plant height was decreased. They have also reported that on stopping stress plant height increases faster. In these experiments only Fenman in Experiment 2 gave similar results to the above. Biryukov and Lyashok (1983) found that water stress at TL-SE decreased number of shoots and plant height in spring wheat varieties. Gales and Wilson (1981) subjected winter wheat plants grown in the field to drought at different stages of growth but none of the treatments significantly decreased grain yield. These workers found that under drought total shoot dry weight and plant height was decreased but effects on straw were greater than effects on grain yield.

If water stress at younger stages causes a reduction in

leaf area, stem area, dry weight per plant and nitrogen uptake per plant, then the plant will have a problem to improve its further development. In these experiments following water stress at TL-SE the measured growth parameters had not recovered at the booting harvest, because only a very short period had elapased since stopping water stress. Some recovery had taken place by anthesis, but still the values of the growth measurments of the TL-SE treatment were lower compared to the control shown in Table 32. Following water stress during TL-SE dry weight per plant at stem extension was 64% and 69% of the control in Experiments 1 and 2 respectively. The corresponding values at booting were 62% and 72% and at anthesis 75% and 87%.

Water stress at TL-SE increased the nitrogen % at booting and at anthesis in both experiments as reported by other workers (Asana and Basu, 1963; Slavik, 1966; Singh and Narang, 1971). Aggrawal and Sinha (1987) found that following early water stress which produced a reduction of growth there can be recovery at later stages. However stressed plants still had decreased yield and yield components. Grain yield and yield components were affected by water stress at TL-SE by different amounts in different varieties as found by other workers (Biryukouv and Lyashok, 1983; Davidson and Campbell, 1984; Beranek, 1986). Grain weight per plant was decreased due to decreases in grain number per plant. This was decreased due to effects on number of ears per plant and number of fertile spiklets per ear as found by Volkova and Udovenko (1985). These workers found that drought at the vegetative stage decreased grain yield, number of grains per plant and other

Table 32 Percentage reduction in growth characters at anthesis due to water stress in both Experiment 1 and 2

Growth characters	Stages TL-SE %	SE-BG %	BG-MT %
Experiment 1			
Leaf area per plant (cm^2)	29.48	29.82	49.36
Flag leaf area per plant (cm^2)	25.33	47.07	28.17
Ear area per plant (cm^2)	23.21	27.09	24.33
Stem area per plant (cm^2)	25.93	32.41	29.82
Dry weight per plant (g)	24.74	34.80	28.09
Nitrogen %	-3.68	-19.85	-5.88
Nitrogen uptake per plant (g)	9.57	11.35	13.12
Soluble carbohydrate %	8.33	6.67	0.00
Soluble carbohydrate content (mg per plant)	33.91	40.93	25.16
Experiment 2			
Leaf area per plant (cm^2)	28.52	51.27	76.87
Flag leaf area per plant (cm^2)	-11.23	40.75	43.61
Ear area per plant (cm^2)	23.79	38.46	5.55
Stem area per plant (cm^2)	11.13	41.70	25.28
Dry weight per plant (g)	13.23	41.99	17.40
Nitrogen %	-12.68	-19.55	7.26
Nitrogen uptake per plant (g)	8.93	17.86	25.00
Soluble carbohydrate %	9.72	11.11	-8.33
Soluble carbohydrate content (mg per plant)	15.03	51.82	13.92

components. The decrease in grain yield due to water stress at TL-SE was greater in Norman in Experiment 1 than in Experiment 2. This was due to a greater decrease in 1000 grain weight and number of grains per plant. Although the stress period was much shorter in Experiment 1 than in Experiment 2, in Experiment 1 the roots started to extract moisture from 46cm 3 weeks after the start of the stress period. In Experiment 2, roots started to extract moisture from 46cm, 8 weeks after the start of the stress period. Average grain weight was significantly decreased by water stress at TL-SE only in Norman in Experiment 1, It was also decreased in Wembley in Experiment 2, but not significantly. Grain number per ear was decreased by water stress at TL-SE in all varieties. The reduction was greater in Norman due to greater decrease in number of fertile spikelets per ear. Water stress at TL-SE decreased the number of fertile spikelets in Norman and Wembley. The decreases are expected as the number of fertile spikelets is being determined at this time. The decrease was significant in Wembley in Experiment 2 and Norman in Experiment 1, possibly due to increased water stress and higher temperature although the same effects were not noted in Fenman in Experiment 1. Frank et al. (1987) found that water stress starting 12 days after seedling emergence produced a shorter spikelet development stage resulting in fewer spiklets per ear. Austin et al. (1980) and Thorne et al. (1988) found that winter wheat produced many spikelets. Similarly in these experiments Norman had more spikelets than Fenman and Wembley. After water stress at TL-SE the growth measurements for Fenman were in between those of Norman and Wembley. In

Fenman harvest index, number of grains per fertile spikelet, fertile spiklets per ear, grains per ear and average weight were not much affected by water stress at TL-SE. During growth of this variety the first few weeks had low temperature then it had a high temperature as shown in Figures 8 and 9. It may be that the contrasting low and high temperature for a shorter period resulted in a smaller effect on these components and measurements. However in Fenman, grain weight per plant, number of the grains per plant and straw dry weight per plant were decreased more in Experiment 2, although temperature was higher and soil moisture % reached lower values in Experiment 1.

3.4.2.2 Effect of water stress during stem extension to booting

Stem extension starts from when the first node is detectable. During this period the embryo ear grows from about 30mm long at the beginning of the phase to 80mm long at anthesis. At the beginning of the phase the plant normally has produced its full complement of tillers, and the main shoot and each tiller has the potential to produce an ear. At this time the final number of spikelet has been determined. SE-BG is also a phase of rapid growth (Kirby and Appleyard, 1981; Kirby et al., 1985b). Because all leaves on the main stem had appeared there was little effect of water stress on number of leaves. Other wokers (Kirby and Faris, 1970, 1972; Kirby and Riggs, 1978; Kirby et al., 1982, 1985a) have reported that if very severe stress occurs at later stages the number of leaves can be decreased.

As reported by other workers (Boyer, 1968; Acevedo et

al., 1971; Watts, 1974) water stress resulted in large decreases in leaf area, possibly because of a decreased rate of leaf expansion. The decreases in leaf area and dry weight due to water stress were greater with water stress at SE-BG than with water stress at TL-SE. Water stress at SE-BG decreased stem area and dry weight per plant similarly in both years as found by Baker et al. (1986). Leaf area was decreased more in Experiment 2 than in Experiment 1, possibly because of higher temperature and greater soil drying. At this stage stem area should also have been affected more in Experiment 2 than Experiment 1. However it was not as affected due to more tillers stem area was higher (Kirby and Faris, 1970, 1972). In Experiment 1 nitrogen percentage was decreased by 11 % but in Experiment 2 it was increased by 3%. The reasons for this difference are not clear. In Experiment 2 nitrogen uptake per plant was higher than in Experiment 1 because of a higher dry weight per plant.

Dry matter production can be decreased due to decreases in leaf area and stem area. In these experiments dry matter production was decreased more due to lower leaf and stem area in Experiment 2 than Experiment 1. During the SE-BG and BG-MT treatments plants were tall and all leaves had appeared (Kirby et al., 1982, 1985a, 1985b). During these treatments temperature was between 16^{o}C and 26^{o}C and duration of bright sunshine was between 4 and 9 hours, so there was a high rate of evaporation from the plant and soil. Soil moisture % was decreased more quickly at SE-BG than at TL-SE, particularly in Experiment 2. Hence stress at this time had large effects on growth, although the stress period was shorter. During the SE-

BG stress period some lower leaves and shoots died. Particularly in Experiment 2, plants of Norman and Fenman also needed watering to avoid death. Singh and Malik (1983) and Jensen and Mogensen (1984) also found that at later stages plants have a higher rate of evapotranspiration. Salter and Goode (1967) also reported that evapotranspiration was faster at later stages than at earlier stages. Cereal crops are short and have a low leaf area in the winter season and have a low water requirement at that time. However in spring they get taller as the season changes. Various workers (Konovalov, 1959; Storrier, 1965; Turner, 1966; Campbell et al., 1969) have concluded from studies of yield components that a plant is most sensitive to water stress during its period of rapid development. Rapid development usually occurs at periods of high temperature (Gallagher, 1979; Kirby et al., 1982). Hence water stress at SE-BG would be expected to cause a large decrease in yield.

In these experiments water stress at SE-BG decreased the tiller number per plant of all varieties. In Experiment 2 the decrease in tillering was faster in all varieties, because of high temperature and more evapotranspiration. Day and Intalap (1970) have also reported that moisture stress during the jointing stage and at later stages accelerated tiller sencescence and reduced grain yield. Aspinall, et al. (1964), Bingham (1966), Campbell et al. (1969), Day and Intalap (1970) and Fischer (1973) have all reported reduction in number of ear bearing tillers with water stress in wheat. Salter and Goode (1967) and Jensen and Mogensen (1984) reported the effects of drought stress at various stage of growth in

different crops. In these experiments death of tillers was possibly because the roots of tillers had not reached the lower horizons of the soil and hence were unable to extract enough moisture. The gypsum block readings showed that there was very little moisture at soil depth 23cm down after three weeks of water stress at SE-BG in all varieties in Experiment 2.

In all varieties plant height was decreased only in Experiment 2 and it did not recover again, possibly because of high temperature and more evapo-transpiration. Water stress at SE-BG caused larger decreases in plant height than at other stages. Similar results have been reported by Salter and Goode (1967).

In these experiments following water stress at SE-BG the measured growth parameters had not recovered at the anthesis harvest because only a very short period had elapased since stopping stress. The growth parameters were much lower at anthesis in both experiments as shown in Table 32. Hower, they showed a little recovery in dry weight per plant at maturity. Following water stress during SE-BG dry weight per plant at booting was 64% and 65% of the controls in Experiments 1 and 2 respectively. The corresponding values at anthesis were 66% and 58% and at maturity 79% and 73%. Water stress at SE-BG increased the nitrogen percentage at anthesis and at maturity in both experiments as reported by other workers (Asana and Basu, 1963; Slavik, 1966; Singh and Narang, 1971). Jensen and Mogensen (1984) found that when moisture stress was applied at any stage of development grain yield was reduced. Moisture stress prior to heading resulted in a

reduction in grain yield. In these experiments nitrogen % was also increased in the grain.

By stem extension total spikelet number is fixed (Kirby and Riggs, 1978; Kirby and Appleyard, 1981; Kirby et al., 1985b). However stress could have an effect on the number of fertile spikelets and this was found in Experiment 2.

Water stress at SE-BG decreased grain yield and most of the yield components in both years. In some varieties the reduction in yield and yield components was greater in Experiment 1 and in others it was greater in Experiment 2, due to different reasons. Grain weight per plant was decreased more in Experiment 2 than in Experiment 1. This was mainly due to greater decrease in number of grains per plant and fertile spikelets per ear. Similarly Singh and Malik (1983) also found that severe stress (-15 bars) imposed during the planting to jointing stage reduced grain yield to about 34%. Straw yield and 1000 grain weight were also both reduced by various levels of moisture stress. Day and Barmore (1971) have observed that grain yield was significantly reduced, when water was withheld at jointing followed by the dough stage. In the experiments here straw yield, average grain weight, harvest index, and grain number per fertile spikelet were not affected by water stress at SE-BG. Some workers (Day and Intalp, 1970; Fischer, 1973; Jensen and Mogensen, 1984) have reported that water stress at earlier stages caused a smaller reduction in yield and yield components than at later stage, such as anthesis time.

With water stress at SE-BG the yield decreases were larger in Norman than in Fenman and larger in Fenman than in

Wembley. These differences between varieties were associated with differences in number of grains per plant and per ear, which were decreased most in Norman and least in Wembley. This suggests that the long duration variety was more sensitive than the other varieties, possibly due to its larger leaf area resulting in more evapotranspiration.

3.4.2.3 Effects of water stress during booting to maturity

By this the time number of ears and spikelets per ear are fixed and stress at this time should mainly affect grain growth. During this time pollination occurs and hence stress at this time may also affect fertile spikelet number and grain number (Sofield et al., 1977; Kirby and Appleyard, 1981). During BG-MT average temperature and hours of bright sunshine were higher than in other water stress periods. The plants were taller and had a large leaf area for transpiration. These conditions favoured evapotranspiration and resulted in rapid drying of soil. Davidson and Campbell (1984) also reported that the rate and amount of water used by the plants was greatest at high day and night temperatures. The gypsum blocks gave no readings 3 weeks after the start of this stress period in all varieties except in Wembley in Experiment 2. Hence stress developed more quickly at this than at earlier periods. Also the plants had no chance to recover as they had at earlier stages. Therefore as a result water stress at this stage had the largest effects on yield as reported by other workers (Salter and Goode 1967; Levitt, 1980).

Aggarwal and Sinha (1987) concluded that maintenance of high leaf area index at anthesis is desirable for obtaining high grain yield in stressed plants. In these experiments

water stress at BG-MT caused large decreases in growth paramters at anthesis, despite the short period under stress from booting to anthesis. Observations showed that water stress at this time resulted in rapid senescence as found by Friend et al. (1962) and Levitt (1981). These workers reported that leaf senescence occurs as plants get taller and this is quicker during booting to maturity, particularly with drought and high temperature. Water stress at BG-MT decreased leaf area more than stem area and the stems remained green as found by Kirby and Faris (1970, 1972) but leaf senescence was rapid. This delayed senescence of the stem after all leaves have died has been found in other crops (Dodd and Scarisbrick, 1986). The decrease in leaf area was greater in Experiment 2, which experienced higher temperature and longer hours of bright sunshine than Experiment 1. The flag leaf is one of the most important leaves of the plant for grain yield. Biswas and Mandal (1987) found that flag leaf removal at any stage of growth hastened senescence and decreased grain mass, grain mass per ear, harvest index and sink activity. In these experiments flag leaf area per plant at anthesis was decreased by water stress at all stages except at TL-SE in Experiment 1. Water stress at SE-BG and BG-MT decreased flag leaf area more than water stress at TL-SE. Water stress at SE-BG decreased flag leaf area most because this stress occurred at the time when the flag leaf was extending. With water stress at TL-SE, compensatory growth occurred in Experiment 2, so that it had higher flag leaf area than the controls at anthesis. In these experiments with water stress at BG-MT nitrogen % was increased in Experiment 1. However the trends of nitrogen %

during growth measurements are not clear. Sometimes stress decreased nitrogen % and sometimes it increased the nitrogen %. Most workers have found that stress increases nitrogen %.

Spiertz and Ellen (1978) found in their experiments that water soluble carbohydrate reserves in the stem can play an important role as a carbohydrate source for the grains when the production of assimilates by current photosynthesis is reduced, due to progressive senescence of the photosynthesising tissue. In these experiments soluble carbohydrate % was not much affected in Experiment 1 but in Experiment 2 soluble carbohydrate % was increased, may be due to high temperature and more drought. Dolnicki and Kukula (1987) in their experiments on rye and triticale showed an increase in sugar content during severe frost. Dougherty et al. (1975a) found that irrigation tended to lower levels of water soluble carbohydrate in preanthesis ears of Aotea and Arawa wheat varieties and reduce grain set. In these experiments the results are very similar. With this water stress at BG-MT resulted in higher soluble carbohydrate % under water stress treatment and fewer grains per plant. The above authors reported that poor grain set occurred in wheat which had a lower level of water soluble carbohydrate in the ear during the period of rapid ear growth. Fisher (1973) and Morgan (1977) have found that anthesis was a more sensitive growth stage in comparison to other growth stages. If water stress occurs at anthesis flowers are injured and the size of seed is reduced.

Water stress at BG-MT resulted in maturity occurring 10 to 20 days earlier than in the other stress treatments and the

control as found by other workers (Salter and Goode, 1967; Levitt 1980; Jensen and Mogensen, 1984). Water stress at booting to maturity also caused greater decreases in average grains weight, grain number per plant, number of grain per ear, fertile spikelets per ear, number of grains per fertile spikelet and increases in number of infertile spikelets per ear than water stress at other periods in both years shown in Table 30 and 31. Plant height was also decreased more by water stress at BG-MT than at other stress periods. These results are in agreement with those of other workers (Asana et al., 1958; Robins and Domingo, 1962; Slavik, 1966; Salter and Goode, 1967; Fisher, 1973; Morgen, 1977; Morgen and Riggs, 1981; Gebeyehou and Knott, 1983). Many other crops are also most sensitive to drought stress at the flowering stage such as barley, sorghum and maize (Salter and Good 1967).

Water stress at BG-MT caused greater decreases in yield and yield components in Experiment 2. This was probably due to higher temperature and more bright sunshine hours quicker evapotranspiration in this experiment. Karmar (1963), Salim, Todd and Schehuber (1965) and Robbins and Domingo (1962) have all suggested that severe soil moisture stress must be avoided from booting to maturity for maximum wheat yield. In these experiments harvest index was decreased by 24 and 34% in Experiments 1 and 2 respectively. At other stages it was decreased by only 2 to 12%. With water stress at BG-MT the decreases in grain weight were much larger than the decreases in straw weight. With water stress at earlier periods the decreases in grain weight and straw weight were more similar, so that harvest index was affected to a lesser extent.

Other workers have also reported that moisture stress decreases harvest index (Passioura, 1977; Hodges, 1978; Rasmussen, 1979; Deloughery and Crookston, 1979).

Water stress at BG-MT increased nitrogen % in the grain. The increase was greater in Experiment 2, possibly due to higher temperature and more moisture stress as found by Laing and Fischer (1977) and Law et al. (1978). Jensen and Mogensen (1984) found that moisture stress prior to heading resulted in an increased percentage of nitrogen in the grain.

The duration of the period from booting to maturity was similar in all varieties except for Norman in Experiment 2. In this case this variety took fewer days than the other varieties possibly due to its earlier sowing. Levitt (1980) also found that early sowing resulted in early maturity.

Water stress at BG-MT decreased grain yield more than at other stages mainly as it caused a larger reduction in average grain weight. Average grain weight was decreased by 35 to 37% with water stress at BG-MT and by only 1 to 7% at other stages. Bruckner and Frohberg (1987) found that high temperatures during grain filling tended to stop grain growth prematurely and hasten physiological maturity. In these experiments water stress at BG-MT decreased the rate of grain growth more than water stress at other stages. However Mogensen and Talukder (1987) found that growth rate of grain was higher with water stress during grain filling compared with unstressed treatments. Duration of grain growth was slightly increased in Experiment 2 but decreased in Experiment 1.

In these experiments (Wembley) average grain weight was lower in the short duration variety than in the longer

duration wheat varieties.

There was little evidence to suggest that water stress at BG-MT decreased yield more in any one variety than another. Water stress decreased grain weight per plant of Norman, Fenman and Wembley by 70%, 58%, and 65%, respectively in Experiment 1 and by 70%, 75%, and 62%, in Experiment 2. Average grain weight was decreased less in Wembley (29%, 21% in Experiment 1 and 2 respectively) than in Norman (47%, 37%) and Fenman (38%, 40%).

The longer duration varieties had larger leaf area at anthesis and as a consequence the soil dried out very quickly, resulting in rapid senescence. In Wembley, leaf area was lower at anthesis, soil drying was less rapid and hence average grain weight was less affected.

3.4.3 INCREASE IN DRY WEIGHT PER PLANT BETWEEN ANTHESIS AND HARVEST AND CONTRIBUTION OF STEM RESERVE TO GRAIN FILLING

The contribution of stem reserve to grain filling and increase in dry weight between anthesis and harvest were calculted by following the method of Gallagher, Biscoe and Scott (1975). If the increase in total crop dry weight is less than grain weight, it means that stem reserves have been used for grain filling. If the increase in total crop dry weight is more than grain weight it means no contribution of stem reserves to grain filling.

Increase in dry weight between anthesis and harvest was calculated as:

Total dry weight per plant at harvest (g) - Total dry weight per plant at anthesis (g)

The contribution of stem reserves to final grain weight was calculated as:

Grain weight per plant at harvest (g) - Increase in dry weight per plant (g)

In the water stress experiments the coefficients of variation for grain weight per plant (11%, 26% in Experiments 1 and 2) were lower than those for increase in dry weight between anthesis and harvest (42.7%, 78.5%) and for contribution of stem reserve to grain filling (369%, 358%). These very high coefficients make it difficult to detect significant differences between treatments.

3.4.3 1 Increase in dry weight per plant between anthesis and harvest.

The increase in dry weight between anthesis and harvest was significantly decreased by water stress at BG-MT in both experiments and at TL-SE in Experiment 2 as shown in Table 33. It was significantly lower in Norman than in other varieties in Experiment 2 only shown in Table 34. The variety X water stress interaction was significant in Experiment 1 but not in Experiment 2 as shown in Table 35. The increase in dry weight between anthesis and harvest was greater in Norman than in Fenman in the control, but not in the stressed treatments.

3.4.3.2 Stem reserve contribution to grain filling.

The interaction between water stress and variety for stem reserve contribution to grain yield was also significant in Experiment 1 but not in Experiment 2 as shown in Table 36. In Experiment 1, in Norman there was no contribution of stem reserves with water stress at TL-SE, SE-BG and in the control but there was a contribution with water stress at BG-MT. In Fenman stem reserves made a larger contribution to grain

Table 33 Main effects of water stress at different growth stages on increase in dry weight between anthesis and maturity and stem reserve contribution to grain yield in Experiments 1 and 2.

	Stages					
	TL-SE	SE-BG	BG-MT	Control	S.E.M.	L.S.D. (P=0.05)
Experiment 1						
Increase in dry weight between anthesis and maturity (g) per plant	2.22	2.81	0.28	2.92	0.25	0.75
Stem reserve contribution to grain yield (g) per plant	0.04	-0.34	0.87	0.34	0.24	0.92
Experiment 2						
Increase in dry weight between anthesis maturity (g) per plant	1.07	2.26	0.21	2.73	0.36	1.36
Stem reserve contribution to grain yield (g) per plant	0.72	-0.49	0.71	0.37	0.34	1.29

Table 34 Main effects of varieties on increase in dry weight between anthesis and maturity and stem reserve contribution to grain yield in water stress Experiments 1 and 2.

	Varieties				
	Norman	Fenman	Wembley	S.E.M.	L.S.D. (P=0.05)
Experiment 1					
Increase in dry weight between anthesis and maturity (g) per plant	2.38	1.75	2.04	0.22	N.S.
Stem reserve contribution to grain yield (g) per plant	-0.22	0.78	0.11	0.21	0.72
Experiment 2					
Increase in dry weight between anthesis and maturity (g) per plant	0.31	2.72	1.68	0.31	1.46
Stem reserve contribution to grain Yield (g) per plant	2.11	-0.82	-0.31	0.30	1.01

Table 35 Effect of varieties and water stress on increase in dry weight (gram per plant) between anthesis and maturity in Experiments 1 and 2.

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	2.38	2.36	1.91
Stem extension to booting	3.09	2.55	2.80
Booting to maturity	-0.08	0.21	0.94
Control	4.37	1.88	2.52
S.E. of means = 0.44; L.S.D. (P = 0.05) = 2.18			
Experiment 2			
Tillering to stem extension	-0.34	2.03	1.53
Stem extension to booting	2.02	2.77	1.99
Booting to maturity	-1.00	0.97	0.67
Control	0.55	5.09	2.54
S.E. of means = 0.62; L.S.D. (P = 0.05) = N.S.			

Table 36 Effect of varieties and water stress on stem reserve contribution to grain yield in Experiment 1 and 2.

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	-0.80	0.36	0.56
Stem extension to booting	-0.71	0.05	-0.38
Booting to maturity	1.39	0.20	0.02
Control	-0.76	1.52	0.26
S.E. of means = 0.42; L.S.D. (P = 0.05) = 2.06			
Experiment 2			
Tillering to stem extension	-0.26	-0.37	-0.17
Stem extension to booting	0.21	-1.00	-0.69
Booting to maturity	-2.15	-1.14	0.10
Control	3.38	-1.76	-0.51
S.E. of means = 0.58; L.S.D. (P = 0.05) = N.S.			

filling with water stress at TL-SE, BG-MT and in the control than with water stress at and SE-BG. In Wembley stem reserve made a contribution to grain filling in the control and with water stress at TL-SE. In the control Fenman had a significantly higher stem reserve contribution than Norman.

In Experiment 2 the main effects of variety and water stress were significant shown in Tables 33 and 34. Stem reserve contribution was significantly higher in Norman than in Fenman and Wembley. In these varieties stem reserves made no contribution to grain filling. Water stress at TL-SE and BG-MT resulted in similar and higher contributions than water stress at SE-BG and in the control shown in Table 33. With water stress at SE-BG stem reserves made no contribution to grain filling.

An attempt was made to relate the data for soluble carbohydrate content at anthesis with the estimated contributions of stem reserve to grain filling. Most of the reserves which are retranslocated are soluble carbohydrate (Rawson and Evans 1971). These workers measured the contribution of soluble carbohydrates to grain yield under different conditions, but found that they could have contributed only a small proportion to grain filling. This was less than 5% in cultivars, and possibly up to 9.3% in Mexico 120 and 12.2% in Sonora. Yu et al. (1964) and Wardlaw and Porter (1967) have reported that reserves contributed 10% at most.

In these experiments comparing tables (12) and (33) shows that there were no relationships between two sets of results. Whereas the total contents of soluble carbohydrate were in the range 9.52 to 19.76 mg per plant, the estimated stem reserve

contribution to grain yield varied between nothing and 870 mg per plant. In Experiment 1 soluble carbohydrate content was decreased by water stress at all stages, whereas stem reserves made a contribution to grain yield only in the plants stressed from BG-MT and in the controls. There was some evidence of a relationship in Experiment 2, in which water stress at SE-BG resulted in a significant decrease in soluble carbohydrate content and no contribution of stem reserves to grain filling. However data for the other treatments were inconsistent. The increase in dry weight between anthesis and harvest were compared with the final average grain weight and rate of grain growth (Tables 14 and 15 were compared with Table 33). It shows that faster rate and lowest increase were observed with water stress BG-MT, which gave lowest average grain weight in both years, as repoted by Spiertz (1977). At other stages the trends were not clear.

In between varieties comparison of (tables 15 and 34) shows that soluble carbohydrate content and stem reserve contribution to grain yield were both greatest in Fenman in Experiment 1 and Norman in Experiment 2. However data for the other varieties were not consistent. In between varieties comparison of increase, rate of grain growth and average grain weight shows no clear trends.

The negative values in the tables show that the incrase in dry weight between anthesis and harvest was greater than grain weight and hence there was no contibution of stem reserve to grain filling.

3.4.4 RELATIONSHIP BETWEEN YIELD AND YIELD COMPONENTS

Values of the correlation coefficient between grain yield and the various yield components were calculated combining the data for all treatments and are shown in Table 37 for Experiment 1 and 2 respectively.

In both experiments grain weight per plant was positively correlated with average grain weight per plant, number of grain per plant, number of grain per ear. Grain weight per plant was not correlated with number of ears per plant in both experiments. Grain weight per plant was correlated with fertile spikelets per ear and number of grains per fertile spikelet in Experiment 2 but not in Experiment 1. Grain weight per plant was also correlated with straw weight per plant in both experiments and harvest index in Experiment 1 only. The number of grains per plant was correlated with the number of fertile spikelets per ear and number of grains per ear in both years. Number of grain per ear was positively correlated with fertile spikelet per ear in both years.

In the tables for yield and yield components, the abbreviations are used:

GWPP = Grain weight per plant (g)

AGWM = Average grain weight (mg)

GNPP = Grain number per plant

ENPP = Number of ears per plant

GNPE = Number of grain per ear

FSPE = Fertile spikelets per ear

GNPFS = Number of grain per fertile spikelets

HIND = Harvest index %

Table 37 Values of the linear correlation coefficient between the grain yield, yield components in water stress Experiments 1 and 2.

	GWPP	AGWM	GNPP	ENPP	GNPE	FSPE	GNPFS	HIND
Experiment 1								
Average grain weight (mg)	0.77*							
Grain number per plant	0.94*	0.58*						
Ear number per plant	0.40NS	0.66*	0.39NS					
Grain number per ear	0.60*	0.04NS	0.68*	-0.41NS				
Fertile spikelet per ear	0.47NS	0.07NS	0.71*	-0.21NS	0.57*			
Grain number per fertile spikelet	0.53NS	0.03NS	0.54NS	-0.54NS	0.96*	0.31NS		
Harvest index %	0.73*	0.86*	0.52NS	0.55NS	0.04NS	-0.04NS	0.06NS	
Straw weight per plant (g)	0.66*	0.22NS	0.79*	-0.08NS	0.86*	0.68*	0.78*	-0.01NS
Experiment 2								
Average grain weight (mg)	0.62*							
Grain number per plant	0.94*	0.32NS						
Ear number per plant	0.39NS	0.20NS	0.39NS					
Grain number per ear	0.79*	0.28NS	0.86*	-0.13NS				
Fertile spikelet per ear	0.70*	0.10NS	0.84*	-0.01NS	0.91*			
Grain number per fertile spikelet	0.77*	0.35NS	0.80*	-0.20NS	0.98*	0.83*		
Harvest index %	0.40NS	0.76*	0.14NS	0.49NS	-0.10NS	-0.28NS	-0.06NS	
Straw weight per plant (g)	0.70*	0.08NS	0.84*	0.03NS	0.89*	0.95*	0.82*	-0.35*

NS = $P > 0.05$

* = $0.01 < P < 0.05$

3.4.5 RELATIONSHIP BETWEEN FINAL AVERAGE GRAIN WEIGHT, RATE AND DURATION OF GRAIN GROWTH AND TOTAL LEAFAREA AT ANTHESIS.

The values of the correlation coefficient between average grain weight, rate and duration of grain growth and total leaf area at anthesis are shown in table 38.

A number of workers (Asana and Basu, 1963; Welbank et al., 1966; Sofield et al., 1977; Spiertz, 1977; Mogensen and Talukder, 1987; Spiertz and Vos, 1984) have reported that grain yield depends on the leaf area index at anthesis and upon how long the leaves and other green parts of the plants stay green. The green leaf area of the plant available for filling the grain depends on the temperature and stress. Therefore the relationship between these characters, final average grain weight, rate and duration of grain growth and total leaf area at anthesis were examined.

In these experiments final average grain weight was positively correlated with total leaf area index in both experiments. Rate and duration of grain growth were correlated with total leaf area index in Experiment 2 only. The correlation between rate and duration of grain growth was only significant in Experiment 2.

This suggests that high leaf area at anthesis increases the rate and duration of grain growth and increases average grain weight. It is also important that the leaves stay green for as long as possible, but leaf area duration was not measured in these experiments.

Table 38 Values of the linear correlation coefficient between the final average grain weight, rate of grain growth, duration of grain growth and total leaf area (leaf+flagleaf+stem+ear) at anthesis in water stress Experiments 1 and 2.

	Final average grain weight (mg)	Rate of grain growth (mg/day)	Duration of grain growth per plant (days)
Experiment 1			
Rate of grain growth (mg/day)	0.75*		
Duration of grain growth per plant (days)	-0.23 N.S.	-0.38 N.S.	
Total leaf area per plant (cm)	0.60*	0.38 N.S.	0.35 N.S.
Experiment 2			
Rate of grain growth (mg/day)	0.95*		
Duration of grain growth per plant (days)	-0.34 N.S.	-0.60*	
Total leaf area per plant (cm)	0.61*	0.71*	-0.55*

N.S. = $P > 0.05$

* = $0.01 < P < 0.05$

3.4.6 DIFFERENCES BETWEEN VARIETIES

In both these experiments, long, medium, and short duration wheat varieties were tested. Long duration wheat varieties (Norman) are sown in October. These varieties produce 11 to 13 leaves although this depends upon the sowing time. These varieties which require vernalization take a long time from germination to stem elongation. Long duration varieties grow under lower temperature for 4 to 6 months compared to mid duration and spring wheat varieties. In these experiments because of low temperature and few hours of bright sunshine the leaves of these varieties were large and narrow. In these experiments the long duration variety (Norman) produced 1 to 3 tillers, a large strong stem, 5 to 6 stem nodes, large ears, more spikelets, higher grain yield, higher average grain weight, higher grain number and dry matter production than spring varieties as found by Austin et al., (1980). Medium duration wheat varieties are normally sown by mid winter, approximately February. These varieties grow for a short time before vernalization, approximately 1 to 2 months. In these experiments, Fenman produced 9 to 10 leaves, 2 to 4 tillers, medium size ear, plant height approximately 70 to 80 cm of main stem, and 4 to 5 detectable stem nodes. Short duration or spring wheat varieties are normally sown after 15th March. They produce more tillers after germination within a few weeks because of more bright sunshine and high temperature. In these experiments, Wembley produced 8 to 9 leaves, had a short straw length and only 3 to 4 detectable stem nodes appeared. In these experiments spring wheat variety (Wembley) had a lower average grain

weight because of short duration during grain filling. In these experiments, Wembley gave lower yield, lower number of grains per plant, lower average grain weight, increased infertile spikelets per ear, increased nitrogen % in grain and straw as found by other workers (Riggs and Hayter, 1975; Laing and Fischer, 1977; Law et al., 1978).

In these Experiments Norman was the most sensitive variety at all stages under water stress. This was because this variety had a long period to grow and to complete each period. The other varieties were mostly sensitive at BG-MT but still less sensitive than Norman. Fenman and Wembley at TL-SE and SE-BG were tolerant varieties.

CHAPTER 4

SALINITY EXPERIMENTS

4.1 INTRODUCTION

The two experiments, Experiment 1 (October 1987-September 1988) and Experiment 2 (October 1988 to September 1989), were carried out at Aber Farm, U.C.N.W., Bangor. The main purpose of the experiments was to determine the effects of salinity at three growth stages on three contrasting wheat varieties. The varieties tested were the same as those used in the water stress experiments, so that the effects of water stress and salinity could be compared.

4.2 MATERIALS AND METHODS

In both experiments plants were grown in unheated glasshouses and no supplementary lighting was used.

4.2.1 Germination: Seeds of all varieties were first tested in an incubator at 25°C to check the germination %. The germination % of each variety was approximately 80 to 90% (details of germination percentage are shown in section 3.2.3). At the start of each sowing sufficient seeds were put in muslin cloth and soaked under running taps overnight. The seeds were placed on capillary matting stretchedover a plastic grid reinforced by wires and placed on top of a plastic bowl. The bowl size was 340 x 270 x 130 mm. There was 5g 'Phostrogen' (Phostrogen Ltd., Corwen, Clwyd) used in the bowls to supply nutrients and the bowls were filled with tap water. To ensure adequate nutrient and moisture supply to the germinating seeds, wicks of capillary matting were always put inside in the water. The seeds were covered with newspaper for two to four days for darkness. When germination started the news-

papers were removed. Pregermination took between 12 to 15 days. It was done in a growth room set at 25°C with continuous lighting. Seedlings were transplanted when the shoots were approximately 8 cm long and had one leaf emerged.

4.2.2 Transplanting: Seedlings were transplanted into holes in polystyrene lids. Each lid was bored with 16 holes using a 9 mm heated cork borer. The lids were placed on 11 litre capacity plastic containers containing the hydroponic solution culture. The containers were 23cm x 23 cm surface by 23 cm deep as shown in Figures 17 to 19. Seeds were supported by foam in each hole. Sixteen plants were sown per lid. The spacing between plants and row to row was approximately 6 cm. The plant density was calculated to be 300 plants per m^2. The pots were painted with bituminised black paint on the outside to prevent growth of algae in the nutrient solution. Also the polystyrene lids were painted black on the surface and sides. Dates of sowing, transplanting and harvesting of all varieties are shown in Table 39.

4.2.3 Nutrient solution culture: The nutrient solution in the pots was changed every two weeks. Ten grams of Phostrogen was added to each pot to supply macro nutrients. The composition of Phostrogen is listed below:

Total nitrogen	10%
Phosphorous pentoxide	10%
Potassium oxide	27%
Magnesium	13%
Manganese	0.02%

Micronutrients were supplied by modified Long Ashton solution (Hewitt, 966). The micronutrients were first prepared

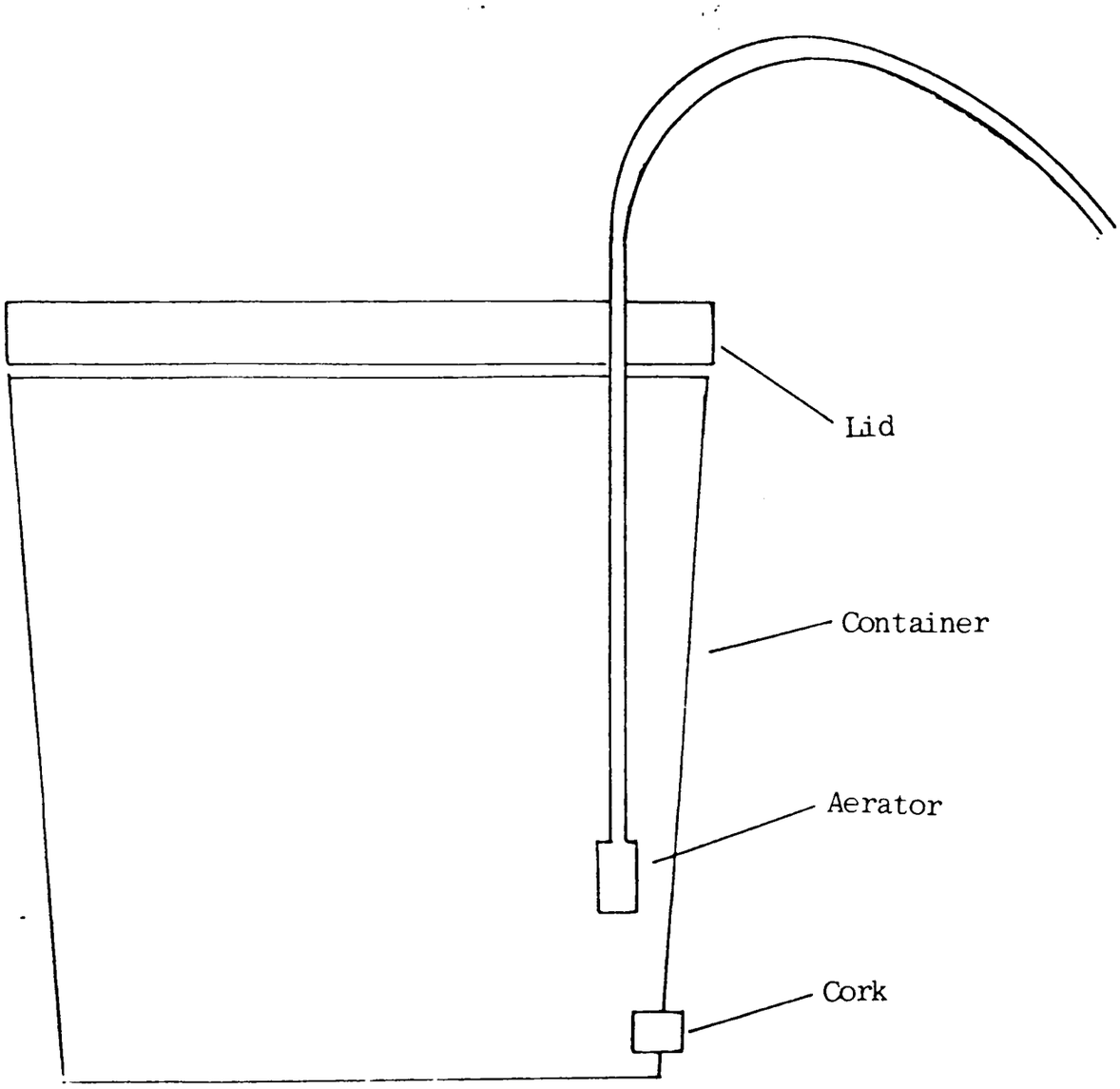


Figure 17 Growth container used in salinity experiments

Growth container, showing aeration line, drainage hole and lid

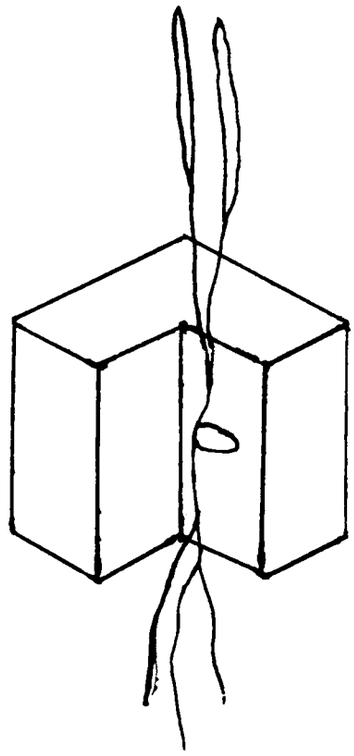


Figure 18 Expanded diagram of supportive foam collar around seedling and position of seed in collar.

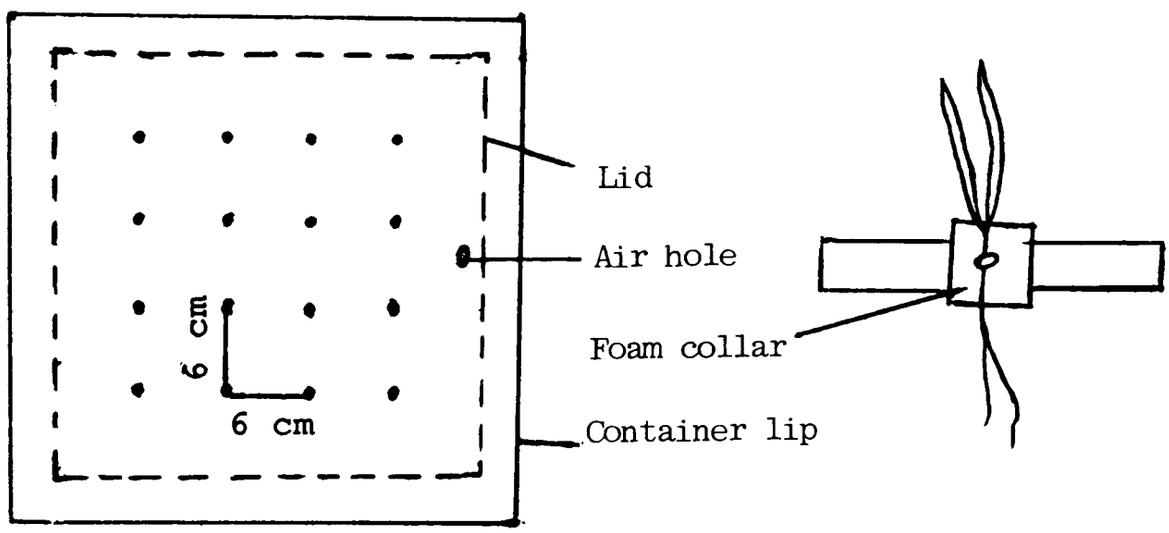


Figure 19 Polystyrene lid, showing spacing between holes, plus sectional view showing foam collar seated in lid.

Table 39 Dates of sowing, transplanting, harvesting and total number of days from sowing to harvest (in parentheses) for the three varieties of wheat and four treatments tested in salinity stress experiments

	Variety		
	Norman	Fenman	Wembley
Experiment 1			
Date pre-germination started	22.10.87	22.2.88	7.4.88
Date of transplanting	6.11.87	8.3.88	17.4.88
Date of harvesting individual treatments			
Tillering to stem extension	22.6.88	9.7.88	7.8.88
Total days	(245)	(138)	(122)
Stem extension to booting	22.6.88	9.7.88	7.8.88
Total days	(245)	(138)	(122)
Booting to maturity	22.6.88	9.7.88	27.7.88
Total days	(245)	(138)	(111)
Control	22.6.88	9.7.88	7.8.88
Total days	(245)	(138)	(122)
Experiment 2			
Date pre-germination started	2.11.88	3.3.89	5.4.89
Date of transplanting	13.11.88	15.3.89	17.4.89
Date of harvesting individual treatments			
Tillering to stem extension	23.6.89	14.7.89	28.7.89
Total days	(233)	(132)	(114)
Stem extension to booting	23.6.89	14.7.89	28.7.89
Total days	(233)	(132)	(114)
Booting to maturity (at anthesis time)	6.6.89	30.6.89	14.7.89
Total days	(216)	(118)	(100)
Control	23.6.89	14.7.89	28.7.89
Total days	(233)	(132)	(114)

as stock solutions which were added to each pot. The quantities of each micronutrient were as follows:

Micronutrient	Stock solution (mM)	Amount added per pot (ml)
$MnSO_4.H_2O$	99.97	1
$CuSO_4.5H_2O$	10.01	1
$ZnSO_4.7H_2O$	10.45	1
H_3PO_4	501.35	1
$Na_2.Mo_4.2H_2O$	5.00	1
Fe.EDTA	101.70	5

Air was supplied from a compressor. It was supplied to each pot for all replications. It was checked regularly for working condition.

4.2.4 Varieties and salinity treatments tested

Three varieties were tested. They were: Norman a winter variety of long duration; Fenman, a mid winter variety, with low vernalization requirement and suitable for spring sowing; Wembley, a spring variety of short duration. The seeds of Norman and Fenman were supplied by the Plant Breeding Institute, Cambridge, U.K. The seed of Wembley was supplied by U.C.N.W., Bangor, U.K. The four treatments tested involved introducing salinity into the nutrient solution during the following growth stages. (1) From the start of tillering to the start of stem extension (first node detectable), (2) from the start of stem extension to the start of booting, (3) from the start of booting to maturity, (4) control (no salt applied). Stress was applied when the

appropriate stage was shown in 75% of all plants and was stopped when the following stage was shown in 75% of plants. The dates of starting and stopping stress are shown in results sections Table 41. The level of salinity introduced was 125 mM NaCl. For convenience 4 Molar solution was used. The sodium chloride salt was mixed with added calcium chloride by proportion 0.2 mM $CaCl_2$: 125 mM NaCl, to maintain the postassium/sodium ratio (Gorham et al., 1985). Both salts were dissolved to make stock solutions when introducing salinity. The salts were applied in two increments. Two-thirds of the salts were applied on the first day of the stress period. After two or three days the remaining one third was applied.

4.2.5 Experimental design: A randomized complete blocks design was used in both experiments. The varieties were sown in separate, but adjacent parts of the glasshouse to avoid shading of late sown plants (e.g. of Wembley) by early sown plants (e.g. of Norman). Blocks were located in similar positions inside the glasshouse. There were six replications in each experiment. Four replications were used for determination of tiller number, leaf number, plant height and for harvesting at maturity. Two replications were used for destructive harvests.

4.2.6 Measurements: Leaf appearance stage, shoot number and plant height were recorded on the central four plants of each pot of four replications at two week intervals. Leaf appearance was counted as the number of leaves appeared on the main shoot. The third, fifth and seventh leaves were marked with white fluid to help in recognizing the leaves. Plant

height was measured from the surface of the polystyrene sheet to the tip of the top leaf.

4.2.7 Growth analysis: For growth analysis two plants were harvested from each pot from two replications at the end of each stress period. Leaf area, stem area, dry weight and nitrogen % were recorded in the same way as the water stress experiments (Section 3.2.5). At anthesis an additional two plants were harvested. At this stage the percentage of water soluble carbohydrates were also determined using the method of Deriaz (1961), Thomas (1977), as in the water stress experiments (Section 3.2.5.4). Nitrogen % was determined using the Kjeldahl method (A.O.A.C., 1955).

4.2.8 Grain growth analysis: Starting fourteen days after anthesis two main shoot ears were harvested each week from each pot of two replications. The ears were dried at 70 to 80^{o}C in an oven for two to three days. After drying the ears were threshed and then the grains were redried. Then the grains were counted and weighed to obtain average grain weight. Rate and duration of grain growth were calculated as in the water stress experiments (Section 3.2.5.6).

4.2.9 Harvest yield and yield components

All 16 plants from each pot of four replications were harvested at maturity. The plants were harvested by cutting the stems at the surface of the polystyrene sheet. The harvesting dates of each treatment are shown in Table 39. The ears were counted and then ten ears were selected at random to count the number of fertile and infertile spikelets. Straw length was measured on 10 stems selected at random. Height was measured from the harvested point to the top of the

ears. The harvested samples were then separated into ears and straw. After drying both samples were weighed. The ears were threshed using a small scale threshing machine.

Grain numbers were counted by using an automatic seed counter (Numigrale-Tecator Hogames, Sweden). Then the grains were weighed. After milling the straw and the flour of wheat was used to determine nitrogen % using the Kjedahl method (A.O.A.C., 1955). Finally all the yield components were calculated. Number of grains per plant, number of ears per plant, grain weight per plant, number of grains per ear, number of grains per spike, number of fertile and infertile spikelets per ear, average grain weight and harvest index were calculated.

4.2.10 Temperature: Daily maximum and minimum temperature were recorded throughout the experiments using a thermometer inside the glasshouse.

4.2.11 Pesticide and insecticide: The plants were checked from time to time for the presence of pests and diseases. Powdery mildew and aphids were the main problems noted. Powdery mildew was controlled using the fungicide fenpropimorph (Mistral, Rhone and Poulenc) at the recommended dose.

Aphids were controlled by spraying dimethoate systematic insecticide (Murphy insecticide, Rhone and Poulenc) at the recommended dose.

4.3 RESULTS

4.3.1 WEATHER CONDITIONS EXPERIENCED DURING THE SALINITY EXPERIMENTS

Salinity Experiment 1 was done in the same glasshouse as water stress Experiment 1, and weather conditions experienced are described in Sections 3.3.1 and 3.3.1.3. Salinity Experiment 2 experienced similar daylength and sun hours as water stress Experiment 2 and these are described in Sections 3.3.1.1, 3.3.1.2 and 3.3.1.4.

4.3.1.1 Average temperature during growing varieties in salinity Experiment 2

Average temperatures recorded in the glass house during salinity Experiment 2 are shown in Figure 20. Average temperature ranged between 6 and 15^{o}C up to 25 weeks. After 25 weeks, it increased up to 32^{o}C. Norman experienced cold temperature up stem extension after which temperature increased. Fenman experienced a shorter time under cold temperature because it was sown in February. When Wembley was sown the temperature was around 16^{o}C. When all varieties were harvested the temperature was more than 24^{o}C.

4.3.1.2 Average temperature at different growth stages in salinity Experiments 1 and 2

Average temperatures (^{o}C) experienced by each variety during stress periods in salinity Experiments 1 and 2 are shown in Table 40. In both years during different stages in different varieties, the temperature trend was very similar. In both years the average temperatures experienced by Norman during TL-SE were approximately half those experienced by

Fig.20. Average weekly temperature during growing varieties in salinity Experiment 2

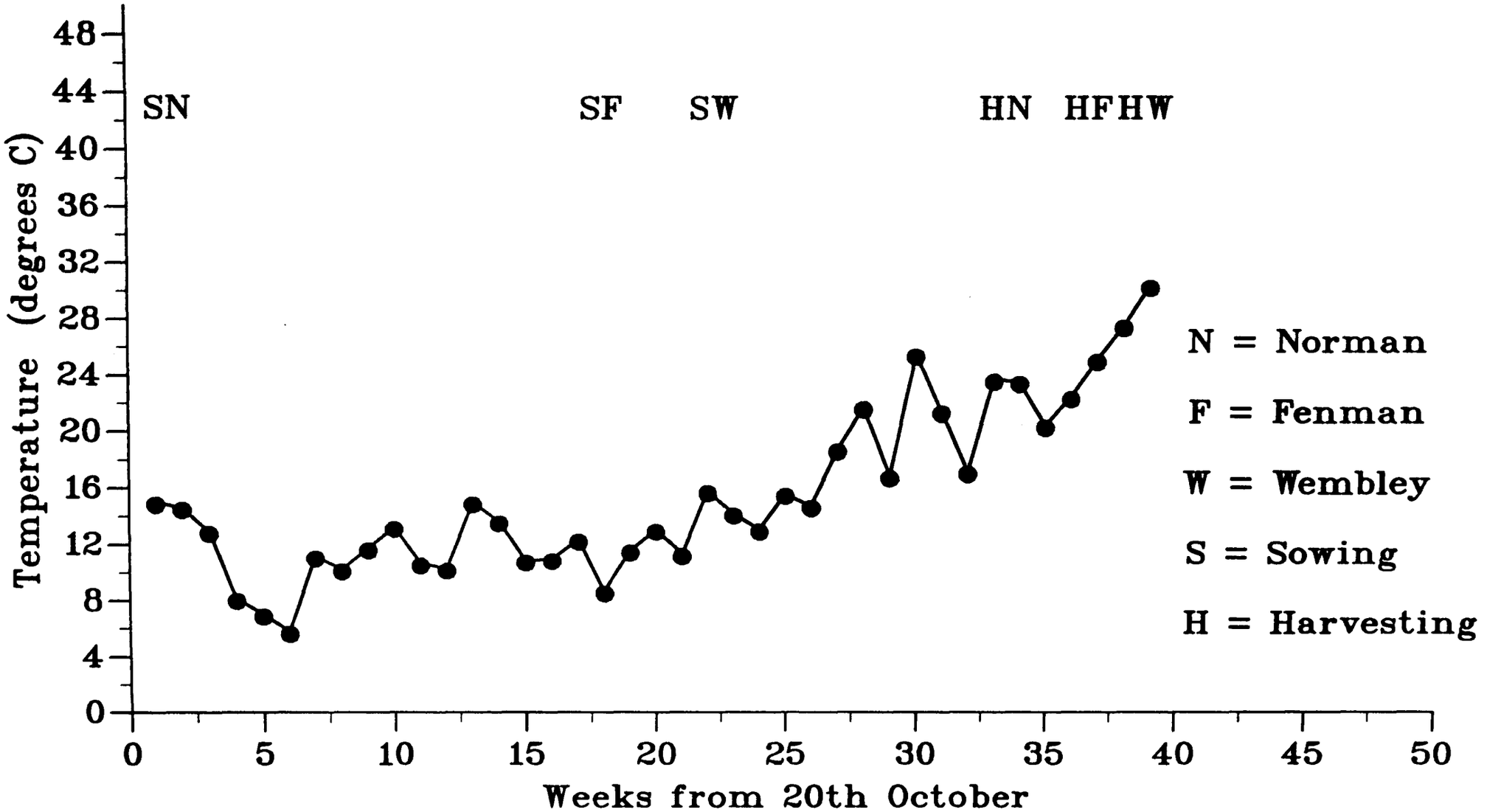


Table 40 Average temperature (^{o}C) experienced by each variety during stress periods in salinity Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	7.80	16.19	20.12
Stem extension to booting	14.01	20.12	21.72
Booting to maturity	21.23	22.44	22.61
Control	13.26	15.95	21.45
Experiment 2			
Tillering to stem extension	11.60	16.39	19.15
Stem extension to booting	14.27	21.4	20.29
Booting to maturity	19.50	22.08	22.90
Control	14.32	18.72	21.18

Wembley. The average temperatures experienced during SE-BG were also much lower in Norman than in Fenman and Wembley. Average temperatures experienced during BG-MT were similar for all varieties. Over the whole growth period the average temperature experienced increased as the duration of the variety decreased. Average temperatures were also higher in Experiment 2 than in Experiment 1. In both years for Norman temperatures were particularly low during TL-SE.

4.3.2 DATES OF STARTING AND STOPPING SALINITY STRESS

The durations of the different stages are shown in table 41. The durations of the stress periods TL-SE and SE-BG were longer in Norman than in Fenman, and generally longer in Fenman than in Wembley. The duration of the period BG-MT showed much smaller variation between varieties. It was longer in Norman than in Wembley in Experiment 1, but there was little difference in the length of this period between varieties in Experiment 2.

4.3.3 NUMBER OF LEAVES APPEARED ON THE MAIN STEM

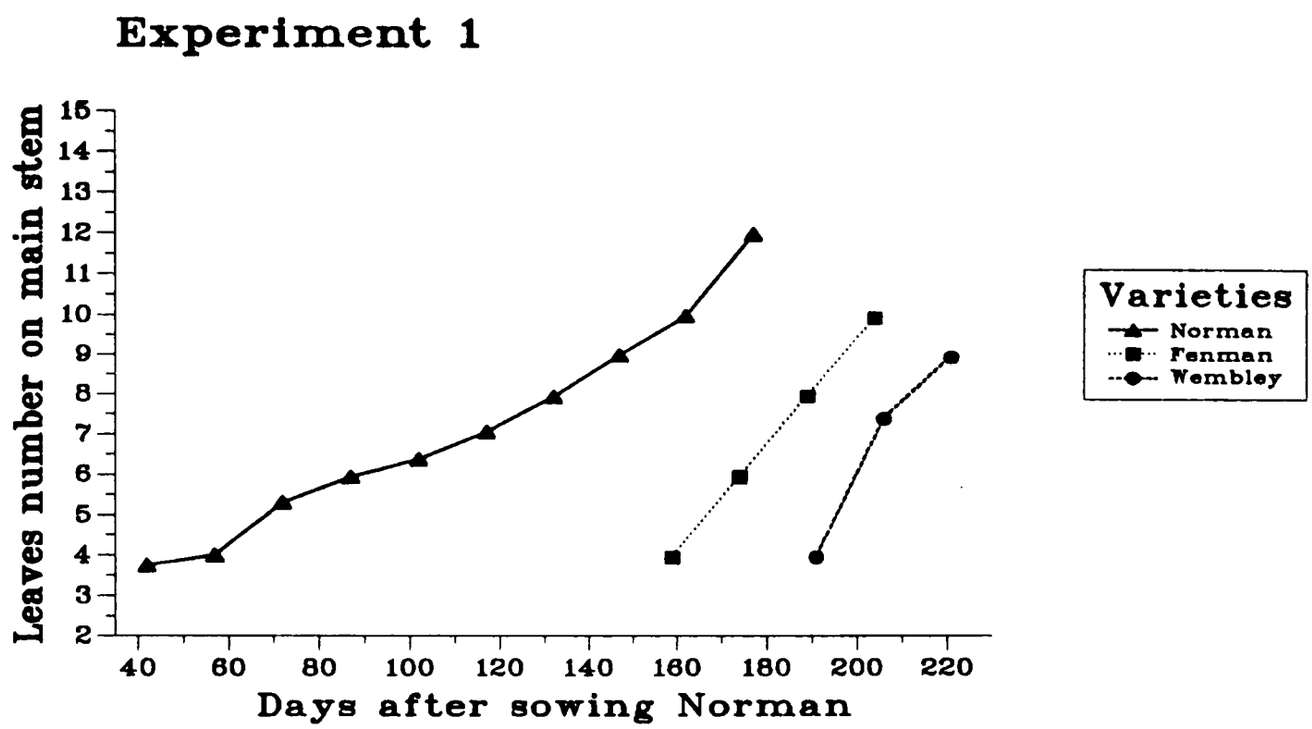
In salinity Experiments 1 and 2, the number of leaves appeared on the main stem of the different varieties are shown in Figure 21. Norman had more leaves than Fenman and Fenman had more leaves than Wembley. In Norman leaf appearance took between 180-190 days, in Fenman it took 80 to 90 days and in Wembley it took 50 to 60 days. During growing of Norman, from germination to stem extension, there was cold season. Up to that time leaves appeared slowly, but after stem extension leaves appeared more quickly. Fenman was sown during

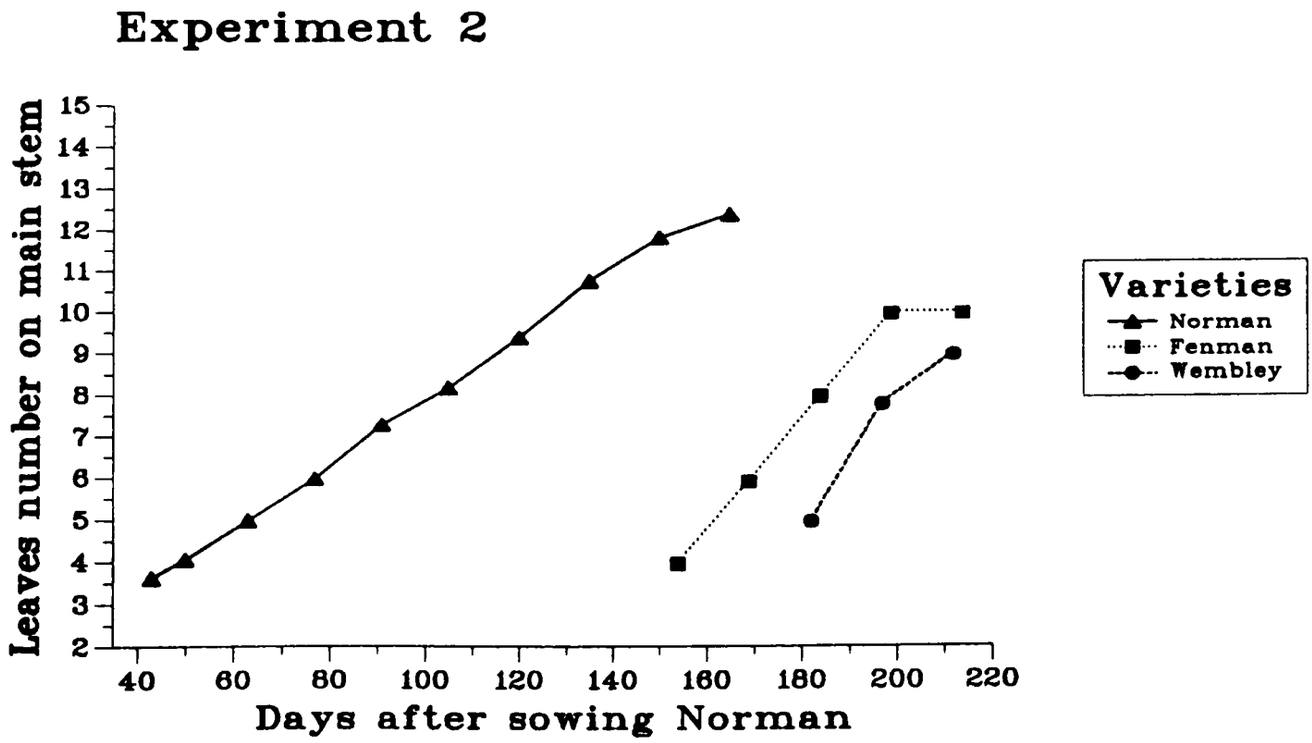
Table 41 Dates of starting and stopping salinity stress and total days under stress at each stage for each variety in Experiments 1 and 2*

	Stages		
	Tillering to stem extension	Stem extension to booting	Booting to maturity
Experiment 1			
Norman			
Date stress started	28.11.87	9.3.88	21.4.88
Date stress stopped	9.3.88	21.4.88	22.6.88
Total days under stress	103	43	63
Fenman			
Date stress started	28.3.88	25.4.88	13.5.88
Date stress stopped	25.4.88	13.5.88	9.7.88
Total days under stress	29	18	57
Wembley			
Date stress started	27.4.88	15.5.88	29.5.88
Date stress stopped	14.5.88	29.5.88	2.7.88
Total days under stress	18	15	35
Experiment 2			
Norman			
Date stress started	14.12.88	3.3.89	25.4.89
Date stress stopped	3.3.89	2.5.89	6.6.89
Total days under stress	80	60	43
Fenman			
Date stress started	3.4.89	9.5.89	22.5.89
Date stress stopped	9.5.89	22.5.89	30.6.89
Total days under stress	66	17	40
Wembley			
Date stress started	27.4.89	16.5.89	5.6.89
Date stress stopped	18.5.89	5.6.89	14.7.89
Total days under stress	22	21	39

* The control plants were not salinity stressed.

Fig.21: Number of leaves appeared on main stem of control plants in salinity Experiment 1 and 2.





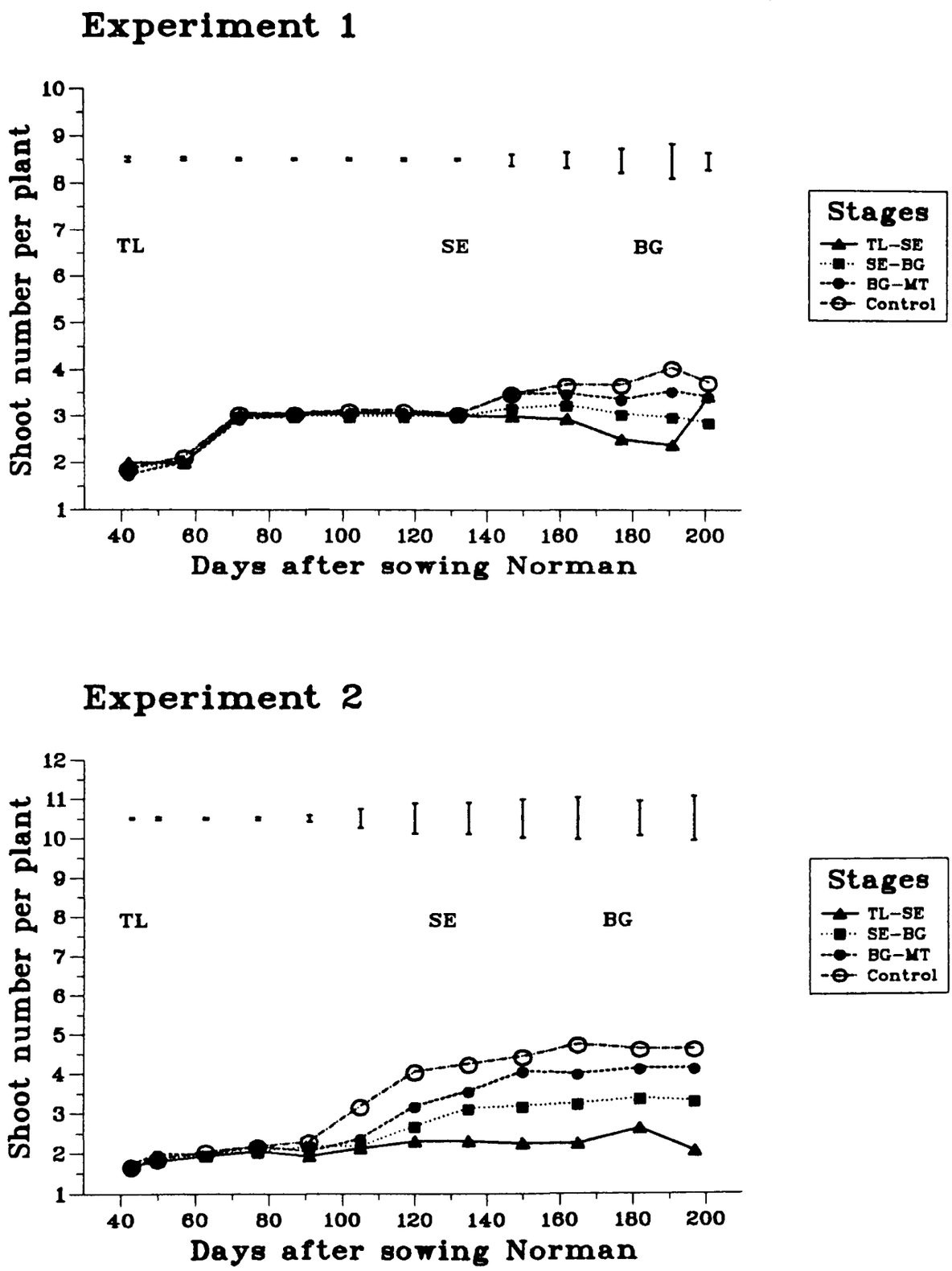
February and experienced short cold periods. In Fenman the first few leaves appeared steadily then other leaves appeared very quickly. In Wembley leaves appeared very quickly, because of high temperatures, long days, and because Wembley is a short duration variety.

In both experiments salinity at TL-SE slightly decreased the number of leaves on the main stem in Norman but not in Fenman and Wembley. The number of leaves was decreased from 12 in the control to 11 with salinity at TL-SE in Norman in Experiment 1 and from 13 to 12 in Experiment 2. Salinity at other stages had no effect on number of leaves. For each treatment the final number of leaves per plant was the same in each replicate, so that for this data the error mean square was zero. It was thus not possible to compute the analysis of variance for this parameter.

4.3.4 NUMBER OF SHOOTS PER PLANT

The effects of salinity at different stages on number of shoots per plant are shown in Figures 22 to 24. At some points there were significant differences between treatments and at some there were not. Salinity at TL-SE generally decreased number of shoots per plant and it did not recover again except in Norman in Experiment 1, where it was slightly increased later on (Figure 22). Applied salinity at SE-BG also decreased number of shoots per plant during the stress period and it did not recover again in all varieties in both years. Salinity at BG-MT decreased number of shoots per plant in Norman (Figure 22) and Fenman (Figure 23) but not in Wembley (Figure 24). Salinity at SE-BG had the greatest

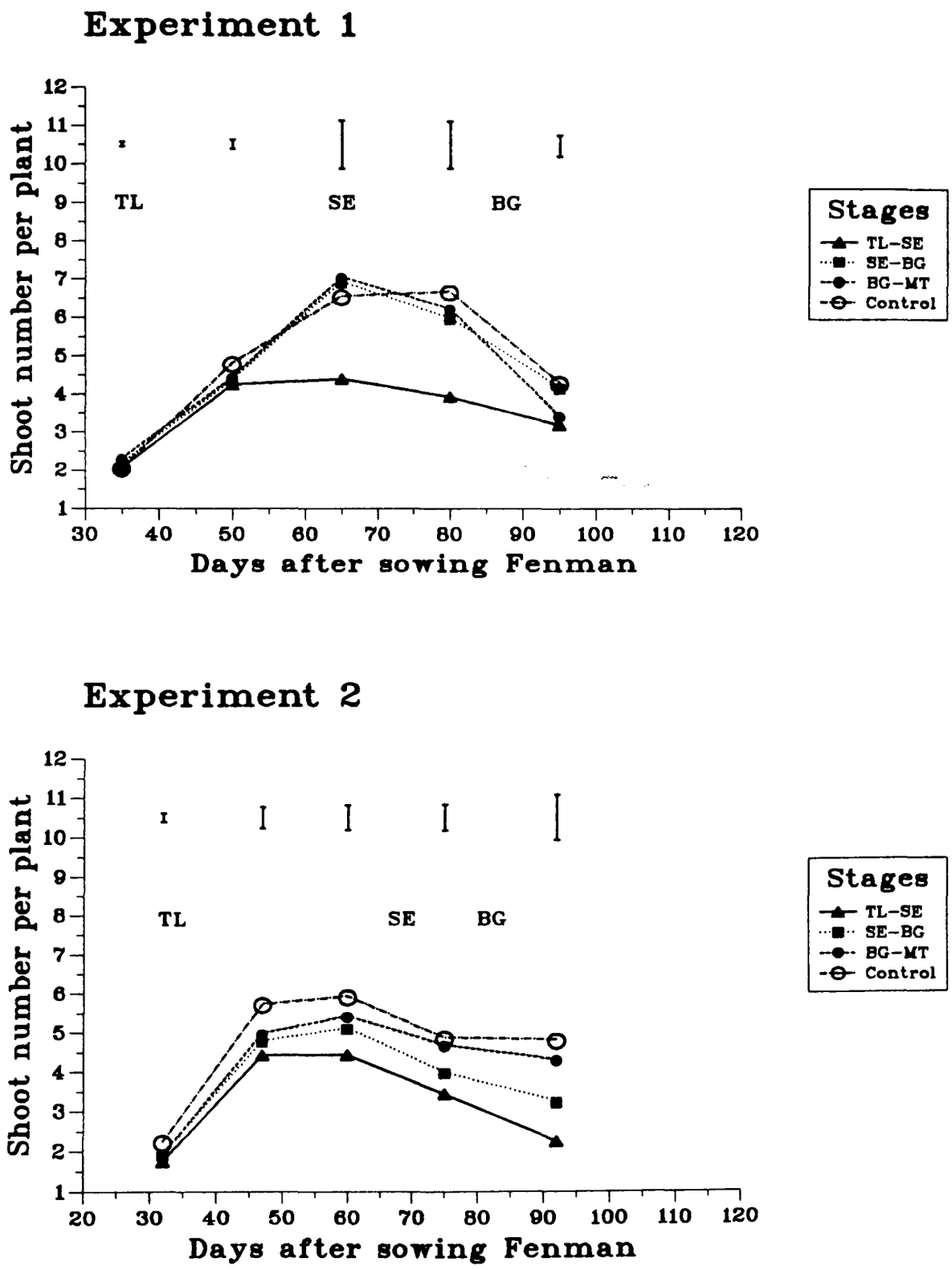
Fig.22: Effect of salinity on shoot number per plant in Norman variety in salinity Experiment 1 and 2.



TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

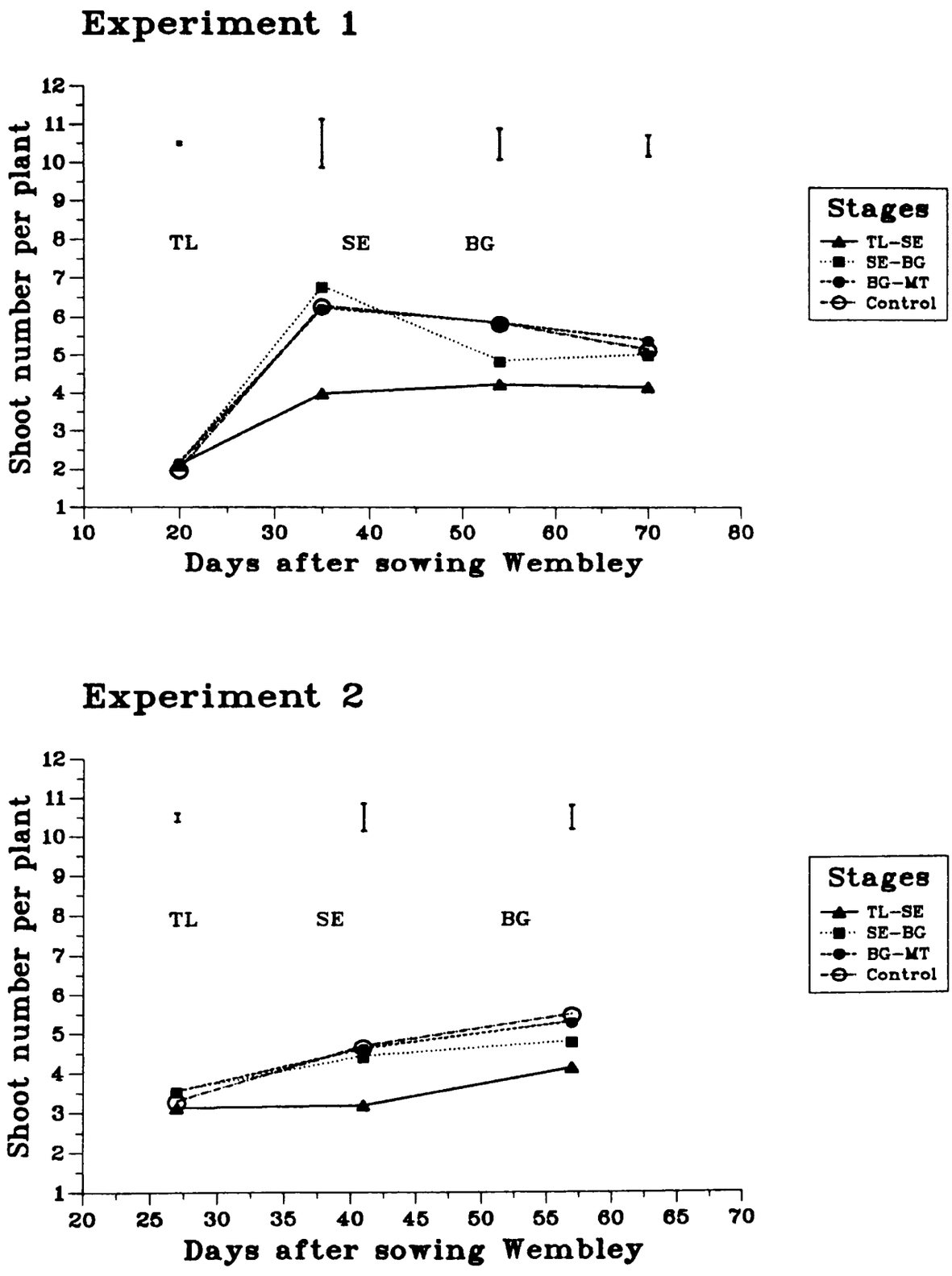
Fig.23: Effect of salinity on shoot number per plant in Fenman variety in salinity Experiment 1 and 2.



TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

Fig.24: Effect of salinity on shoot number per plant in Wembley variety in salinity Experiment 1 and 2.



TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

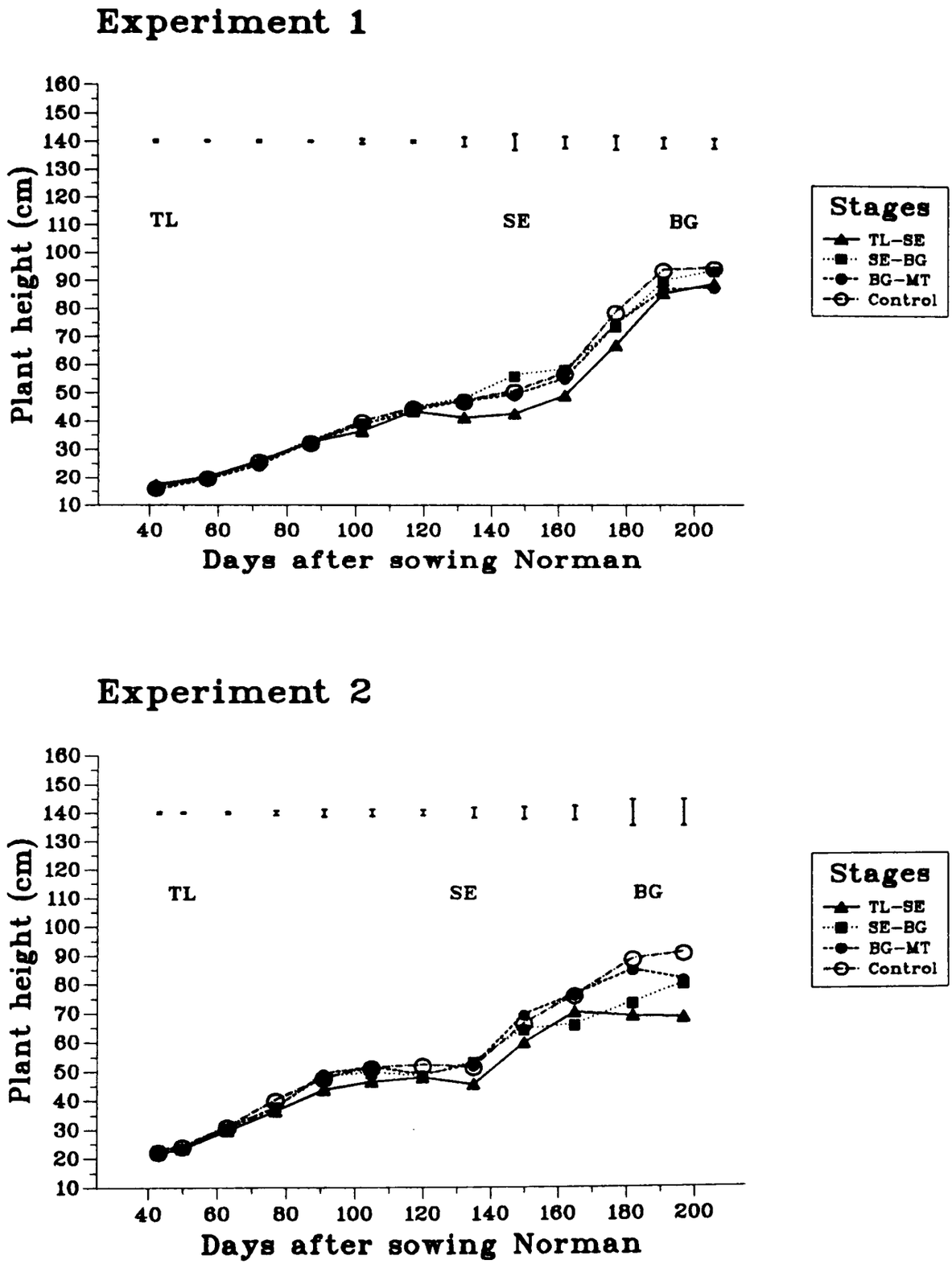
effects on number of shoots per plant and also on number of ears per plant. There was little tiller death in Norman and some in Fenman and Wembley. However in Experiment 2 in Norman number of shoots was increased, and then it was constant all the time in control. In Fenman and Wembley the control has given very similar results in both years to Norman.

4.3.5 PLANT HEIGHT OF MAIN STEM

The affect of salinity on plant height at different stages are shown in Figures 25 to 27.

In both experiments in all varieties generally all salinity treatments significantly decreased plant height during the stress period. In both Experiments 1 and 2 in Norman salinity at TL-SE decreased plant height and it did not recover (Figure 25). In Fenman salinity at TL-SE decreased plant height then it recovered again only in Experiment 1 (Figure 26). In both Experiments 1 and 2 in Wembley, salinity at TL-SE gave a similar plant height during the stress period then after 55 days it increased plant height but not significantly (Figure 27). In both Experiments 1 and 2, in Norman, salinity at SE-BG decreased plant height during the stress period then it did not recover again (Figure 25). In Fenman, salinity at SE-BG slightly decreased plant height in Experiment 1 (Figure 26). In Experiment 2, salinity at SE-BG had a greater effect and significantly decreased plant height (Figure 26). In Wembley, salinity at SE-BG showed very similar results to Fenman in both experiments (Figure 27. Generally in both experiments in all varieties salinity at BG-MT gave similar plant height to control. This was sometimes significant and sometimes not significant.

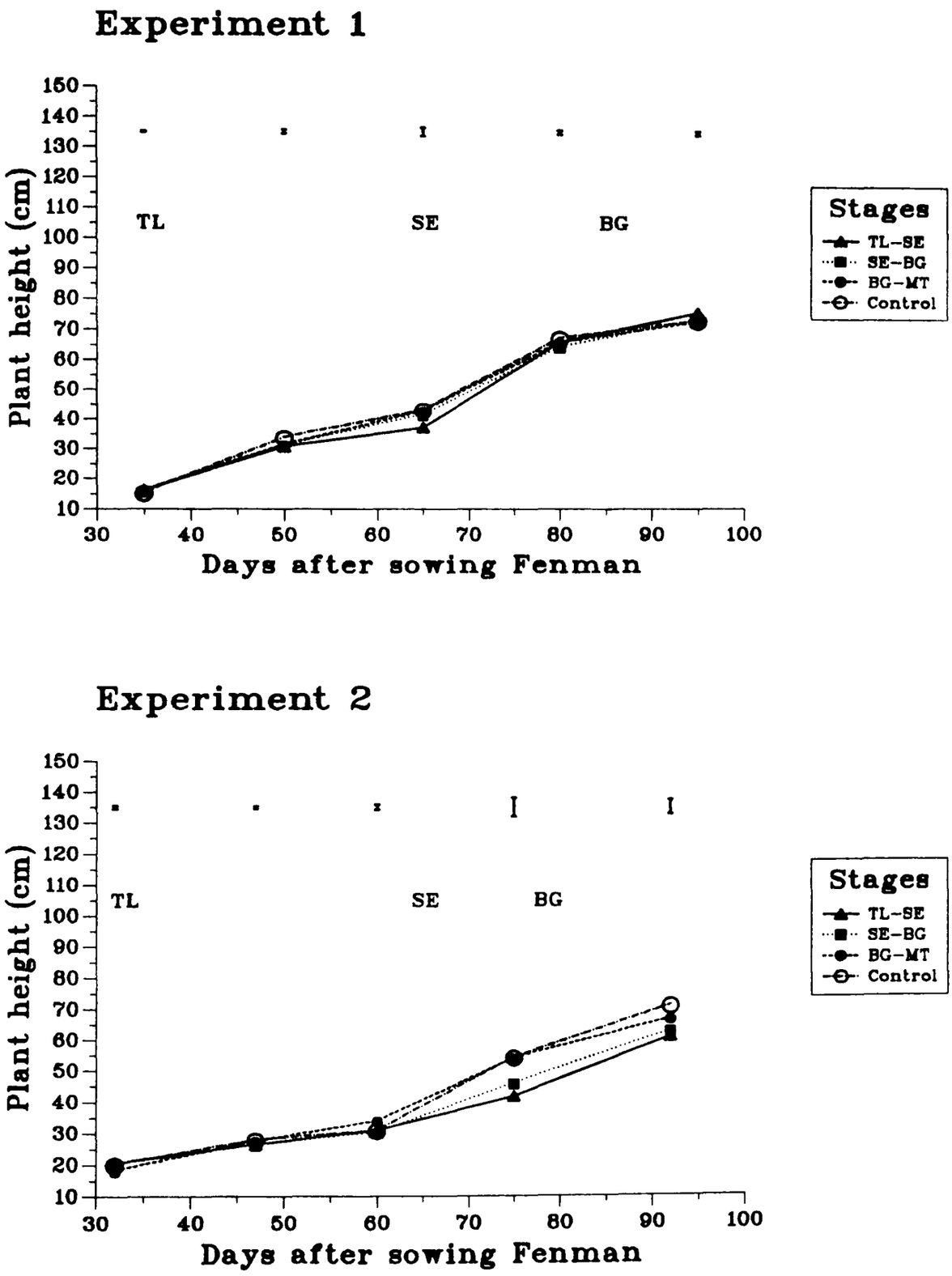
Fig.25: Effect of salinity on plant height of main stem of Norman variety in salinity Experiment 1 and 2.



TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

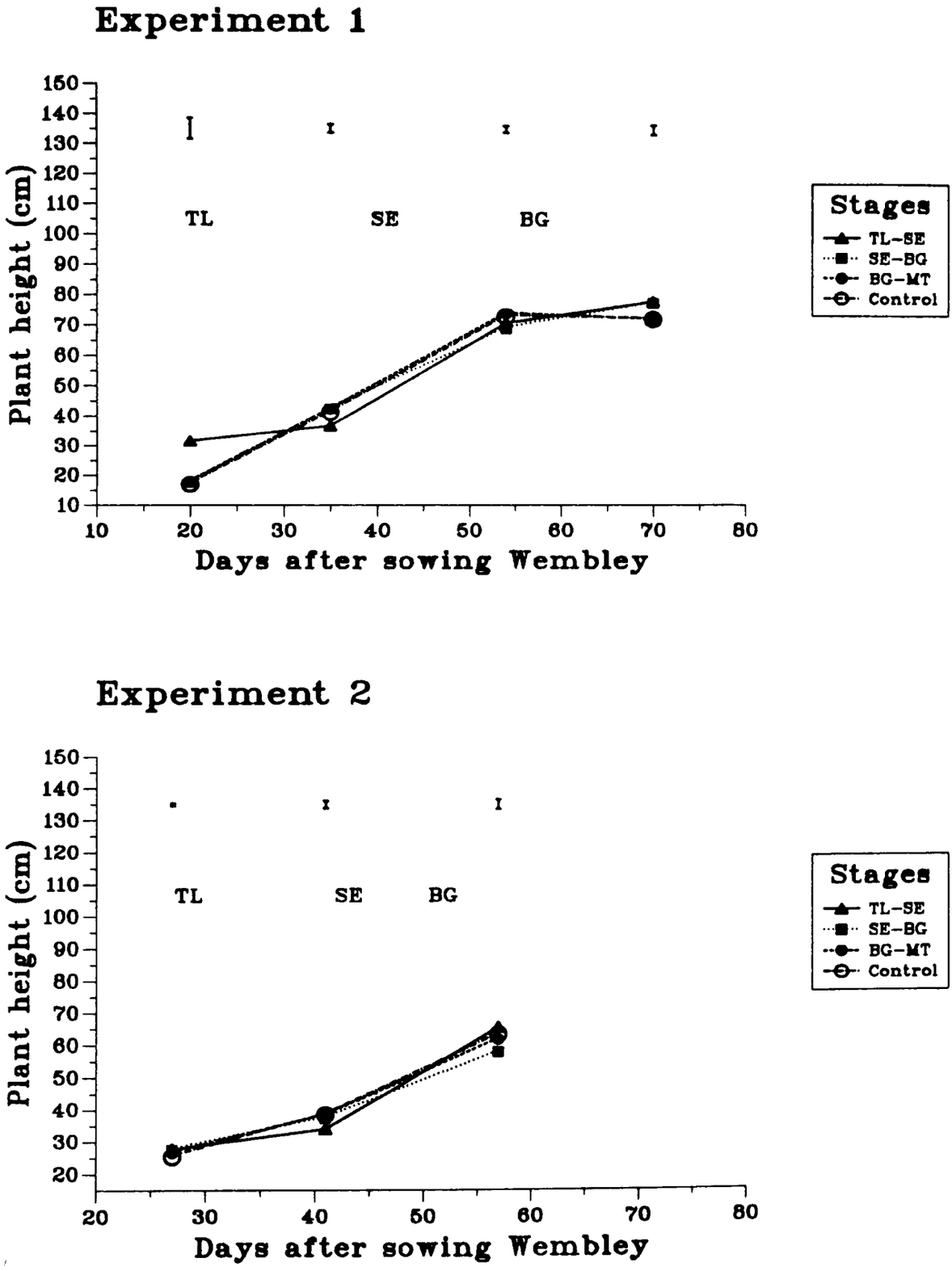
Fig.26: Effect of salinity on plant height of main stem of Fenman variety in salinity Experiment 1 and 2.



TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

Fig.27: Effect of salinity on plant height of main stem of Wembley variety in salinity Experiment 1 and 2.



TL = Tillering; SE = Stem extension; BG = Booting

I = S.E. of mean

4.3.6. SIGNIFICANCE OF MAIN EFFECTS AND INTERACTIONS

As reported earlier (section 3.3.7) in the growth analysis data collected at stem extension, booting and anthesis the interactions between variety and salinity were N.S. Hence data are presented as main effects only.

4.3.7. MAIN EFFECT OF SALINITY AT DIFFERENT STAGES FOR GROWTH CHARACTERISTICS IN SALINITY EXPERIMENTS 1 AND 2

4.3.7.1 Main effect of salinity at stem extension

In general, in both years, salinity at TL-SE resulted in significant decreases in leaf area, stem area, dry weight and nitrogen uptake per plant (Table 42). Nitrogen % was also decreased by salinity but this was not significant.

4.3.7.2 Main effect of salinity at booting

In general, in both years, salinity at TL-SE and SE-BG significantly decreased leaf area, stem area and dry weight per plant (Table 43). In general, salinity at TL-SE resulted in significantly lower values of these parameters than salinity at SE-BG. Nitrogen % was increased by salinity but this was not significant. In both Experiments 1 and 2, nitrogen uptake per plant was significantly lower with salinity at TL-SE compared to SE-BG, and SE-BG gave significantly lower values compared to the control.

4.3.7.3 Main effect of salinity at anthesis

At anthesis, leaf area, stem area, flag leaf area, ear area, dry weight per plant and nitrogen uptake per plant were decreased by all salinity treatments (Table 44). In both years generally salinity at TL-SE caused the greatest decrease

Table 42 Main effects of salinity at different stages on growth characters at stem extension in Experiments 1 and 2

	Stages			
	TL-SE	Control	S.E.M.	L.S.D. (P=0.05)
Experiment 1				
Leaf area per plant (cm^2)	134.80	216.20	8.04	27.82
Stem area per plant (cm^2)	27.90	27.90	9.05	N.S.
Dry weight per plant (g)	0.97	1.58	0.30	1.022
Nitrogen %	4.38	4.63	0.097	N.S.
Nitrogen uptake per plant (g)	0.043	0.073	0.0038	0.013
Experiment 2				
Leaf area per plant (cm^2)	109.00	266.00	10.04	34.74
Stem area per plant (cm^2)	28.70	86.60	9.13	31.59
Dry weight per plant (g)	0.93	2.01	0.07	0.25
Nitrogen %	3.92	4.04	0.06	N.S.
Nitrogen uptake per plant (g)	0.036	0.081	0.0034	0.012

Table 43 Main effects of salinity at different stages on different growth characters at booting in Experiments 1 and 2

	Stages				
	TL-SE	SE-BG	Control	S.E.M.	L.S.D. (P=0.05)
Experiment 1					
Leaf area per plant (cm^2)	239.00	515.00	847.00	40.03	158.11
Stem area per plant (cm^2)	49.00	79.00	241.00	68.38	N.S.
Dry weight per plant (g)	2.81	5.29	9.18	0.62	2.46
Nitrogen %	3.15	2.97	2.76	0.13	N.S.
Nitrogen uptake per plant (g)	0.085	0.150	0.240	0.016	0.063
Experiment 2					
Leaf area per plant (cm^2)	204.00	364.00	519.00	24.75	97.76
Stem area per plant (cm^2)	41.50	62.80	83.30	4.47	17.65
Dry weight per plant (g)	2.66	4.29	7.07	0.47	1.87
Nitrogen %	2.64	2.42	2.12	0.10	N.S.
Nitrogen uptake per plant (g)	0.06	0.11	0.15	0.0096	0.038

Table 44 Main effect of salinity at different stages on different growth characters at anthesis in Experiments 1 and 2

	Stage					
	TL-SE	SE-BG	BG-MT	Control	S.E.M.	L.S.D. (P=0.05)
Experiment 1						
Leaf area per plant (cm^2)	191.00	408.00	357.00	524.00	36.63	153.85
Flag leaf area per plant (cm^2)	75.90	164.40	171.20	195.30	16.77	70.43
Ear area per plant (cm^2)	72.20	157.40	128.20	185.30	14.79	62.13
Stem area per plant(cm^2)	87.70	151.30	137.50	195.20	8.97	37.67
Dry weight per plant (g)	6.08	11.70	10.34	14.82	0.26	1.079
Nitrogen %	2.62	2.35	2.06	2.03	0.14	0.58
Nitrogen uptake per plant (g)	0.16	0.26	0.21	0.30	0.12	0.049
Soluble carbohydrate %	0.37	0.37	0.50	0.57	0.04	N.S.
Soluble carbohydrate content (mg per plant)	17.00	39.90	42.10	68.20	8.17	34.31
Experiment 2						
Leaf area per plant (cm^2)	86.00	293.00	309.00	367.00	21.22	89.11
Flag leaf area per plant (cm^2)	50.10	83.60	126.50	178.50	6.34	26.64
Ear area per plant (cm^2)	60.00	84.80	110.90	137.90	7.46	31.33
Stem area per plant (cm^2)	71.90	95.40	103.20	154.80	6.004	25.22
Dry weight per plant (g)	4.71	6.61	9.57	12.28	0.76	3.179
Nitrogen %	2.17	2.21	1.97	1.89	0.12	0.149
Nitrogen uptake per plant (g)	0.10	0.14	0.19	0.21	0.0091	0.038
Soluble carbohydrate %	0.55	0.49	0.61	0.69	0.04	N.S.
Soluble carbohydrate content (mg per plant)	7.50	9.40	16.80	24.30	1.52	6.39

in all parameters compared to the control.

In both years, salinity at SE-BG and BG-MT decreased leaf area, stem area, ear area and nitrogen uptake per plant compared to the control, but this was not always significant.

Nitrogen % was significantly higher at TL-SE compared to control, but not significantly higher than SE-BG, BG-MT. Salinity at TL-SE and SE-BG increased nitrogen % but this was not always significant.

In both Experiments 1 and 2, salinity had no significant effects on soluble carbohydrate %, although salinity at SE-BG resulted in less soluble carbohydrate % compared to the control. There were significant effects of salinity on soluble carbohydrate content in both years. All salinity treatments decreased soluble carbohydrate content. In Experiment 1 and 2 salinity at TL-SE resulted in significantly less soluble carbohydrate content compared to the control. In Experiment 2 salinity at SE-BG and BG-MT significantly decreased soluble carbohydrate content compared to the control.

4.3.8 MAIN EFFECT OF VARIETIES FOR GROWTH CHARACTERISTICS IN SALINITY EXPERIMENTS 1 AND 2

4.3.8.1 Main effect of varieties on growth characteristics at stem extension

In Experiment 1, leaf area per plant and nitrogen uptake per plant at stem extension were significantly higher in Norman than Fenman (Table 45). Fenman had a leaf area significantly higher than Wembley, but nitrogen uptake was not significantly higher than Wembley. In Experiment 1, the effects of variety on stem area, dry weight, and nitrogen %

Table 45 Main effect of varieties on growth characters at stem extension in salinity Experiments 1 and 2

	Varieties				
	Norman	Fenman	Wembley	S.E.M.	L.S.D. (P=0.05)
Experiment 1					
Leaf area per plant (cm^2)	196.10	180.40	150.00	3.21	13.93
Stem area per plant (cm^2)	29.10	19.20	35.40	11.089	N.S.
Dry weight per plant (g)	1.50	1.23	1.10	0.36	N.S.
Nitrogen %	5.30	3.75	4.46	0.12	N.S.
Nitrogen uptake per plant (g)	0.080	0.046	0.048	0.0047	0.020
Experiment2					
Leaf area per plant (cm^2)	130.00	223.00	211.00	12.30	53.38
Stem area per plant (cm^2)	125.80	23.30	23.80	11.18	48.52
Dry weight per plant (g)	1.35	1.83	1.24	0.089	0.39
Nitrogen %	4.31	3.62	3.99	0.076	0.33
Nitrogen uptake per plant (g)	0.059	0.066	0.049	0.0041	N.S.

were not significant. In Experiment 2, leaf area per plant was significantly lower in Norman than in Fenman and Wembley. Stem area was significantly higher in Norman than in Fenman and Wembley. Norman gave dry weight per plant and nitrogen % significantly higher than Fenman. Mostly in all parameters there were no significant differences between Fenman and Wembley. Nitrogen uptake per plant showed no significant differences between varieties.

4.3.8.2 Main effect of varieties on growth characteristics at booting

In Experiment 1, leaf area, dry weight, nitrogen % and nitrogen uptake per plant has given significant results (Table 46). For stem area there were no significant differences between varieties. In Norman, leaf area and dry weight per plant were significantly higher than in Fenman and Wembley. Between Wembley and Fenman there were no significant differences. Norman had a significantly lower nitrogen % than Fenman but not significantly lower than Wembley. Nitrogen uptake per plant was significantly higher in Norman than in Wembley and Fenman. In Experiment 2, at SE-BG the effects of variety on leaf area, stem area, dry weight, nitrogen uptake per plant were significant. Wembley had a significantly higher leaf area and stem area than Norman and Fenman. Dry weight and nitrogen uptake per plant were significantly higher in Norman compared to Fenman in Experiment 2. Nitrogen % was not significantly affected by variety.

4.3.8.3 Main effect of varieties on growth characteristics at anthesis

At anthesis in both experiments all parameters showed

Table 46 Main effect of varieties on growth characters at booting in salinity Experiments 1 and 2

	Varieties				
	Norman	Fenman	Wembley	S.E.M.	L.S.D. (P=0.05)
Experiment 1					
Leaf area per plant (cm^2)	785.00	367.00	449.00	40.028	158.11
Stem area per plant (cm^2)	123.00	58.00	184.00	68.39	N.S.
Dry weight per plant (g)	9.86	3.58	3.85	0.62	2.46
Nitrogen %	2.67	3.28	2.93	0.13	0.52
Nitrogen uptake per plant (g)	0.26	0.12	0.11	0.016	0.063
Experiment 2					
Leaf area per plant (cm^2)	313.00	266.00	508.00	24.75	97.76
Stem area per plant (cm^2)	46.70	57.80	83.20	4.46	17.62
Dry weight per plant (g)	6.91	2.19	4.93	0.47	1.87
Nitrogen %	2.30	2.30	2.59	0.10	N.S.
Nitrogen uptake per plant (g)	0.15	0.05	0.12	0.0096	0.038

significance, except nitrogen % which showed no significant effects (Table 47). In Experiment 1, Norman had a significantly higher leaf area, stem area, flag leaf area, dry weight and nitrogen uptake per plant than Wembley and Fenman. Nitrogen % was not significantly affected by variety in both Experiments. In Experiment 2 at anthesis Norman had a significantly higher leaf area, stem area, flag leaf area, ear area, dry weight and nitrogen uptake per plant than Fenman. Wembley had a significantly higher stem area, flag leaf area per plant than Fenman. In Wembley dry weight and nitrogen uptake per plant were not significantly different to Fenman.

Soluble carbohydrate % was not significant in Experiment 1 but it was significant in Experiment 2. In Experiment 2, Fenman had a soluble carbohydrate % significantly lower than Norman and Wembley. Soluble carbohydrate content showed significant differences between varieties in both Experiments 1 and 2.

In both years, Norman had a significantly higher soluble carbohydrate content than Fenman and Wembley. In Experiment 2, Wembley had a significantly higher soluble carbohydrate content than Fenman.

4.3.9 SIGNIFICANCE OF MAIN EFFECTS AND INTERACTIONS FOR GRAIN YIELD, YIELD COMPONENTS AND OTHER CHARACTERS RECORDED AT HARVEST

Generally in salinity Experiments 1 and 2, the interaction between varieties and stages was significant for grain yield and most yield components. In some cases, the interaction was not significant in one but not both years, but

Table 47 Main effect of varieties on growth characters at anthesis in salinity Experiments 1 and 2

	Varieties				
	Norman	Fenman	Wembley	S.E.M.	L.S.D. (P=0.05)
Experiment 1					
Leaf area per plant (cm^2)	553.00	230.00	327.00	31.75	119.69
Flag leaf area per plant (cm^2)	222.50	127.20	105.20	14.52	54.74
Ear area per plant (cm^2)	199.90	108.20	99.20	12.81	48.28
Stem area per plant (cm^2)	202.80	99.20	126.90	7.77	29.29
Dry weight per plant (g)	17.46	7.61	7.13	0.93	3.52
Nitrogen %	2.14	2.25	2.42	0.12	N.S.
Nitrogen uptake per plant (g)	0.36	0.16	0.17	0.010	0.04
Soluble Scarbohydrate %	0.51	0.49	0.36	0.035	N.S.
Soluble carbohydrate content (mg per plant)	73.30	31.30	20.70	7.072	26.66
Experiment 2					
Leaf area per plant (cm^2)	314.00	206.00	271.00	18.38	69.32
Flag leaf area per plant (cm^2)	113.80	82.40	132.90	5.49	20.71
Ear area per plant (cm^2)	103.20	43.80	148.20	6.46	24.34
Stem area per plant (cm^2)	125.00	69.90	124.10	5.20	19.59
Dry weight per plant (g)	11.09	6.47	7.31	0.66	2.47
Nitrogen %	1.89	2.23	2.06	0.10	N.S.
Nitrogen uptake per plant (g)	0.19	0.14	0.15	0.0079	0.030
Soluble carbohydrate %	0.66	0.45	0.64	0.033	0.12
carbohydrate content (mg per plant)	21.80	8.40	13.40	1.32	4.96

the main effects of variety or salinity were significant. These results are interpreted from the main effects of varieties and main effects of salinity where appropriate.

4.3.10 MAIN EFFECTS OF SALINITY AT DIFFERENT STAGES, ON GRAIN YIELD, YIELD COMPONENTS, AND OTHER CHARACTERISTICS

To show the main trends for varieties and salinity stress at stages the main effects of these factors are presented and discussed briefly.

The effects of salinity stress at different stages on yield and yield components other characteristics recorded at harvest in Experiments 1 and 2 are shown in Tables 48 and 49 respectively. Generally all grain yield and yield components were significantly decreased in both Experiments 1 and 2 except number of grains per fertile spikelet and harvest index in Experiment 1. Particularly salinity at TL-SE in Experiment 2 significantly decreased grain weight per plant, number of grains per plant, number of ears per plant, number of grains per ear, fertile spikelets per ear, number of grains per fertile spikelet, harvest index, straw dry weight per plant and plant height more than salinity at other stages. Average grain weight was significantly decreased by salinity at BG-MT in both Experiments 1 and 2.

In Experiment 1, salinity at BG-MT significantly increased the number of infertile spikelets per ear. Salinity at TL-SE and SE-BG gave no significant effects. In Experiment 2 all salinity treatments significantly increased the number of infertile spikelets per ear. In Experiment 1 salinity at

Table 48 Main effects of salinity at different growth stages on yield, yield components and other characters recorded at harvest - Experiment 1

	Stages					
	TL-SE	SE-BG	BG-MT	Control	S.E.M.	L.S.D. (P=0.05)
Grain weight per plant (g)	5.31	6.72	5.77	9.15	0.33	1.25
Average grain weight (mg)	39.26	38.06	34.32	42.51	0.84	3.21
Number of grains per plant	135.9	177.0	166.1	214.7	7.051	26.93
Number of ears per plant	3.39	3.99	3.92	4.35	0.13	0.49
Number of grains per ear	44.24	46.29	45.47	52.11	1.48	5.66
Fertile spikelet per ear	17.43	18.30	17.79	19.29	0.29	1.10
Number of grains per fertile spikele	2.52	2.51	2.51	2.65	0.066	N.S.
Infertile spikelet per ear	2.39	2.78	3.32	2.23	0.13	0.49
Harvest index %	46.89	43.29	44.06	46.17	1.39	N.S.
Straw dry weight per plant (g)	6.18	8.91	7.43	10.98	0.40	1.53
Plant height of main stem (cm)	78.14	80.36	76.94	81.59	0.93	3.55
Number of leaves on main stem	10.00	10.33	10.33	10.33	-	N.S.
Nitrogen % in grain	2.78	2.83	2.93	2.67	0.67	N.S.
Nitrogen % in straw	1.70	1.62	1.15	1.23	0.094	0.36
Nitrogen uptake per plant (grain + straw) (g)	0.25	0.33	0.26	0.38	0.013	0.05
Final average grain weight of grain growth (mg)	39.48	40.64	33.99	42.56	1.12	4.70
Rate of grain growth growth (mg/day)	1.16	1.21	0.96	1.33	0.065	0.21
Duration of grain growth (days)	34.44	34.37	36.71	31.88	1.84	N.S.

Table 49 Main effects of salinity at different growth stages on yield, yield components and other characters recorded at harvest - Experiment 2

	Stages					
	TL-SE	SE-BG	BG-MT	Control	S.E.M.	L.S.D. (P=0.05)
Grain weight per plant (g)	2.09	4.32	4.44	7.36	0.17	0.66
Average grain weight (mg)	33.40	34.34	30.59	38.51	1.00	3.79
Number of grains per plant	61.9	125.4	146.2	190.7	4.92	18.80
Number of ears per plant	2.34	3.49	4.07	4.45	0.11	0.43
Number of grains per ear	28.02	38.26	39.40	45.04	1.72	6.57
Fertile spikelet per ear	14.44	15.80	15.95	18.01	0.25	0.9
Number of grains per fertile spikelet	1.92	2.39	2.44	2.46	0.086	0.33
Infertile spikelet per ear	3.83	4.00	4.25	2.44	0.17	0.66
Harvest index %	36.41	42.40	41.54	45.96	1.17	4.46
Root dry weight per plant (g)	0.68	1.10	1.26	1.53	0.086	0.327
Straw dry weight per plant (g)	3.55	5.91	6.30	9.20	0.32	0.98
Plant height of main stem (cm)	65.05	74.05	74.36	79.65	0.82	3.14
Number of leaves on main stem	10.29	10.65	10.69	10.67	0.033	0.13
Nitrogen % in grain	2.86	2.88	3.02	2.60	0.054	0.20
Nitrogen % in straw	2.00	1.66	1.07	1.24	0.089	0.34
Nitrogen uptake per plant (grain + straw) (g)	0.13	0.23	0.20	0.30	0.008	0.032
Final Average grain weight of grain growth (mg)	40.26	41.44	39.37	44.72	1.37	N.S.
Rate of grain growth (mg/day)	0.89	0.97	0.98	1.10	0.098	N.S.
Duration of grain growth (days)	41.7	46.1	42.6	40.9	4.31	N.S.

all stages decreased plant height (length of straw and ears) at maturity but this was significant for BG-MT only. In these experiments root dry weight per plant was measured only in Experiment 2. It was significantly lower with salinity at TL-SE than with salinity at other stages and in the control. In Experiment 2 all salinity treatments resulted in a significant decrease in plant height but plant height was decreased most by salinity at TL-SE. There were no significant effects of salinity on leaf number in Experiment 1. In Experiment 2 salinity at TL-SE resulted in significantly fewer leaves than the other treatments and the control. In Experiment 1, there were no significant effects of salinity on the nitrogen % of grain. In Experiment 2, all salinity treatments significantly increased nitrogen % in grain. Salinity at BG-MT had higher nitrogen % in grain. In both years salinity at TL-SE and SE-BG resulted in a significant increase in straw nitrogen %.

In Experiment 1 all salinity treatments decreased nitrogen uptake per plant (straw + grain) but the greatest decreases were observed with salinity at TL-SE and BG-MT. The same trends were present in Experiment 2.

In Experiment 1, salinity at BG-MT resulted in a significantly lower average grain weight and rate of grain growth compared to the control. Salinity at TL-SE and SE-BG had no significant effects on average grain weight and rate of grain growth. Duration of grain growth was not significantly affected by salinity. In Experiment 2, average grain weight, rate and duration of grain growth were not significantly affected by salinity.

4.3.11 MAIN EFFECTS OF VARIETIES ON GRAIN YIELD, YIELD COMPONENTS AND OTHER CHARACTERS

The main effects of varieties on grain yield and yield components and other characteristics recorded at harvest for salinity stress Experiments 1 and 2 are shown in Tables 50 and 51 respectively. The main effect of variety was generally significant for grain yield and yield components in these experiments except for grain number per plant in Experiment 2. In both Experiments 1 and 2, Norman had significantly higher number of grains per ear, fertile spikelets per ear, number of grains per fertile spikelet and straw dry weight per plant than other varieties. Also in Experiment 1 only Norman had significantly higher grain weight per plant and number of grains per plant. In Experiment 2 only Fenman had a significantly increased grain weight per plant. In both Experiments 1 and 2, Fenman had the higher average grain weight and harvest index. However, Wembley had a significantly higher number of ears per plant and infertile spikelets per ear in both Experiments 1 and 2.

There were significant differences between the varieties in number of infertile spikelets per ear, Fenman had least and Wembley had the most. Dry weight of root per plant was significantly higher in Norman than Fenman and Wembley, and Fenman had non significantly lower than Wembley. Effect of salinity on plant height showed significant differences in Experiments 1 and 2. In both years, Norman gave plant height significantly higher compared to Fenman and Wembley. Fenman had a significantly higher plant height than Wembley in Experiment 1 but not in Experiment 2. In Experiment 1 Norman

ble 50 Main effects of varieties on yield and yield components and other characters recorded at harvest in salinity - Experiment 1

	Varieties				
	Norman	Fenman	Wembley	S.E.M.	L.S.D. (P=0.05)
:ain weight per plant (g)	8.21	6.40	5.60	0.28	0.98
'erage grain weight weight (mg)	39.41	39.52	36.69	0.73	2.53
ımber of grains per plant	205.80	161.70	151.40	6.10	21.18
ımber of ears per plant	3.16	3.39	5.18	0.11	0.39
ımber of grains per ear	64.13	47.75	29.19	1.28	4.45
ertile spikelet per ear	19.72	17.88	17.02	0.25	0.86
ımber of grains per fertile spikelet	3.25	2.67	1.72	0.057	0.20
ıfertile spikelet per ear	2.39	1.66	3.98	0.11	0.39
ırvest index %	40.73	49.89	44.68	1.20	4.17
:raw dry weight per plant (g)	11.66	6.61	6.85	0.35	1.2
lant height of main stem (cm)	88.90	76.87	72.00	0.81	2.79
ımber of leaves on main stem	12.00	10.00	9.00	-	N.S.
itrogen % in grain	2.73	2.75	2.93	0.058	0.20
itrogen % in straw	1.48	1.24	1.55	0.081	0.28
itrogen uptake per plant (grain + straw) (g)	0.39	0.26	0.27	0.11	0.04
inal Average grain eight of grain growth (mg)	41.14	39.66	36.71	0.97	3.65
ate of grain growth (mg/day)	1.29	1.12	1.08	0.057	0.21
ıration of grain growth (days)	31.95	36.59	34.50	1.60	N.S.

Table 51 Main effects of varieties on yield, yield components and other characters recorded at harvest in salinity - Experiment 2

	Varieties				
	Norman	Fenman	Wembley	S.E.M.	L.S.D. (P=0.05)
Grain weight per plant (g)	4.31	5.06	4.29	0.15	0.56
Average grain weight (mg)	32.25	37.31	33.07	0.86	2.98
Number of grains per plant	133.50	129.70	129.90	4.26	N.S.
Number of ears per plant	2.49	3.56	4.72	0.095	0.33
Number of grains per ear	51.13	34.43	27.48	1.49	5.17
Fertile spikelet per ear	17.59	15.78	14.78	0.21	0.75
Number of grains per fertile spikelet	2.88	2.17	1.86	0.074	0.26
Infertile spikelet per ear	3.27	2.92	4.71	0.15	0.52
Harvest index %	32.85	46.95	44.94	1.01	3.50
Root dry weight per plant (g)	1.26	1.00	1.17	0.074	0.26
Straw dry weight per plant (g)	8.36	5.18	5.19	0.27	0.96
Plant height of main stem (cm)	82.25	69.63	67.96	0.75	2.62
Number of leaves on main stem	12.67	10.00	9.05	0.029	0.099
Nitrogen % in grain	2.96	2.72	2.59	0.046	0.16
Nitrogen % in straw	1.69	1.34	1.44	0.077	0.27
Nitrogen uptake per plant (grain + straw) (g)	0.25	0.20	0.19	0.0074	0.03
Final Average grain weight of grain growth (mg)	37.42	48.06	38.87	1.18	4.47
Rate of grain growth (mg/day)	0.94	1.24	0.79	0.084	0.32
Duration of grain growth (days)	40.00	39.70	48.70	3.73	N.S.

had 12 leaves, Fenman 10 leaves and Wembley 9 leaves on the main stem. In Experiment 2, leaf number was significantly different. Norman had significantly more leaves than Fenman and Fenman had non significantly higher leaf number than Wembley on the main stem. In Experiment 1, Norman and Fenman had a grain nitrogen % lower than Wembley. In Experiment 2, Norman had a grain nitrogen % higher than Fenman and Wembley. There were significant differences between the varieties in nitrogen % in the straw. In both years straw nitrogen % was greater in Norman and Wembley than in Fenman. In both Experiments 1 and 2, Norman had a significantly higher nitrogen uptake per plant than Fenman and Wembley. However, Fenman and Wembley had nitrogen uptake per plant similar to each other in both years. In Experiments 1 and 2, average grain weight and rate of grain growth and rate of showed significant differences between varieties. Wembley had a significantly lower average grain weight (from grain growth analysis) than Norman in Experiment 1. In Experiment 2, Fenman had a significantly higher average grain weight than Norman and Wembley. Rate of grain growth were lowest in Wembley in both years. In both Experiments 1 and 2, duration of grain growth was not significantly different in the varieties.

In these experiments, at final harvest there were no significant effects of salinity in Experiments 1 and 2 on the number of detectable stem nodes on the main stem as shown in Table 52. The values of this character were similar in both experiments, but were different between varieties. In both years in both experiments Norman had more dectable stem nodes than Fenman and Fenman had more than Wembley, as found by

Table 52 Detectable stem nodes on the main stem of plants of different wheat varieties, Norman, Fenman and Wembley in salinity Experiments 1 and 2.

Variety	Salinity Experiments Mean	S.E.of mean
Experiment 1		
Norman	5.7	0.153
Fenman	4.7	0.153
Wembley	3.7	0.153
Experiment 2		
Norman	5.6	0.163
Fenman	4.6	0.163
Wembley	3.6	0.163

Kirby et al. (1985b).

The numbers of detectable stem nodes were similar for each variety in the salinity experiments.

4.3.12 EFFECTS OF VARIETIES AND SALINITY ON YIELD AND YIELD COMPONENTS AND OTHER CHARACTERISTICS IN SALINITY EXPERIMENTS 1 AND 2

4.3.12.1 Grain weight per plant (g)

In Experiments 1 and 2 there were significant differences in grain weight per plant between varieties and stages (Table 53). In both years in all varieties salinity decreased grain weight per plant. In Experiments 1 and 2, in Norman salinity at TL-SE resulted in a significantly lower grain weight per plant than salinity at SE-BG, BG-MT and control. Salinity at SE-BG and BG-MT has given significantly less grain weight per plant compared to the control in Norman in both years. In Fenman in Experiment 1, salinity at TL-SE gave non-significantly less grain weight per plant compared to SE-BG and control. In Experiment 1, in Fenman salinity at SE-BG and BG-MT nonsignificantly decreased grain weight per plant compared to the control. However, in Experiment 2, grain weight per plant was significantly decreased by salinity at SE-BG and BG-MT compared to the control. In Experiment 1, in Wembley salinity at TL-SE gave non-significantly less than the control but in Experiment 2 it gave significantly less than the control. In Wembley salinity at SE-BG resulted in a grain weight per plant which was not significantly lower the control in both years. In both years in Wembley salinity at BG-MT has given significantly less grain weight per plant

Table 53 Effect of varieties and salinity on grain weight per plant (g) in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	4.97	5.56	5.42
Stem extension to booting	7.67	6.83	5.68
Booting to maturity	7.75	5.47	4.08
Control	12.45	7.75	7.26
S.E. of means = 0.57; L.S.D. (P = 0.05) = 2.80			
Experiment 2			
Tillering to stem extension	1.54	1.30	3.44
Stem extension to booting	3.38	5.23	4.35
Booting to maturity	4.17	5.29	3.87
Control	8.14	8.43	5.51
S.E. of means = 0.30; L.S.D. (P = 0.05) = 1.48			

compared to the control. In the controls in both years Norman had a significantly higher grain weight per plant than Wembley. Fenman gave significantly higher grain weight per plant than Wembley in Experiment 2 but not in Experiment 1.

4.3.12.2 Average grain weight (mg)

In Experiment 1, the variety x salinity interaction for average grain weight was not significant, but it was in Experiment 2 (Table 54). However in Experiment 1, the main effects of stage and variety were significant. Salinity at BG-MT significantly decreased average grain weight compared to TL-SE, SE-BG and control. Salinity at SE-BG gave significantly lower average grain weight than the control. Salinity at SE-BG gave similar average grain weight to TL-SE, but not significant. In varieties average grain weight was significantly higher in Norman and Fenman than in Wembley. Between Norman and Fenman there was no significant difference in average grain weight.

In Experiment 2, in Norman salinity at BG-MT gave average grain weight, which was nonsignificantly lower than salinity at TL-SE and SE-BG. Salinity at BG-MT gave significantly lower average grain weight than the control. Salinity at SE-BG resulted in a non-significantly lower average grain weight compared to salinity at TL-SE. In Fenman salinity at TL-SE gave an average grain weight which was significantly lower compared to salinity at SE-BG and the control but not significantly lower than salinity at BG-MT. Salt stress at BG-MT gave average grain weight significantly less compared to control. In Wembley salinity at TL-SE has given average grain weight similar to control. Salinity at SE-BG gave

Table 54 Effect of varieties and salinity on average grain weight (mg) in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	39.28	41.71	36.79
Stem extension to booting	38.61	39.04	36.54
Booting to maturity	36.81	34.98	31.17
Control	42.93	42.34	42.25
S.E. of means = 1.46; L.S.D. (P = 0.05) = N.S.			
Experiment 2			
Tillering to stem extension	34.80	30.30	35.00
Stem extension to booting	29.80	40.90	32.30
Booting to maturity	27.40	34.50	29.60
Control	36.61	43.60	35.40
S.E. of means = 1.72; L.S.D. (P = 0.05) = 8.51			

average grain weight which was not significantly lower than the control. Salinity at BG-MT has given average grain weight non significantly less than the control and all stage in wembley. Norman and Wembley control had non-significantly similar average grain weight and both varieties had non-significantly less than Fenman.

4.3.12.3 Number of grains per plant

In both years the interaction was significant for number of grains per plant (Table 55). All salinity treatments decreased number of grains per plant in all varieties. In Experiment 1, in Norman all salinity treatments significantly decreased number of grains per plant. Salinity at TL-SE gave significantly lower number of grains per plant than salinity at SE-BG and BG-MT. Salinity decreased number of grains per plant in Fenman and Wembley at all stages but this was not statistically significant. In the control Norman gave significantly higher number of grains per plant than Fenman and Wembley.

In Experiment 2, in Norman, salinity at TL-SE resulted in significantly lower number of grains per plant compared to salinity at SE-BG, BG-MT and control. Salinity at SE-BG resulted in number of grains per plant which was non-significantly lower compared to salinity at BG-MT. Salinity at BG-MT resulted in a significantly lower number of grains per plant than the control in Norman. In Fenman salinity at TL-SE had significantly lower number of grains per plant than salinity at SE-BG. Salinity at SE-BG resulted in a lower number of grains per plant than salinity at BG-MT but this was not significant. Salinity at BG-MT resulted in a number of

Table 55 Effect of varieties and salinity on number of grains per plant in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	126.4	133.3	148.0
Stem extension to booting	196.1	174.3	154.7
Booting to maturity	211.3	156.2	130.9
Control	289.6	182.9	171.8
S.E. of means = 12.21; L.S.D. (P = 0.05) = 60.46			
Experiment 2			
Tillering to stem extension	45.3	42.9	97.6
Stem extension to booting	113.3	128.3	134.6
Booting to maturity	152.5	154.0	132.0
Control	223.0	193.5	155.5
S.E. of means = 8.52; L.S.D. (P = 0.05) = 42.18			

grains per plant which was non-significantly lower than the control. In Wembley also salinity at TL-SE resulted in a number of grains per plant which was non-significantly lower than salinity at SE-BG. Salinity at SE-BG resulted in number of grains per plant which was not significantly lower than in the control in Wembley. In the control Norman had a number of grains per plant significantly higher than Wembley. In Fenman the control had a number of grains per plant which was not significantly higher than in Wembley and not significantly less than in Norman.

4.3.12.4 Number of ears per plant

In both years the interaction of salinity x variety was significant for number of ears per plant (Table 56). In both years all salinity treatments in all varieties decreased number of ears per plant except in Fenman salinity at SE-BG in Experiment 1.

In both years in Norman salinity at TL-SE has given a significantly lower number of ears per plant than the control. In Norman salinity at SE-BG and BG-MT non-significantly decreased the number of ears per plant. In Experiment 2 in Norman salinity at SE-BG gave significantly less number of ears per plant than the control. With salinity at BG-MT the number of ears per plant was not significantly lower than the control. In Fenman the number of ears per plant was not significantly lower at TL-SE in Experiment 1, but in Experiment 2 salinity at TL-SE significantly decreased the number of ears per plant compared to other stages and the control. In Experiments 1 and 2, in Fenman salinity at BG-MT gave a similar number of ears per plant to the control, but

Table 56 Effect of varieties and salinity on number of ears per plant in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	2.1	3.1	5.0
Stem extension to booting	3.2	3.6	5.2
Booting to maturity	3.4	3.4	5.1
Control	4.0	3.5	5.5
S.E. of means = 0.22; L.S.D. (P = 0.05) = 1.11			
Experiment 2			
Tillering to stem extension	1.3	1.8	3.9
Stem extension to booting	2.3	3.5	4.6
Booting to maturity	2.7	4.4	5.1
Control	3.6	4.5	5.2
S.E. of means = 0.20; L.S.D. (P = 0.05) = 0.95			

little less than the control. In Experiment 1, in Fenman, salinity at SE-BG slightly increased the number of ears per plant but not significantly. In Wembley all salinity treatments decreased the number of ears per plant but in most cases this was not significant. In Wembley in Experiment 2, salinity at TL-SE significantly decreased the number of ears per plant. In both experiments in the control, Norman had significantly lower number of ears per plant than Wembley. In Experiment 1 Fenman had non-significantly lower than Norman and in Experiment 2 Fenman had non-significantly higher than Norman control.

4.3.12.5 Fertile spikelets per ear

In Experiment 1 the variety x salinity interaction was not significant for fertile spikelets per ear but in Experiment 2 it was (Table 57). In Experiment 1, the main effects of salinity and variety were significant. All salinity treatments gave significantly less fertile spikelets per ear than the control. All salinity stress treatments had no significant differences between each other. In varieties Norman had significantly more fertile spikelets per ear than Fenman and Wembley. Fenman and Wembley had no significant differences in fertile spikelets per ear.

In Experiment 2, salinity at TL-SE has given significantly lower fertile spikelets per ear compared to the control in all varieties. In Norman, salinity at SE-BG and BG-MT also gave significantly less fertile spikelets per ear than the control. In Experiment 2, in Fenman and Wembley salt stress at SE-BG and BG-MT has given non-significantly less fertile spikelets compared to the control in both varieties.

Table 57 Effect of varieties and salinity on fertile spikelet per ear in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	18.4	17.4	16.5
Stem extension to booting	20.0	17.3	17.6
Booting to maturity	19.0	18.2	16.2
Control	21.5	18.6	17.8
S.E. of means = 0.50; L.S.D. (P = 0.05) = N.S.			
Experiment 2			
Tillering to stem extension	15.4	14.2	13.7
Stem extension to booting	17.6	15.2	14.7
Booting to maturity	16.5	16.9	14.5
Control	20.9	16.9	16.3
S.E. of means = 0.43; L.S.D. (P = 0.05) = 2.12			

In the control in both years Norman had more fertile spikelets per ear than Fenman and Wembley.

4.3.12.6 Number of grains per fertile spikelet

For number of grains per fertile spikelet the variety x salinity interaction was not significant in Experiment 1, but in Experiment 2 it was (Table 58). In Experiment 1, only the main effect of variety was significant. Norman had significantly more grains per fertile spikelet than Fenman and Fenman had more than Wembley.

In Experiment 2, in Norman salinity at TL-SE and SE-BG the number of grains per fertile spikelet was not significantly less than in the control. Salinity at BG-MT gave a grain number per fertile spikelet which was not significantly higher than salinity at SE-BG and control. Salinity at TL-SE in Fenman significantly decreased number of grains per fertile spikelet lower than the control. In Fenman salinity at SE-BG and BG-MT gave non-significantly less number of grains per fertile spikelet than the control. In Wembley salinity at TL-SE and BG-MT gave number of grains per fertile spikelet similar to control, but not significantly. In Wembley salinity at SE-BG non-significantly increased number of grains per fertile spikelet compared to salinity at BG-MT and the control. In the control, Norman had a non-significantly higher number of grains per fertile spikelet than Fenman and Wembley. Wembley control had a lower number of grains per fertile spikelet than Fenman but this was not significant.

4.3.12.7 Harvest index %

In Experiment 1, for harvest index there was a significant interaction between varieties and stages, but it was not

Table 58 Effect of varieties and salinity on number of grains per fertile spikelet in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	3.25	2.48	1.83
Stem extension to booting	3.00	2.82	1.70
Booting to maturity	3.35	2.57	1.60
Control	3.39	2.81	1.75
S.E. of means = 0.11; L.S.D. (P = 0.05) = N.S.			
Experiment 2			
Tillering to stem extension	2.30	1.66	1.81
Stem extension to booting	2.82	2.36	2.00
Booting to maturity	3.46	2.09	1.78
Control	2.96	2.56	1.85
S.E. of means = 0.15; L.S.D. = 0.73			

significant in Experiment 2 (Table 59). In Experiment 1 in Norman, salinity had no significant effect on harvest index. In Experiment 1, in Fenman, salinity at TL-SE, SE-BG and BG-MT resulted in a non-significant increase in harvest index compared to the control. In Experiment 1 in Wembley, salinity at TL-SE gave a harvest index slightly higher than the control but this was not significant. In Experiment 1, in Wembley, salinity at SE-BG and BG-MT gave non-significantly lower harvest index than the control. In the controls all varieties were not significantly different to each other in Experiment 1.

In Experiment 2, the main effects of stages and variety were significant. Salinity at TL-SE significantly decreased the harvest index compared to SE-BG, BG-MT and control. Salinity at SE-BG and BG-MT had no significant difference to each other and the control. In varieties Norman had a significantly lower harvest index than Fenman and Wembley. Fenman and Wembley had a non significant higher in harvest index.

4.3.12.8 Straw dry weight per plant (g)

In both years for straw weight per plant, the variety x stages interaction was significant (Table 60). Generally all salinity treatments decreased straw dry weight per plant in both years. In Experiments 1 and 2, in Norman, salinity TL-SE, SE-BG and BG-MT gave significantly lower straw weight than the control. The straw dry weights for salinity at SE-BG and BG-MT were not significantly different to each other. In Fenman in Experiments 1 and 2, salinity at TL-SE gave significantly lower straw dry weight per plant than the

Table 59 Effect of varieties and salinity on harvest index % in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	39.30	52.51	48.86
Stem extension to booting	37.72	48.06	44.08
Booting to maturity	42.74	51.75	37.69
Control	43.16	47.23	48.10
S.E. of means = 2.40; L.S.D. (P = 0.05) = 11.90			
Experiment 2			
Tillering to stem extension	27.92	37.26	44.05
Stem extension to booting	31.87	49.71	45.63
Booting to maturity	34.69	47.79	42.14
Control	36.90	53.04	47.94
S.E. of means = 2.022; L.S.D. = N.S.			

Table 60 Effect of varieties and salinity on straw dry weigth per plant (g) in Experiments 1 and 2

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	7.76	5.12	5.66
Stem extension to booting	12.16	7.39	7.18
Booting to maturity	10.46	5.10	6.74
Control	16.28	8.83	7.83
S.E. of means = 0.70; L.S.D. (P = 0.05) = 3.05			
Experiment 2			
Tillering to stem extension	4.14	2.22	4.31
Stem extension to booting	7.32	5.24	5.17
Booting to maturity	7.85	5.77	5.29
Control	14.13	5.29	5.98
S.E. of means = 0.55; L.S.D. (P = 0.05) = 2.71			

control. Salinity at SE-BG in both years gave a lower straw dry weight per plant than the control, but this was not significant. In Fenman in Experiment 1 salinity at BG-MT gave a significantly lower straw dry weight per plant than the control. In Wembley in Experiments 1 and 2 all salinity treatments decreased straw weight per plant but not significantly. All salinity treatments were not significantly different to each other.

In both Experiments 1 and 2, the Norman control had a significantly higher straw dry weight per plant than Fenman and Wembley. In both years, Fenman and Wembley had straw weight per plant, which were not significantly different to each other.

4.4 DISCUSSION

4.4.1 DIFFERENCES BETWEEN SALINITY EXPERIMENTS 1 AND 2

Generally in both experiments, salinity at all stages, in all varieties, decreased grain yield, yield components and growth characters. In Experiment 2 there were greater reductions in yield, yield components and growth characters than in Experiment 1. Norman was sown earlier in Experiment 1 so it had more time under salt during TL-SE than in Experiment 2. There was higher temperatures during growing of Fenman and Wembley in Experiment 2. Temperature was also higher during growing of Norman after stem extension. These higher temperatures possibly resulted in faster uptake of water and salt and more severe internal water deficits and effects of toxic concentrations of Na and Cl.

4.4.2 BEHAVIOUR OF VARIETIES UNDER SOLUTION CULTURE AND IN SALT STRESS

In solution culture the plants were affected straight away by applied salt at any stage (Bower and Wadleigh, 1948; Bernstein, 1963). Generally all varieties produced a large leaf area during the growing time. All varieties produced coleoptile tillers in solution culture but not in the water stress experiments. Wembley produced more tillers than other varieties because during this time the temperature was higher, days were long with more sunshine. Fenman produced more tillers than Norman. In Norman during TL-SE leaves were large and narrow, because of the cold weather. In solution culture small tillers continually appeared until maturity.

Approximately 5 to 15 tillers were always noticed on the control plants. Fewer tillers were produced on the plants grown in pots in the water stress experiments. These tillers some times died during growing then new ones appeared. This death and re-emergence of tillers is probably because of light interception and the solution culture technique used. In field crops small tillers at the base of the crop often die due to shading by taller main stems. There was no shading effect in these experiments. Sunlight was present at the base of the plants as they were grown in pots. Tillers may also die due to shortage of nutrients, but in these experiments in solution culture, water and nutrients were freely available. These small tillers always produced 2 to 4 leaves. Because of more tillers, higher plant height and more leaves, the straw weight per plant after stem extension was always much higher in the control in all varieties than in the water stress experiments. In solution culture after stem extension plants of Norman were much stronger and had thicker stems than those of Fenman and Wembley varieties. Fenman and Wembley plants were stronger in solution culture than in the water stress experiments. There was a lodging problem in Norman, particularly it was noticed at BG-MT stage and in the control.

At maturity there were 4 to 5 green leaves in all varieties in the control. Some upper leaves were also green with salinity at TL-SE, and SE-BG. However the ears were mature and had turned yellow in colour and contained filled grains. This lack of senescence of leaves did not occur in the water stress experiments where maturity developed naturally. It was due to continued supply of nutrients and water in

solution culture experiments. In the stressed plants leaf colour changed to dark green. Salt stressed plants also had more wax on upper and lower surfaces and on the stem (Hayward and Magistad, 1946). It was also noticed that aphids were first attacking the stressed plants (Gauch and Wadleigh, 1944; Rush and Epstein, 1976).

4.4.3 EFFECT OF SALINITY AT DIFFERENT STAGES

The effect of salinity depends on the stage of plant growth, period of exposure to salt, weather conditions and salt concentration (Maas and Hoffman, 1977).

In these experiments generally salinity at all stages decreased shoot number, plant height, leaf area, other growth measurements, and grain yield and yield components in both experiments, either less or more (Rawson, 1986). When salt was applied at any stage it decreased growth measurements during the stress period. At some stages a small amount of recovery occurred and at some stages the plant did not recover completely again. Particularly salt stress at TL-SE much decreased growth measurements (Gauch and Wadleigh, 1944).

4.4.3.1 Effect of salinty during tillering to stem extension

Crop development during the from phase tillering to stem extension has been described in the literature review in sections 3.23.1, 3.23.2, 3.23.3 and discused in relation to water stress in sections 3.4.2.1, 3.4.2.2, 3.4.2.3.

This section discusses how salinity during this phase affects growth and yield. During the phase TL-SE number of leaves on the main stem increased from 7 to 8 in Norman, 5 to 6 in Fenman and 4 to 5 in Wembley. AT TL-SE Norman experienced

a long stress period. This was because during this stage temperature was low and there were fewer hours of bright sunshine and shorter days, so that the first stem node appeared very late. In Fenman and Wembley at TL-SE it was vice versa. These experienced higher temperature, more bright sunshine and longer days. A number of workers (Kirby et al., 1982; Bakerr et al., 1986; Wright and Hughes, 1987b) have shown that in cereals development rate is influenced by temperature and daylength, and that development rate increases as these factors increase. The differences in temperature and bright sunshine would also influence rate of transpiration and hence salt uptake. Salt uptake would be expected to be slower in Norman, but faster in Fenman and Wembley, as these varieties experienced warmer and sunnier conditions during the TL-SE stage.

Salinity at TL-SE slightly decreased leaf number on the main stem only in Norman in both experiments. This variety was under stress for a long time and it has been shown that severe stress can affect leaf number by affecting primoridia production during the vegtative stage (Maas and Poss, 1989). Rawson (1986) also found that salinity decreased vegetative growth. The reductions in shoot number per plant, number of leaves and other growth characters resulted in the decreases in yield and yield components. With salinity at this stage some leaf death occured. More leaves died in Norman during TL-SE than in Fenman and Wembley. Particularly in Norman, salinity at TL-SE stunted growth and leaves were smaller as found by Shainberg and Oster (1978). Salinity at TL-SE decreased number of shoots in all varieties in both

experiments as found by other workers (Elkady et al., 1981; Rawson, 1986 and Kumar et al., 1983; and Haqqani et al., 1984). Number of tillers did not recover again except in Norman in Experiment 1. These tillers appeared very late possibly because of the continued water supply in the solution culture. Although they produced ears these remained green and did not contribute to yield . In these experiments with salinity at TL-SE more shoots died in Fenman in both experiments than in Norman and Wembley. A similar trend was observed in the water stress Experiment 1, although here shoot death also occurred in Wembley. In field grown wheat crops the plants normally produce more tillers than survive to produce ears. This death of shoots is attributed partly to competition for light within the crop as it is the smaller shoots at the base of the crop which die. Shoot death was probably lower in these experiments than in normal field crops because the plants were grown in pots, which were spaced apart and hence received light at the base. In these experiments at TL-SE root growth was not measured in both years. Root dry weight was recorded in Experiment 2 only at final harvest. However observations showed that there was much less root growth at the stem extension stage in Norman than in the other varieties. In Experiment 2 salinity during TL-SE resulted in significantly lower dry weight of root at final harvest than salinity at other stages. Abdul halim et al., (1988) found that root growth showed more sensitivity to both available soil water and soil salinity level than other components in wheat varieties. Similarly Asana and Kale (1974) established that salinity depressed root growth more than shoot growth and

it also reduced tillering, leaf size, shoot height, 1000 grain weight, grain yield and dry matter production.

Salinity at TL-SE decreased plant height during the stress period more than at other stages in all varieties, and as found by other workers (Asana and Kale 1974). It was decreased most in Experiment 2. It did not recover again in Norman and Fenman in Experiment 2. In Wembley in both experiments after stopping salt stress, plant height recovered faster possibly because the stress period was shorter. Maas et al., (1986) also found in two sorghum cultivars that plant height was decreased by salinity during the vegetative stage but was not affected by salinity at later stages. Total grain yield per plant was decreased most by salination during the vegetative stage and least during maturation stage.

Salinity at TL-SE decreased leaf area, stem area, dry weight per plant, nitrogen % in straw and nitrogen uptake per plant in both experiments. Salinity at TL-SE decreased leaf area, stem area and dry weight per plant at stem extension more in Experiment 2 than in Experiment 1. In Norman this may be due to high temperature and more bright sunshine. Leaf area was decreased more because at this stage more leaves died. Rawson (1986) found that leaf area, number of tillers and dry matter production were reduced by salininty. Maas (1986) reported that barley, corn, cowpeas, rice, sorghum and wheat were most sensitive during early seedling growth and then became increasingly tolerant during later stages of growth and development. Salinity had no significant effect on nitrogen percentage, but decreased total nitrogen uptake in both experiments because it decreased dry matter production. Torres

and Bingham (1973), Heikal (1977) and Gorham et al. (1986) also found total plant nitrogen decreased by salinity.

Recovery at later stages is important. If plants do not recover at later stages then yield and yield components, will be markedly affected. Recovery depends upon growth stage, crop and how much stress is applied. Maas (1986) reported that cereal crops are most sensitive to salinity during the vegetative stage. They are unable to achieve full recovery from this early stress. In these experiments with salinity at TL-SE plants did not recover at later growth stages as reported by Maas (1986). Plants stressed at TL-SE had lower values of growth parameters than those stressed at later gowth periods in the harvests carried out at booting and anthesis and also had lower yield even though the TL-SE stress period had finished much earlier. Salinity at TL-SE decreased all growth parameters at the booting harvest. These growth parameters could have recovered at anthesis but in fact they were decreased more as shown in Table 61. This suggests that salts are remained in the roots and in plants after the stress period had finished. A number of workers have reported that cereal crops are most sensitive to salt stress during vegetative stages (Ayers et al., 1952; Danielson and Russell, 1957; Kingsbury et al., 1984; Maas, 1986; Larik and Saheel, 1986).

In Experiment 1 the dry weight per plant of the stressed plants was 61%, 31%, 42%, and 56% of the control at stem extension, booting, anthesis, and at maturity values respectively. The corresponding values in Experiment 2 were 46%, 38%, 38%, 39%. This suggests that some recovery occured, but also this

Table 61 Percentage decrease in growth measurement recorded at anthesis due to salinity stress at different stages in salinity Experiments 1 and 2

Growth characters	Stages TL-SE %	SE-BG %	BG-MT %
Experiment 1			
Leaf area per plant (cm^2)	63.55	22.14	31.87
Flag leaf area per plant (cm^2)	61.14	15.82	12.34
Ear area per plant (cm^2)	61.04	15.06	30.82
Stem area per plant (cm^2)	55.07	22.49	29.56
Dry weight per plant (g)	58.97	21.05	30.23
Nitrogen % in straw	-29.06	-15.76	-1.48
Nitrogen uptake per plant (g)	46.67	13.33	30.00
Soluble carbohydrate %	35.09	35.09	12.28
Soluble carbohydrate content (mg per plant)	75.07	41.50	38.27
Experiment 2			
Leaf area per plant (cm^2)	76.57	20.16	20.16
Flag leaf area per plant (cm^2)	71.93	53.17	53.17
Ear area per plant (cm^2)	56.49	38.51	38.51
Stem area per plant (cm^2)	53.55	38.37	38.37
Dry weight per plant (g)	61.65	46.17	46.17
Nitrogen % in straw	-14.81	-16.93	-16.93
Nitrogen uptake per plant (g)	52.86	33.33	33.33
Soluble carbohydrate %	20.29	28.99	28.99
Soluble carbohydrate content (mg per plant)	69.14	61.32	61.32

recovery was not complete due to the reductions in leaf area and dry weight per plant at later stages. Soluble carbohydrate % and soluble carbohydrate content were decreased by salinity at TL-SE shown in Table 61. Frank et al. (1989) found that concentrations of water soluble carbohydrates were greater in stems, increasing rapidly as plants developed. Concentration of water soluble carbohydrate in leaf tissue changed only slightly during development and was smaller than in stems. Main plant stems had a higher water soluble carbohydrate concentration than tiller stems. Water soluble carbohydrate of tillers stems decreased as tiller position increased from the main stem. They suggested that water soluble carbohydrate concentration in the stem is an important factor in determining total tiller number and survival. In these Experiments the concentration of water soluble carbohydrate in separate leaves and stems was not determined, but it is assumed that most of these were in the stem. Lowest production and greatest death of tillers was observed with salinity at TL-SE. This treatment also had the lowest concentration and total content of water soluble carbohydrate. In these experiments with salinity at TL-SE stems were shorter and had a lower leaf area, due to salt stress so they had a lower soluble carbohydrate % at anthesis. Nelson and Spollen (1987) reported that wheat normally accumulates carbohydrate as fructans, particularly in stem tissue. Similarly other workers (Archbold, 1940; Archbold and Mukerjee, 1942) also reported the phenomenon of carbohydrate accumulation in the stems of cereals as well as in many other grasses at the stage of flowering. In these experiments the decreases in soluble carbhydrate % and soluble carbohy-

drate content were greatest in Experiment 1, but the reduction in growth was greatest in Experiment 2. Some other workers (Munns et al., 1982) found that NaCl treatments increased the concentration of soluble carbohydrate in the elongating tissues of the growing leaf, while starch did not change. These findings disagree with the results of the present study. In these experiments Norman had higher soluble carohydrate than other varieties as rported by Daniels et al., (1982), larger stems had a more carbohydrates.

In these Experiments salinity at TL-SE decreased grain weight per plant, number of grains per plant, number of ears per plant, number of spikelets per ear, straw dry weight per plant, and nitrogen uptake per plant more than at other stages. These characters were decreased more in Experiment 2 than Experiment 1 shown in Tables 62 and 63. In Norman this may be due to high temperature and more bright sun hours at this stage. The several workers (Ayers et al., 1952; Asana and Kale, 1974; Bernal Bingham and Oertli, 1974; Joshi, 1976; Kumar et al., 1983; Haqqani, Rauf and Zahid, 1984; Rawson, 1986) all found that salinity at the vegetative stage decreased number of tillers, plant height, yield and yield components more than at other stages. Most crops are more sensitive to salinity under hot, dry conditions than under cool humid ones Maas (1986).

Rate of grain growth and average grain weight were decreased by salinity but not significantly. Brucker and Frohberg (1987) and Mogensen and Talukder (1987) have reported that average grain weight, rate and duration of grain growth are mostly decreased if stress occurs during BG-MT or at

Table 62 Percentage decrease in yield and yield component and other characters recorded at harvest due to salinity stress at different stages in Experiment 1

	Stages		
	TL-SE %	SE-BG %	BG-MT%
Experiment 1			
Grain weight per plant (g)	41.97	26.58	36.94
Average grain weight (mg)	7.65	10.47	19.27
Grain number per plant	36.70	17.56	22.64
Ears number per plant	22.07	8.28	9.89
Grain number per ear	15.10	11.17	12.74
Fertile spikelet per ear	9.64	5.13	7.78
Grain number per fertile spikelet	4.91	5.28	5.28
Infertile spikelet per ear	-7.17	-24.66	-48.88
Harvest index %	-1.56	6.24	4.57
Straw dry weight per plant (g)	43.72	18.85	32.33
Plant height of main stem (cm)	4.22	1.51	5.67
Leaf number on main stem	3.19	0.00	0.00
Nitrogen % grain	-4.12	-5.99	-9.74
Nitrogen % in straw	-38.21	-31.71	6.50
Nitrogen uptake per plant (g)	34.21	13.16	31.58
Final average grain weight of grain growth (mg)	7.24	4.51	20.14
Rate of grain growth (mg/day)	12.78	9.02	27.82
Duration of grain growth (days)	-8.03	-7.81	-15.15

Table 63 Percentage decrease in yield and yield component and other characters recorded at harvest due to salinity stress at different stages in Experiment 2

	Stages		
	TL-SE %	SE-BG %	BG-MT %
Experiment 2			
Grain weight per plant (g)	71.60	41.30	39.67
Average grain weight (mg)	13.27	10.83	20.57
Grain number per plant	67.54	34.24	23.34
Ears number per plant	47.42	21.57	8.54
Grain number per ear	37.79	15.05	12.52
Fertile spikelet per ear	19.82	12.27	11.44
Grain number per fertile spikelet	21.95	2.85	0.81
Infertile spikelet per ear	-56.97	-63.93	-74.18
Harvest index %	20.78	7.75	9.62
Straw dry weight per plant (g)	61.41	35.76	31.52
Plant height of main stem (cm)	18.33	7.03	6.64
Leaf number on main stem	3.56	0.19	-0.19
Nitrogen % in grain	-10.00	-10.00	-16.15
Nitrogen % in straw	-61.29	-33.87	13.71
Nitrogen upake per plant (g)	56.67	23.33	33.33
Final average grain weight of grain growth (mg)	9.97	7.33	11.96
Rate of grain growth (mg/day)	19.09	11.82	10.91
Duration of grain growth (days)	-1.56	-12.71	-4.16

flowering, or at anthesis. Similarly stem reserves are an important character during grain filling. They can be decreased due to early stress, which will help to decrease average grain weight (Rawson and Hofstra, 1969; Rawson and Evans, 1971; Jensen and Mogensen, 1984). In Experiment 1 grain weight per plant, number of grains per plant, number of ears per plant, harvest index and straw dry weight per plant were decreased more in Norman than in other varieties. A similar trend was evident in Experiment 2. However the decreases in these characters were larger in Experiment 2 than in Experiment 1. In Fenman this was because during TL-SE the stress period was longer with more bright sun hours in Experiment 2. These components were decreased more in Norman at TL-SE because the stress lasted longer in Norman. As found by Francois et al. (1988) salinity reduced vegetative growth less than grain yield. These results suggest that a long stress period, with relatively low evaporative conditions (and hence low salt uptake) is possibly more damaging to yield than a short period of stress at higher temperature.

4.4.3.2 Effect of salinity stress during stem extension to booting

At this stage the terminal spikelet has been formed and the floral structures develop as the ear grows and the stem elongates as has been discussed in the literature review (3.23.1, 3.23.2, 3.23.3) and in the water stress experiments section (3.4.2.1, 3.4.2.2, 3.4.2.3). In the salinity experiments at stem extension the plants were taller, had more tillers and more biomass than plants in the water stress experiments. This is probably due to the solution culture

technique used, which meant that plants were continuously supplied with water and nutrients. The phase SE-BG in the salinity experiments was shorter, than other phases for all varieties in both experiments, except in Norman in Experiment 2 where the phase was longer, due to late sowing. During this phase Fenman and Wembley experienced higher temperature and more bright sun hours than Norman in both years. Norman experienced higher temperature and more bright sun hours than during TL-SE. This would be expected to result in faster uptake of salt than during TL-SE. Salinity at SE-BG had no effect on number of main stem leaves in all varieties as all leaves were formed on the apex when stress started as has been disscussed in section (3.23.1, 3.23.2, 3.23.3).

Salinity at SE-BG decreased number of shoots at the start of salt stress. This suggests that salt affected the plants straight away, possibly because high temperature and long days resulted in rapid salt uptake. It could also be due to an osmotic effect. The decreases in number of shoots were less than those brought about by salinity at TL-SE, as found by Abdul Halim et al. (1988).

Salinity at SE-BG had a small effect on plant height in Experiment 1, and a slightly larger effect in Experiment 2 in all varieties. Abdel Halim et al. (1976) and Abdul Halim et al. (1985; 1988) also found that salinity had a small effect on plant height at booting, and at later stages and at harvest. However the decreases in plant height at harvest were smaller than at other stages. Maas et al. (1986) also reported that plant height in sorghum was not affected by salinity at later stages.

In these experiments it was noticed that root growth was rapid after stem elongation as found by Ma (1987). Salinity at SE-BG significantly decreased, leaf area, dry weight and nitrogen uptake per plant. All these characters showed similar reductions in Experiment 1 and 2. Stem area showed a greater decrease in Experiment 1 in Norman. Salinity at this stage had a smaller effect than at TL-SE, because this stage had a shorter stress period. Many workers (Asana and Kale, 1974; Abdel Halim et al., 1976; Francois et al., 1986; Maas, 1986; Rawson, 1986; Abdul Halim et al., 1985, 1988) have reported that salinity decreases growth measurements, yield and yield components at this stage, but less than at TL-SE.

Various workers have reported that the effects of salinity are different in different crops at different stages, and that different growth characters are affected. Heikal (1977) found that total nitrogen content of leaves of safflower and sunflower increased progressively with increase in salinity levels. Bernstein (1962) has reported an increased nitrogen content of plants at high levels of NaCl, and Chen et al. (1964) demonstrated that total nitrogen concentration in the aerial parts of citrus seedlings due to translocation from roots. On the other hand Heikal (1977) reported that salinity induced a reduction in the total nitrogen content of wheat and radish. Similarly Hutton (1971) with leguminous plants, Lashin and Atanasiu (1972) with cotton and Shimose (1973) with rice reported that salinity resulted in a reduction in total nitrogen content. In these experiments salinity at SE-BG resulted in a small increase in the nitrogen % at SE-BG as found by Mashhady et al. (1982) and Heikal (1977). However

nitrogen uptake per plant was decreased due to decrease in the dry weight per plant.

Salinity at SE-BG caused reductions in growth parameters, leaf area, stem area, ear area, dry weight per plant at anthesis shown in Table 61. They were decreased similarly in both experiments, except flag leaf area per plant which was decreased less in Experiment 1, may be due to compensatory growth after the end of the stress period. These growth parameters had not recovered fully by anthesis because only a short time had elapsed since stopping stress. However these parameters were decreased less than with salinity at TL-SE. Many workers (Maas 1986; Mass et al., 1986; Francois et al., 1986; Maas and Poss, 1989) have reported that applied salinity during growth periods decreases the growth parameters at later stages. Maas et al. (1986) also reported in sorghum that salinity during the booting stage decreased flag leaf area, yield and yield components, and hastened complete plant maturity. Similarly in these experiments salinity at SE-BG decreased the flag leaf area, and yield and yield components. Grain yield from plants stressed during either the vegetative, reproductive or maturation stage became less sensitive to salinity the later plants were stressed. In the experiments here at anthesis time soluble carbohydrate % was decreased (although not significantly) by salinity at SE-BG, similar to TL-SE although the stress period was shorter. Aslam et al. (1986) found that plants grown at higher NaCl often contain more carbohydrates than plants grown at low NaCl. Munns et al. (1982) found in barley that carbohydrate status of the youngest leaf was higher after 5 days of salt treatment than

in the control, especially in the most rapidly elongating region, while that of the older leaves was slightly lower. Water stressed plants also have higher total reserve of carbohydrate concentration than controls (eg. Ackerson, 1981). However in these experiments soluble carbohydrate content was lower in the stressed plants than controls due to the lower soluble carbohydrate % and lower dry weight per plant.

The total dry weight per plant of the stressed plants expressed as a percentage of the controls was 58%, and 61% at booting, 79%, and 54%, at anthesis and 81%, and 64% at maturity respectively in Experiments 1 and 2. This suggest that some recovery took place in Experiment 1 but there was no recovery in Experiment 2, In Norman and Wembley this is possibly because they had a longer stress period at SE-BG in Experiment 2 than in Experiment 1.

In both Experiments 1 and 2 salinity at SE-BG caused reductions of yield and yield components, grain weight per plant, number of grains per plant, fertile spikelets per ear, number of grains per fertile spikelet, straw dry weight per plant and nitrogen uptake per plant shown in Tables 62 and 63. All these yield components were significantly decreased in both experiments except number of grains per plant in Experiment 1. Francois et al. (1989) showed that straw yield was more sensitive than was grain yield in rye crop. Harvest index was not significantly affected by salinity at SE-BG in both years. These yield components were decreased more in Experiment 2. In Norman and Wembley the stress period at SE-BG was longer in Experiment 2 than in Experiment 1, but at this stage in both years the temperature was similar.

Grain yield was decreased more than other yield components. It was mainly due to decreases in number of grains per plant, grain number per ear and number of ears per plant. These yield and yield components were decreased less at SE-BG than at TL-SE shown in Tables 62 and 63. Many workers (Maas and Hoffman, 1977; Haqqani, Rauf and Zahid, 1984; Maas, 1986; Maas et al., 1986; Rawson, 1986; Francois et al., 1986; Abdul Halim, 1988; Francois et al., 1988, 1989; Maas and Poss, 1989) have reported that yield and yield components were less affected with salinity applied at later growth stages. In these experiments nitrogen percentage in grain and nitrogen percentage in straw increased under salt stress at SE-BG. It was increased more in straw than in grain yield. Salinity at SE-BG resulted in decreases in average grain weight due to decrease in rate of grain growth although this was not always significant. Duration of grain growth was not significantly affected. As mentioned in earlier sections (3.4.2.1, 3.4.2.2, 4.4.3.1) these factors were little affected during earlier growth periods by applied stress. These characters can be more affected by stress during development of grain (Kirby and Appleyard, 1981; Mogensen and Talukder, 1987).

In Fenman and Wembley the SE-BG stress period was much shorter than in Norman. The plants were exposed to salinity for only 2 to 3 weeks yet yield was still significantly decreased. These results suggest that the processes of tillering and ear development are very sensitive to salinity.

Grain weight per plant was decreased due to decreases in number of grains and ears per plant. Number of fertile spikelets per ear and average grain weight were relatively

little affected as these components are determined at other times in the life of the crop. The decreases in numbers of grains and ears per plant were less in Fenman and Wembley , which experienced a short stress period, than in Norman, in which the stress period was longer. Norman reached this stage earlier than Fenman and Wembley , at a time when temperature was lower, and sun hours were shorter and hence when salt uptake was probably slower. However yield was decreased. All varieties were sensitive to salinity at this stage.

4.4.3.3 Effect of salinity stress during booting to maturity

During this stage ear emergence occurs. and the anthers and pollen become visible on the ears. Afterwards grain filling occurs (Kirby and Appleyard, 1981) and average grain weight, duration and rate of grain growth can be decreased by stress at this stage (Kirby and Appleyard, 1981; Mogensen and Talukder 1987). At anthesis the plants grown in solution culture were taller and had a larger green leaf area than plants grown in pots in the water stress experiments. During this stage mean temperature experienced was similar in both years, but was 2 to 3^{o}C lower in Norman than in Fenman and Wembley. Hours of bright sunshine were longer in Experiment 2 than in Experiment 1, and hence in Experiment 2 all varieties stressed at this stage were harvested 10 to 14 days earlier than in Experiment 1. At this stage Norman and Fenman had a longer stress period in Experiment 1 than in Experiment 2, possibly due to the earlier sowing period. When plants stressed at this stage were harvested, some leaves were still green. Only the ears had completely senesced naturally. This is due to the solution culture technique used as found by

Hayward and Magistad (1946). With water stress at this stage all plants died quickly in both years as found by Mothes (1928), Gates (1964, 1968) and Slatyer (1967). Salinity at BG-MT had smaller effects on tillering than at earlier growth stages. Some tillers with an ear were dead at final harvest. These were counted as ears but they contained no grain at this stage. Salinity at BG-MT had no chance to decrease tiller production as this had ceased by this time. Many workers (Francois et al., 1986; 1988; Maas 1986) have reported that salinity has a smaller effect on number of tillers, plant height, yield and yield components when applied at later growth stages, booting and at anthesis. Haqqani et al. (1984) found that increasing soil salinity and sodicity reduced the number of ear bearing and non ear bearing, the number of spikelets per ear, 1000 grain weight, straw weight and grain yield.

Final height was decreased significantly in both experiments, although the decrease was small. Abdul Halim et al. (1988) found that in mexipak wheat cultivars salinity caused a small decrease in height at later growth stages. Similarly Maas et al., (1986) found that plant height was not affected by salinity at later stages in sorghum.

Salinity at BG-MT decreased leaf area, flag leaf area, stem area, dry weight, nitrogen uptake, soluble carbohydrate % and soluble carbohydrate content per plant at anthesis in both experiments shown in Table 61. However the decreases in these characters were smaller than with salinity at TL-SE because this stage had a shorter stress period as found by many workers (Francois et al., 1986, 1988, 1989; Abdul Halim

et al., 1986). In these experiments flag leaf area and dry weight per plant were decreased more in Experiment 2, possibly because there were more sun hours. Maas et al. (1986) found that salinity during the booting stage decreased flag leaf area in sorghum. Soluble carbohydrate % was not significantly affected in both experiments. However, Downton (1977), found that carbohydrate concentration (sugar and starch on a dry weight basis) was decreased by 20 to 40% in leaves of grapevines at 75 mM NaCl, showing the reduced growth was due to reduction in photosynthesis. Munns et al. (1982) on the other hand found for barley that the carbohydrate status of the youngest leaf was higher after 5 days of salt treatment than in the control, especially in the most rapidly elongating region, while that of the older leaves was slightly lower. Soluble carbohydrate content was decreased more in Experiment 2 than in Experiment 1, due to greater reduction in dry weight per plant and soluble carbohydrate %.

At anthesis nitrogen % was increased but not significantly. It was increased more in Experiment 2. In both experiments salinity at all stages increased nitrogen % at anthesis. However nitrogen uptake was significantly decreased due to decreases in dry weight per plant. Nitrogen uptake was decreased most with salinity at TL-SE. Similarly other workers (Heikal, 1977; Torres and Bingham, 1973; Mashhady, Sayed and Heikal, 1982) have reported decreased nitrogen content in wheat under salinity stress.

Recovery was calculated by expressing dry weight per plant of the stressed treatments as a % of the unstressed controls. With salinity at BG-MT dry weight per plant at

anthesis was 70% and 78% of the controls in Experiments 1 and 2 respectively. At maturity the corresponding values were 68% and 69% respectively. With salinity at this stage there was no chance for recovery because stress continued up to maturity.

In both experiments grain yield and straw dry matter production was decreased more than other yield components. In both years salinity at SE-BG and BG-MT decreased yield and yield components less than salinity at TL-SE shown in Tables 62 and 63. A number of workers (Asana and Kale, 1974; Bernal, Bingham and Oertli, 1974; Kumar, Chauhan and Singh, 1981; Kumar, 1983; Maas, 1986; Maas, et al., 1986; Francois et al., 1986, 1988, 1989; Abdul Halim et al., 1988) have reported that salinity decreases yield and yield components less, when it occurs at booting, anthesis and at later stages. Salinity at BG-MT also decreased yield and yield components more than salinity at SE-BG in Experiment 1. This is also possibly because there was no recovery time and salt stress continued up to maturity. However with salinity at BG-MT the numbers of infertile spikelets per ear were increased more than with salinity at TL-SE and SE-BG. As reported by Kirby and Appleyard (1981) during BG-MT any stress can affect spiklet number. Haqqani et al. (1984) also reported that similar decreases in spikelets per ear, 1000 grain weight, and straw and grain yield.

Average grain weight is a major factor of grain yield. It depends on the rate and duration of grain growth and amount of reserve carbohydrate. These processes depend on the leaf area index present at anthesis and depend upon how long the leaves and other parts of the plant stay green as reported by Nass and Reiser (1975) and Bruckner and Frohberg (1987). The

reduction in rate of grain growth due to salinity is probably due to the large reduction in leaf area. In these experiments average grain weight was less affected by salinity at BG-MT compared to water stress. This is possibly due to the solution culture technique used. In this system plant leaves did not senesce quickly as in the water stress experiments as reported by Mogensen and Talukder (1987). Salinity at BG-MT had similar effects on average grain weight, decreasing it by 19% and 21% as shown in Tables 62 and 63 respectively in Experiments 1 and 2. Salinity at BG-MT caused a greater reduction in average grain weight than salinity at TL-SE and SE-BG. The duration of grain growth was not significantly affected in the experiments although it was increased. However in the water stress experiments it was decreased. In salinity Experiment 2 it was increased due to earlier harvesting of plants. Therefore in these salinity experiments average grain weight, rate and duration of grain growth were less affected by salinity than by water stress as the plants stayed greener for longer due to the solution culture technique used. Nass and Reiser (1975) and Bruckner and Frohberg (1987) reported that salinity reduced the rate of grain growth and decreased the average grain weight. In these experiments with salinity at BG-MT, grain weight per plant, average grain weight and number of grains per plant were more affected than other yield components in all varieties. The decreases in yield components of the three varieties were not consistent in the two experiments. Grain number per plant, ear number per plant, fertile spikelet per ear and straw dry weight per plant were decreased more in Norman than in other varieties. However

grain weight per plant and average grain weight were decreased most in Norman in Experiment 2 and in Wembley in Experiment 1. Fenman had grain weight per plant between Norman and Wembley. These results suggest that at BG-MT Norman is more sensitive than other varieties in most yield components. However for grain weight per plant there was no consistent trend in Experiments 1 and 2. Results obtained by other workers (Joshi, 1976; Chipa and Lal, 1985; Francois et al., 1988)., also this suggests that variety differences in response to salinity do exist.

4.4.4 INCREASE IN DRY WEIGHT PER PLANT BETWEEN ANTHESIS AND HARVEST AND CONTRIBUTION OF STEM RESERVES TO GRAIN FILLING

The increase in dry weight per plant between anthesis and harvest and contribution of stem reserves to grain filling was calculated using the method of Gallgher, Biscoe and Scott (1975) and following the procedure used in the water stress experiments (section 3.4.3).

Increases in dry weight per plant between anthesis and maturity are shown in Table 64. The increases in this experiment were much larger than those noted in the water stress experiment (shown in Table 35). This is possibly a consequence of the growing technique used. In the water stress experiment all shoots died, whereas in solution culture plants continued to grow and tiller. Therefore the increase in dry weight noted is made up of 2 components: (1) The increase in dry weight of stems and ears present at anthesis (2) Increase in dry weight due to extra tillers produced between anthesis

Table 64 Effect of varieties and salinity stress on increase in dry weight (gram per plant) between anthesis and maturity in Experiment 1 and 2.

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	5.02	6.54	6.02
Stem extension to booting	3.70	7.94	7.42
Booting to maturity	3.05	2.94	8.49
Control	9.78	6.99	4.45
S.E. of means = 2.50; L.S.D. (P = 0.05) = N.S.			
Experiment 2			
Tillering to stem extension	1.47	0.75	3.23
Stem extension to booting	5.56	6.03	5.20
Booting to maturity	2.86	6.25	1.68
Control	6.54	8.73	4.84
S.E. of means = 2.75; L.S.D. (P = 0.05) = N.S.			

and harvest. This means that where many extra tillers were produced than the increase in dry weight between anthesis and maturity is an over estimate of the true increase. Hence the calculated contribution from stem reserves is an under estimate of the true contribution.

There were no significant effects of salinity X variety interaction on increase in dry weight and an stem reserve contribution to grain yield (Table 64 and 65). Generally the main effects of salinity and the main effects of variety were not significant (Table 66 and 67). In Experiment 1 the contribution of stem reserves to grain filling was greater in Norman than in Fenman and Wembley, where they made no contribution. All other effects were not significant.

The coefficients of variation for grain weight in the salinity experiments (13%, 18% in Experiment 1 and 2) were much lower than those for the increase in dry weight between anthesis and harvest (58%, 88%) and the calculated contribution of stem reserve to grain filling (622%, 3732%). These very high coefficients make it difficult to detect significant differences between treatments.

This is possiably a consequence of the small sample size which was used to determine dry weight at anthesis. Grain weight at harvest, which was determined on a much larger sample, had a much lower coefficient of variation. It is suggested that in any future work much larger samples should be taken at anthesis. This may not be possible in pot experiments where sample size is limited by the number of plants available in a pot, as was the case in these experiments. An alternative would be to increase the number of

Table 65 Effect of varieties and salinity stress on stem reserve contribution to grain yield (g) per plant in Experiments 1 and 2.

Stress period	Varieties		
	Norman	Fenman	Wembley
Experiment 1			
Tillering to stem extension	-0.16	-1.05	-1.48
Stem extension to booting	4.92	-1.92	-1.82
Booting to maturity	4.83	1.74	-4.33
Control	2.98	0.42	2.67
S.E. of means = 2.50; L.S.D. (P = 0.05) = N.S.			
Experiment 2			
Tillering to stem extension	-0.09	0.50	-0.24
Stem extension to booting	-0.13	-0.61	-0.71
Booting to maturity	1.33	-1.10	2.05
Control	1.99	-0.25	0.44
S.E. of means = 2.35; L.S.D. (P = 0.05) = N.S.			

Table 66 Main effects of salinity stress at different growth stages on increase in dry weight between anthesis and maturity and stem reserve contribution to grain yield in salinity Experiments 1 and 2.

	Stages					
	TL-SE	SE-BG	BG-MT	Control	S.E.M.	L.S.D. (P=0.05)
Experiment 1						
Increase in dry weight between anthesis and maturity (g) per plant	5.86	6.35	4.83	7.07	1.44	N.S.
Stem reserve contribution to grain yield (g) per plant	-0.89	0.39	0.75	2.02	1.44	N.S.
Experiment 2						
Increase in dry weight between anthesis maturity (g) per plant	1.82	5.59	3.60	6.70	1.58	N.S.
Stem reserve contribution to grain yield (g) per plant	0.06	-1.15	0.76	0.69	1.35	5.19

Table 67 Main effects of varieties on increase in dry weight between anthesis and maturity and stem reserve contribution to grain yield in salinity Experiments 1 and 2.

	Varieties				
	Norman	Fenman	Wembley	S.E.M.	L.S.D. (P=0.05)
Experiment 1					
Increase in dry weight between anthesis and maturity (g) per plant	5.39	6.10	6.59	1.24	N.S.
Stem reserve contribution to grain yield (g) per plant	3.14	-0.20	-1.24	1.24	4.33
Experiment 2					
Increase in dry weight between anthesis and maturity (g) per plant	4.11	5.44	3.74	1.38	N.S.
Stem reserve contribution to grain Yield (g) per plant	0.26	-0.37	0.38	1.18	N.S.

replicates, and to have separate replicates for growth analysis and yield determination. However, in practise, this would probably result in being able to test fewer treatments.

The negative values in the tables show that the incrase in dry weight between anthesis and harvest was greater than grain weight and hence there was no contibution of stem reserve to grain filling.

4.4.5 RELATIONSHIPS BETWEEN YIELD AND YIELD COMPONENTS

In these experiments yield was significantly correlated to all yield components except grains per fertile spikelet and harvest index in Experiment 1 shown in Table 68. In Experiment 2 the correlation between yield and number of grains per fertile spikelet was not significant. Number of grains per plant were significantly correlated with fertile spikelet per ear in both year. Fertile spikelets were significantly correlated with grain number per fertile spikelet.

In the tables for yield and yield components, the abbreviations are used:

GWPP = Grain weight per plant (g)

AGWM = Average grain weight (mg)

GNPP = Grain number per plant

ENPP = Number of ears per plant

FSPE = Fertile spikelets per ear

GNPFS = Number of grain per fertile spikelets

HIND = Harvest index %

Table 68 Values of the linear correlation coefficient between the grain yield, yield components in salinity Experiments 1 and 2.

	GWPP	AGWM	GNPP	ENPP	FSPE	GNPFS	HIND
Expriment 1							
Average grain weight (mg)	0.63*						
Grain number per plant	0.97*	0.44NS					
Ear number per plant	-0.05NS	-0.23NS	-0.15NS				
Fertile spikelet per ear	0.85*	0.52NS	0.84*	-0.40NS			
Grain number per fertile spikelet	0.57*	0.04NS	0.56*	-0.82*	0.77*		
Harvest index %	-0.06NS	0.31NS	-0.14NS	0.08NS	-0.29NS	-0.19NS	
Straw weight per plant (g)	0.89*	0.41NS	0.91*	-0.13NS	0.90*	0.61*	-0.50NS
Experiment 2							
Average grain weight (mg)	0.63*						
Grain number per plant	0.95*	0.37NS					
Ear number per plant	0.60NS	0.28NS	0.63*				
Fertile spikelet per ear	0.65*	0.19NS	0.71*	-0.01NS			
Grain number per fertile spikelet	0.36NS	-0.04NS	0.46NS	-0.31NS	0.67*		
Harvest index %	0.58*	0.61*	0.46NS	0.80*	-0.16NS	-0.35NS	
Straw weight per plant (g)	0.62*	0.04NS	0.74*	0.11NS	0.92*	0.67*	-0.18NS

NS = P > 0.05

* = 0.01 < P < 0.05

4.4.6 RELATIONSHIP BETWEEN FINAL AVERAGE GRAIN WEGHT, RATE AND DURATION OF GRAIN GROWTH AND TOTAL LEAF AREA AT ANTHESIS

In both experiments final average grain weight was significantly correlated with rate of grain growth and with duration of grain growth in Experiment 1 shown in Table 69. Final average grain weight was not significantly correlated with total leaf area at anthesis in both experiments. Rate of grain growth was significantly negatively correlated with duration of grain growth. Duration of grain growth was significantly negatively correlatedwith total leaf area at anthesis in Experiment 1 but not in Experiment 2.

This means that high average grain weight is achieved by having a fast rate and short duration of grain growth. This was correlated with a high leaf area at anthesis in one experiment. The results also suggest that salinity decreases average grain weight by decreasing rate of grain growth.

4.4.7 EFFECTS OF SALINITY ON DIFFERENT VARIETIES

Comparing the three varieties used in these experiments, Norman had increased grain weight per plant in Experiment 1 only. In both experiments Norman had a higher grain number per plant, grain number per ear, grain number per fertile spikelet, fertile spikelet per ear, straw weight per plant, leaf number on main stem, nitrogen uptake per plant. Norman also had more infertile spikelets per ear and faster rate of grain growth.

All varieties were particularly sensitive to salinity at TL-SE, which decreased growth measurements and yield components,

Table 69 Values of the linear correlation coefficient between the final average grain weight, rate of grain growth, duration of grin gorwth and total leaf area (leaf+flag leaf+stem+ear) at anthesis in salinity Experiments 1 and 2.

	Final average weight (mg)	Rate of grain growth (mg/day)	Duration of grain growth per plant (days)
Experiment 1			
Rate of grain growth (days)	0.94*		
Duration of grain growth per plant (days)	-0.83*	-0.92*	
Total leaf area per plant (cm)	0.40 N.S.	0.59*	-0.58*
Experiment 2			
Rate of grain growth (days)	0.85*		
Duration of grain growth per plant (days)	-0.44 N.S.	-0.70*	
Total leaf area per plant (cm)	0.23 N.S	-0.15 N.S	0.15 N.S

N.S. = $P > 0.05$

* = $0.01 < P < 0.05$

particularly grain number per plant and ear number per plant more than at SE-BG, BG-MT. In varieties Norman was most sensitive at TL-SE. It had much greater reduction in shoot number, plant height, leaf number, leaf area, ear number per plant and harvest index at maturity (Tables, 45, 46, 59, 61, 62, 63). Wembley variety was less sensitive at TL-SE. It had more shoot numbers and higher values of growth measurements than other varieties at this stage. As it had more shoots it had more ears per plant at maturity. Wembley variety was most sensitive in yield and yield components at maturity. Wembley showed the greatest decrease in grain weight per plant, grain number per plant, grain number per ear, grain number per fertile spikelet, fertile spikelets per ear, nitrogen % in grain, nitrogen uptake per plant. Wembley showed an increased number of infertile spikelets per ear, and duration of grain growth. Fenman was generally between Norman and Wembley in growth measurements, yield and yield components.

Therefore, Norman or other long duration varieties which have a long TL-SE period are less useful for breeding work. However these varieties may be more suitable for plant breeders during the stages SE-BG and BG-MT. Possibly a growth retardant could be used to stop lodging, and increase yield, yield components and dry matter production under salinity. Fenman, Wembley and other shorter duration varieties which have shorter periods at TL-SE and SE-BG may be more suitable for plant breeding work, where stress is normally experienced during these periods.

CHAPTER 5

CONCLUSIONS AND SUGGESTIONS FOR FURTHER EXPERIMENTS

5.0 CONCLUSIONS AND SUGGESTIONS FOR FURTHER EXPERIMENTS

Generally in both experiments, both stresses decreased growth measurements, yield and yield components at all stages in all varieties. In the water stress experiments, yield and yield components of all varieties were most susceptible at BG-MT. Growth measurements were decreased most by water stress at SE-BG. In the salinity experiments all varieties showed the greatest decrease in growth measurements, yield and yield components with salinity at TL-SE rather than at SE-BG or BG-MT.

Grain weight per plant, average grain weight, grain number per ear, fertile spikelets per ear, grain number per fertile spikelet were decreased more by water stress than by salinity at BG-MT. However leaf area, stem area, dry weight per plant, grain weight per plant, number of grains per ear, fertile spikelets, number of grains per fertile spikelets were decreased more by salinity than by water stress at TL-SE.

In varieties, Norman was more sensitive at TL-SE in the salinity experiments than in the water stress experiments. This variety was less affected at SE-BG and BG-MT in the salinity experiments but not in the water stress experiments. Generally Norman was more sensitive than other varieties at BG-MT in the salinity experiments.

In these experiments, the varieties were not tested under similar climatic conditions. As weather conditions can influence the effect of stress, then ideally we should compare long, medium and short duration varieties under identical climatic conditions.

Different amounts of water at different stages could also be tested in these varieties because sometimes in tropical countries drought occurs for a very short period. Water potential measurements in plants, leaves and shoots are also important because sometimes water is present in the soil but hot wind and high temperature cause injury straightaway to the plants by desiccation. This was not measured in these experiments.

In the salinity experiments ion (Na^+, Cl^-) uptake was not measured. It should be measured in long, medium and short duration varieties at different stages. In these experiments apical development was also not recorded. It is quite important to look at apical development to see how the primordia are affected at different stages by water stress and salinity stress in long, medium and short duration varieties. In these experiments salt was applied in only one quantity and only one salt (NaCl) was tested. Testing other salts in different amounts may give different results. Growth regulators may also be helpful during stress conditions. One more important and good suggestion is that these stresses should be applied together in these varieties in a randomized factorial split plot design, with hormones and nitrogen fertilizer, because in most tropical countries the salt and drought problems occur together. Farmers are also crying about the nitrogen fertilizer effect during growing crops, under drought and salinity problems.

In addition, the effects of stress on stem reserve contribution to yield and its relationship with water soluble

carbohydrate should be examined in more detail using larger samples than were used in these experiments. The effects of stress on the number of endosperm cells in the grain should also be examined. Early stress may limit yield by limiting the number of these cells.

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APPENDIX 1

APPENDEX

EQUIPMENT USED

Aerators: 'Supa' Aquatic Supplies Ltd, 'Conway' Hawthorne Close, Barlborough, Chesterfield, G.B.

Air Compressor: Comair-Brown Wade, High Wycombe, England.

Air Supply Unit: IRGA (The Analytical Development Co.)

Air Supply Generator WG-600:Ltd., Pinder Rd, Hoddeson.

Automatic Area Meter: Model NAM7, Hayashi Denkoh Co. Ltd., Tokyo, Japan.

Balances: Satorius, west Germany.

Conductivity Meter: Model P335, Portland Electronics Ltd., 18 Greenacres Road, Oldham, England.

Fluorescent Lights in growth room: 125W ' Warm White', Philips, Einhover, Holland.

Fridge: Vindon Scientific Ltd., Diggle, Oldham, England.

Gypsum block for soil moisture: Model 200, Soil Moisture Equipment Co., P.O. Box 30.

Lamps in glasshouse: High pressure Mercury Vapour Lamp.

Large Drying Ovens: Unitherm, Drying Oven, Russell-Lindsey.

Large Mill: Allenest Type SCIS, Brighton, England.

Nitrogen Analyser: Kjeltec Auto 1030 Analyser, West Germany.

pH Meter: Ionalyzer - Specific ion meter, Model 407A, Orion Research Inc, Cambridge, Mass, USA.

'Phostrogen': Phostrogen Ltd., Corwen, Clwyed, UK.

Pipettes: Eppendorf Varipipette (4720) and Multipipette (4780), Eppendorf Geratenbau, Netherland, Hirz Bmbh, Postfach 65, 0670, 2000, Hambrug 65, West Germany.

Salinity Bridge Measuring Instrument: Cat. No. 5500. Soil Moisture Equipment Corporation, P.O. Box 30025.

Seed Counter: Numigral-Tecator, Box 70, 5-26301, Hoganas, Sweden.

Small Mill: Cyclotec 1093, Sample Mill, Tecator, Sweden.

Vortex Stirrer: Gallenkamp Spinmix, England.