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Studies of leaf growth in barley

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STUDIES OF LEAF GROWTH IN BARLEY

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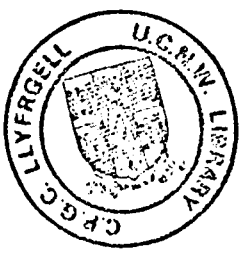

IN THE NAME OF

GOD

MOST GRACIOUS MOST MERCIFULL

DEDICATION

I dedicate this thesis to the loving memory

of my late parents

Asif Maan

DECLARATION PAGE NOT SCANNED AT THE REQUEST OF THE UNIVERSITY

CONTENTS

		Page
SUMMARY		i
ACKNOWLEDGEMENTS		iii
LIST OF TABLES		iv
LIST OF FIGURES AND PLATES		x
LIST OF ABBREVIATIONS AND SYMBOLS		xiv
CHAPTER 1.	GENERAL INTRODUCTION	1
CHAPTER 2.	REVIEW OF LITERATURE	6
2.1	APICAL DEVELOPMENT	7
2.2	PHYSIOLOGICAL ASPECTS OF LEAF GROWTH AND DEVELOPMENT	15
2.2.1	Cell division and expansion	15
2.2.2	Ontogenetic changes in leaf size	18
2.2.3	Nitrogen nutrition	20
2.2.4	Light intensity and photoperiodic effects	22
2.2.5	Temperature effects	25
2.2.6	Interactions between light and temperature	27
2.2.7	Effects of plant density	28
2.2.8	Effects of water stress	29
2.2.9	Conclusions	29
2.3	PHYSIOLOGICAL ASPECTS OF TILLERING	30
2.4	YIELD DETERMINATION OF CEREALS	37
2.5	TECHNIQUES OF EXPERIMENTATION	41
2.6	MAIN OBJECTIVES OF THIS STUDY	46
CHAPTER 3.	EXPERIMENT 1.	
	Effects of nitrogen supply and sowing date on growth of the first five main shoot leaves of spring barley.	48

3.1	INTRODUCTION	49
3.2	MATERIALS AND METHODS	49
3.2.1	Cultivation of plants and experimental treatments tested.	49
3.2.2	Metreological observations	51
3.2.3	Leaf extension measurements	54
3.2.4	Plant growth analysis	55
3.2.5	Pests and diseases	58
3.3	RESULTS	58
3.3.1	Environmental conditions during the course of the experiments	58
3.3.1.1	Water and nutrient supply	58
3.3.1.2	Temperature	58
3.3.1.3	Photoperiod	59
3.3.1.4	Solar radiation	59
3.3.1.5	Time taken to different growth stages	61
3.3.2	Statistical analysis	61
3.3.3	Main effects and interactions	64
3.3.3.1	Main effects of sowing date	64
3.3.3.2	Main effects of nitrogen	67
3.3.3.3	Main effects of leaf position	67
3.3.4	Interactions between nitrogen supply, sowing date and leaf position	70
3.3.4.1	Lamina area and dry weight	70
3.3.4.2	Specific lamina area	72
3.3.4.3	Leaf extension rate and duration of 5th main shoot leaf	74
3.3.4.4	Nitrogen content of 5th main shoot leaf	77
3.3.4.5	Main shoot total dry weight	77
3.3.4.6	Tiller number and dry weight	79
3.3.4.7	Plant dry weight	79
3.4	CONCLUSIONS	82

CHAPTER 4. EXPERIMENT 2.

Apical development and leaf growth in relation to nitrogen supply and environments. 84

4.1	INTRODUCTION	85
4.2	MATERIALS AND METHODS	86
4.2.1	Cultivation of plants and experimental treatments tested	86
4.2.1.1	Plant material	86
4.2.1.2	Growing medium	86
4.2.1.3	Sowing procedure	87
4.2.1.4	Details of treatments	87
4.2.2	Apical development	89
4.2.3	Leaf extension measurements	94
4.2.4	Plant growth analysis	97
4.2.5	Metreological observations	98
4.2.6	Pests and diseases	99
4.3	RESULTS	99
4.3.1	Environmental conditions during the course of the experiment	99
4.3.1.1	Temperature	99
4.3.1.2	Photoperiod	99
4.3.1.3	Radiation	101
4.3.1.4	Crop development	101
4.3.2	Statistical analysis	103
4.3.3	Apical development	104
4.3.3.1	Primordia initiation and Julian time	106
4.3.3.2	Primordia initiation and thermal time	106
4.3.3.3	Leaf appearance and Julian time	108
4.3.3.4	Leaf appearance and thermal time	108
4.3.4	Leaf extension and leaf nitrogen content of first 6 main shoot leaves	108
4.3.4.1	Main effects of sowing date	110
4.3.4.2	Main effects of nitrogen application	110
4.3.4.3	Main effects of leaf position	112
4.3.4.4	Sowing date and leaf position interaction	112
4.3.4.5	Nitrogen and leaf position interaction	114
4.3.4.6	Sowing date and nitrogen interaction	114
4.3.4.7	Sowing date, nitrogen and leaf position interaction	114
4.3.5	Lamina area,dry weight,specific	

lamina area and lamina:sheath ratio 120
4.3.5.1 Main effects of sowing date 123
4.3.5.2 Main effects of nitrogen 123
4.3.5.3 Main effects of leaf position 123
4.3.5.4 First order interactions 125
4.3.5.4.1 Sowing date and leaf position interaction 125
4.3.5.4.2 Nitrogen and leaf position interaction 127
4.3.6 Plant size and dry weight at different Growth stages 131
4.3.6.1 Sowing date and time of harvest interaction 131
4.3.6.2 Nitrogen and time of harvest interaction 135
4.3.6.3 Sowing date and nitrogen interaction 137
4.4 CONCLUSIONS 137

CHAPTER 5. EXPERIMENT 3.

The effects of plant density and nitrogen supply on apical development, leaf growth and yield of spring barley 141

5.1 INTRODUCTION 142
5.2 MATERIALS AND METHODS 143
5.2.1 Cultivation of plants and experimental treatments tested 143
5.2.1.1 Plant material 143
5.2.1.2 Growing medium 143
5.2.1.3 Details of treatments and experimental design 143
5.2.1.4 Sowing method 144
5.2.2 Apical development 144
5.2.3 Leaf extension measurements 145
5.2.4 Plant growth analysis 145
5.2.5 Yield analysis 146
5.2.6 Metreological observations 147

5.2.7	Pests and disease control	148
5.3	RESULTS	148
5.3.1	Environmental conditions during the course of the experiment	148
5.3.2	Time taken to various growth stages	148
5.3.3	Statistical analysis	151
5.3.4	Apical development	152
5.3.4.1	Primordia initiation	152
5.3.4.2	Leaf appearance	155
5.3.5	Leaf extension of first 6 main shoot leaves	155
5.3.5.1	Main effects of plant density, nitroge amount and leaf position	155
5.3.5.2	First order interactions	158
5.3.6	Lamina area, dry weight, specific lamina area and lamina:sheath ratio	158
5.3.6.1	Main effects of plant density, nitrogen supply and leaf position	160
5.3.6.2	First order interactions	160
5.3.7	Growth analysis : Plant size and dry weight at different growth stages	165
5.3.7.1	Main effects of plant density	165
5.3.7.2	Main effects of nitrogen amount	168
5.3.7.3	Main effects of time of harvest	168
5.3.7.4	Plant density and harvest interaction	168
5.3.7.5	Nitrogen and harvest interaction	172
5.3.8	Yield analysis	172
5.3.8.1	Main effects of plant density on grain yield and its components	175
5.3.8.2	Main effects of nitrogen amount on grain yield and its components	175
5.4	YIELD DETERMINATION	175
5.5	CONCLUSIONS	180
CHAPTER 6.	GENERAL DISCUSSION	183
6.1	PREFACE	184
6.2	ADVANTAGES AND DISADVANTAGES OF USING	

	THIS PARTICULAR EXPERIMENTAL APPROACH	185
6.3	EFFECTS OF GROWTH MEDIA	186
6.4	GROWTH OF THE FOLIAGE CANOPY	187
6.4.1	Leaf appearance	189
6.4.2	Final number of leaves	191
6.4.3	Leaf area	192
6.4.4	Extension of leaf 5 of main shoot	193
6.4.4.1	Relationship between LER, LED and FLL of leaf 5	195
6.4.4.2	Effect of nitrogen supply on LER of leaf 5	195
6.4.4.3	Factors influencing LED of leaf 5	200
6.4.5	Leaf growth of other main shoot leaves	203
6.4.5.1	Relationship between LER and leaf nitrogen content for other main shoot leaves	203
6.4.5.2	Relationship between LED and mean air temperature for other main shoot leaves	206
6.4.6	Effects of sowing date, nitrogen and plant density on ontogenetic changes in leaf size	209
6.5	Relationship between lamina area, lamina length and lamina dry weight	213
6.6	Tillering	217
6.7	Primordia production	218
BIBLIOGRAPHY		220
APPENDIX I	Recipe of the nutrient solution	252
APPENDIX II	Length of day light for 54° N	253

S U M M A R Y

The yield of crop dry matter is closely dependent upon the amount of solar radiation intercepted by the crop canopy. This in turn is primarily determined by the amount of leaf area and its persistence. This study was concerned with the influence of environments, nitrogen supply and plant density in controlling apical development and leaf growth and development in barley. Three series of experiments were carried out on sequentially sown spring barley (cv. Claret) to cover the whole range of the natural variation in environmental variables. In the first series of experiments there were 4 sowing dates, 4 levels of nitrogen and plants were grown in perlite in small pots. In the second series there were 3 sowing dates, 4 levels of nitrogen and plants were grown in soil and sand compost in small pots. In the third series of experiments there were 3 plant densities, 2 levels of nitrogen and plants were grown in soil and sand compost in large tanks.

A strong effect of growth media and size of pot on leaf growth was observed. The plants grown in soil had longer leaves and had more tillers than plants grown in perlite. Leaves were even longer when plants were grown in large tanks.

Primordia initiation on the main shoot apex, leaf appearance and leaf extension were best described as linear function of thermal time rather than Julian time. Rate of leaf appearance on the main shoot was found to be linearly related to the rate of change of daylength at crop emergence.

Final leaf length depended upon both the rate and duration of leaf extension. However, most of the variation in final leaf length was due mainly to variation in leaf extension rate.

Leaf extension rate increased with nitrogen supply. A significant quadratic relationship between leaf extension rate and leaf nitrogen content was observed. It is suggested that irrespective of growing conditions leaf extension rate (in mm $^{o}Cd^{-1}$) is most probably controlled by the nitrogen content in the leaf rather than external nitrogen supply.

High temperatures, long days and fast leaf appearance rates all resulted in shorter leaf extension duration. Of these variables variation in temperature accounted for the greatest proportion of variation in leaf extension duration.

In general all the plant parameters recorded were affected by nitrogen supply, but the effect was more pronounced in perlite. There was a smaller response to applied nitrogen in soil because of the residual nitrogen supplied by the breakdown of organic matter.

Lamina area and dry weight increased with the position of leaf on the main shoot up to 2 leaf insertions before the flag leaf. The flag leaf was always much smaller than the subtending leaves. This ontogenetic drift in leaf size was associated with variations in leaf extension rate and leaf extension duration of the leaves. Final leaf size was affected by plant density. As density increased the size of the first three leaves was increased but the size of upper leaves was dramatically decreased. As density increased, final leaf number and the position of the largest leaf on the main shoot were decreased.

Nitrogen affected the position of the largest leaf on the main shoot. As nitrogen supply increased the position of longest leaf moved higher up the main stem. This pattern was also modified by sowing date. In sowings made in June, where rate of crop development was fastest, leaf 4 was the first leaf to show response to nitrogen. In sowings made in September, which developed more slowly, leaf 6 was the first leaf to show response to nitrogen. These effects are attributed to effects of internal competition for nitrogen. This suggests that the size of the later leaves is reduced due to lower availability of nitrogen. Early stem extension will also result in greater competition for nitrogen. On this basis one would expect a large response to nitrogen in fast developing crops and this was the pattern observed in these experiments.

For most of the leaf growth parameters recorded in these experiments there were significant sowing date * nitrogen supply * leaf position interactions, which have not been reported in previously published investigations. This indicates the complex way in which these factors control leaf growth.

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LIST OF TABLES

Table number	Title	Page
CHAPTER 3		
3.1	An example of the method of determining leaf extension rate (LER in mm $^{o}Cd^{-1}$) and apparent extension duration (LED in ^{o}Cd) for a particular pot.	56
3.2	Time taken from sowing date to the date when leaf 5 ceased extension growth	61
3.3	An example of analysis of variance table for the data from experiment 1	63
3.4	Significance levels of the main effects of sowing date (SD), nitrogen level (N) and leaf position (LP) and their interactions on the different plant growth parameters recorded	65
3.5	The main effects of sowing date on the various plant growth parameters recorded	66
3.6	The main effects of nitrogen supply on the various plant growth parameters recorded	68
3.7	The main effects of leaf position on lamina area, lamina dry weight and specific lamina area of individual main shoot leaves	69
3.8	The effects of sowing date and nitrogen supply on leaf extension rate (LER), apparent extension duration(LED) and final leaf length(FLL) of leaf 5	76
3.9	The effects of sowing date and nitrogen supply on the nitrogen content (mg $leaf^{-1}$) of leaf 5	78

Tables (contd...)

CHAPTER 4

4.1 Leaf length (mm) of first 6 leaves on main shoot as measured during growth analysis time (length of and linear measurements (apparent length from soil surface) 96

4.2 The effect of sowing date on the crop development in experiment 2 102

4.3 Summary of the significance of the main effects of sowing date (SD), nitrogen amount (N), leaf position (LP), growth stages (H) and their interactions on plant growth parameters recorded during experiment 2 105

4.4 Mean rate of primordia initiation (R_p), apparent duration of primordia initiation (D_p) and mean number of primordia in relation to Julian time (days after sowing) and thermal time (^oCd) for different sowing dates together with their appropriate correlation coefficient (r) 107

4.5 Mean rate of leaf appearane (R_l) , apparent duration of leaf appearance (D_l) and final number of leaves on main shoot in relation to Julian time and thermal time for different sowing dates with their appropriate correlation coefficient (r) 109

4.6 Main effects of sowing date, nitrogen amount and leaf position on leaf extension rate (LER), leaf extension duration (LED), final leaf length (FLL) and leaf nitrogen content (LN) of main shoot leaves 111

4.7 The effects of sowing date and leaf position on leaf extension rate (LER), leaf extension duration

Tables (contd...)

(LED) and final leaf length (FLL) of main shoot leaves 113

4.8 The effects of nitrogen application and leaf position on leaf extension rate (LER), leaf extension duration (LED) and final leaf length (FLL) of main shoot leaves 115

4.9 The effects of sowing date and nitrogen application on leaf extension rate (LER), leaf extension duration (LED) and final leaf length (FLL) of main shoot leaves 116

4.10 The effects of nitrogen supply and leaf position on leaf nitrogen content of main shoot leaves 117

4.11 The effects of sowing date and nitrogen supply on leaf nitrogen content of main shoot leaves 118

4.12 Main effects of sowing date, nitrogen amount and leaf position on lamina area (LA), lamina dry weight (LWT), specific lamina area (SLA) and lamina length:sheath length ratio (LSR) of the individual main shoot leaves 124

4.13 The effects of sowing date and leaf position on main shoot lamina area (cm^2 $leaf^{-1}$) 126

4.14 The effects of sowing date and leaf position on main shoot lamina dry weight (mg $leaf^{-1}$) 128

4.15 The effects of sowing date and leaf position on main shoot specific lamina are (mm^2 mg^{-1}) 129

4.16 The effects of sowing date and leaf position on main shoot lamina length:sheath length ratio 130

Tables (contd...)

4.17 The effects of nitrogen amount and leaf position on main shoot lamina area (cm^2 $leaf^{-1}$) 132

4.18 The effects of nitrogen amount and leaf position on main shoot lamina dry weight (mg $leaf^{-1}$) 133

4.19 The effects of sowing date on plant growth parameters recorded at different growth stages during experiment 2 134

4.20 The effects of nitrogen amount on plant growth parameters recorded at different growth stages during experiment 2 136

4.21 The effects of sowing date and nitrogen amount on plant growth parameters recorded at awn emergence stage during experiment 2 138

CHAPTER 5

5.1 The effect of plant density on the time taken from sowing to various growth stages 150

5.2 Summary of significance levels of main effects of plant density (D), nitrogen amount (N), leaf position (LP) and harvest (H) and their interactions on plant growth parameters recorded during experiment 3 153

5.3 The effects of plant density and nitrogen amount on primordia initiation on main shoot apex 154

5.4 The effects of plant density and nitrogen amount on leaf appearance on main shoot 156

5.5 Main effects od plant density, nitrogen amount and leaf position on the rate of leaf extension (LER),

Tables (contd...)

duration of leaf extension (LED) and final leaf length (FLL) of main shoot leaves 157

5.6 The effects of plant density and leaf position on leaf extension rate (LER), leaf extension duration (LED) and final leaf length (FLL) of main shoot leaves 159

5.7 Main effects of plant density, nitrogen amount and leaf position on lamina area (LA), lamina dry weight (LWT), specific lamina area (SLA) and lamina length:sheath length ratio (LSR) of main shoot leaves 161

5.8 The effects of plant density and nitrogen amount on lamina area (LA), lamina dry weight (LWT), specific lamina area (SLA) and lamina length:sheath length ratio (LSR) of main shoot leaves 163

5.9 The effects of plant density and leaf position on lamina area (LA), lamina dry weight (LWT), specific lamina area (SLA) and lamina length:sheath length ratio (LSR) of main shoot leaves 164

5.10 The effects of nitrogen amount and leaf position on lamina area (LA), lamina dry weight (LWT), specific lamina area (SLA) and lamina length:sheath length ratio (LSR) of main shoot leaves 166

5.11 Main effects of plant density on different plant growth parameters recorded during experiment 3 167

5.12 Main effects of nitrogen amount on different plant growth parameters recorded during experiment 3 169

Tables (contd...)

5.13 Main effects of time of growth analysis on different plant growth parameters recorded during experiment 3 170

5.14 The effect of plant density on plant growth parameters recorded at different growth stages during experiment 3 171

5.15 The effect of nitrogen amount on plant growth parameters recorded at different growth stages during experiment 3 173

5.16 Main effects of plant density on grain yield and its components of spring barley 174

5.17 Main effects of nitrogen amount on grain yield and its components of spring barley 176

CHAPTER 6

6.1 Effect of growing media on extension growth of leaf 5 of main shoot 188

6.2 Values of correlation coefficient between leaf nitrogen content and lER obtained when linear and quadratic models were fitted to the data of experiments 1, 2 and 3 198

6.3 The linear correlation coefficient matrix between mean air temperature and mean daylength during the phase of appearance of leaf 5, mean leaf appearance rate (LAR) and leaf 5 extension duration (LED) 201

LIST OF FIGURES AND PLATES

Figure number	Title	Page
CHAPTER 3		
3.1	Graphic presentation of the method of determining leaf extension rate (LER in mm $^{o}Cd^{-1}$) and apparent duration of leaf extension (LED in ^{o}Cd) for a particular pot	57
3.2	Showing average weekly mean air temperature (A), photoperiod (B) and solar radiation (C) experienced by the plants during the course of experiment 1	60
3.3	Lamina area (a) and lamina dry weight (b) in relation to sowing date, its position on the main shoot and nitrogen supply	71
3.4	The effects of nitrogen supply and sowing date on lamina area (a) and lamina dry weight (b) of individual main shoot leaves	73
3.5	The effects of nitrogen supply, sowing date on specific lamina area (SLA) of individual main shoot leaves	75
3.6a	The effect of nitrogen supply and sowing date on dry weight of main shoot leaves (MSLWT); dry weight of tillers (TWT); dry weight of pseudostem (SWT) and dry weight of whole plant (PWT)	80
3.6b	The effects of nitrogen supply and sowing date on number of tillers per plant	81

Figures (contd...)

CHAPTER 4

4.1 Showing average weekly mean air temperature (A), photoperiod (B) and solar radiation (C) experienced by the plants during the course of experiment 2 100

4.2 Effects of sowing date, nitrogen supply and leaf position on final length of first 6 main shoot leaves 119

4.3 Effects of sowing date, nitrogen supply and leaf position on leaf extension rate of first 6 main shoot leaves 121

4.4 Effects of sowing date, nitrogen supply and leaf position on leaf extension duration of first 6 main shoot leaves 122

CHAPTER 5

5.1 Showing average weekly mean air temperature (A), photoperiod (B) and solar radiation (C) experienced by the plants during the course of experiment 3 149

5.2 Relationship between number of tillers per plant and number of ears per plant 177

5.3 Relationship between number of ears per plant and number of grain per plant 177

5.4 Relationship between number of grains per plant and grain yield per plant 178

5.5 The effect of plant density and nitrogen supply on grain yield per plant 180

Figures (contd...)

5.6 Relationship between plant density and reciprocal of grain yield per plant 180

CHAPTER 6

6.1 Main shoot leaf appearance rate as a function of rate of change of daylength at crop emergence 190

6.2 The effects of sowing date, nitrogen supply and growing media on leaf length of leaf 5 on the main shoot (sheath+lamina) 194

6.3 Relationship between LER and final length of leaf 5 on the main shoot 196

6.4 Relationship between LED and final length of leaf 5 on the main shoot 196

6.5 Effect of nitrogen supply on LER of leaf 5 on the main shoot in experiment 1 197

6.6 Effect of nitrogen supply on LER of leaf 5 on the main shoot in experiment 2 and 3 197

6.7 Relationship between nitrogen content and LER of leaf 5 on the main shoot in experiments 1, 2 and 3 199

6.8 Relationship between mean air temperature and apparent extension duration (LED) of leaf 5 on the main shoot 202

6.9 Relationship between LER and final leaf length of leaves 1-4 & 6 on the main shoot 204

6.10 Relationship between LED and final leaf length of leaves 1-4 & 6 on the main shoot 204

Figures (contd...)

6.11 Relationship between LER and nitrogen content of leaves 1-4 & 6 of main shoot 205

6.12 Relationship between mean air temperature and LED of leaves 1-4 & 6 on main shoot 208

6.13 Ontogenetic and sowing date effects on the leaf size of main shoot leaves 211

6.14 Linear relationship between lamina length and lamina area of main shoot leaves 214

6.15 Linear relationship between lamina dry weight and lamina area of main shoot leaves 214

6.16 Quadratic relationship between lamina length and lamina area of main shoot leaves 216

6.17 Quadratic relationship between lamina dry weight and lamina area of main shoot leaves 216

Plates

CHAPTER 4

Plate 1 Scanning electron micrograph of main shoot apex at 'late vegetative stage' 91

Plate 2 Scanning electron micrograph of main shoot apex at 'double ridge stage' 92

Plate 3 Scanning electron micrograph of main shoot apex at 'awn primordium stage' 93

LIST OF ABBREVIATIONS AND SYMBOLS

At	thermal time
ADLL	adjusted leaf length
^{o}Cd	day degree centigrade (thermal time unit)
DAS	days after sowing
D_{LA}	apparent duration of leaf appearance
D_{P}	apparent duration of primordia initiation
FLL	final leaf length
HI	harvest index
HSD	honestly significant difference (from Zar, 1984)
LA	lamina area per leaf
LED	apparent leaf extension duration
LER	apparent leaf extension rate
LN	leaf nitrogen content
LSR	lamina length:sheath length ratio
LWT	lamina dry weight per leaf
MSLWT	main shoot lamina dry weight
NS	not significant (at P=0.05)
OLL	observed leaf length
P	probability level
PWT	plant dry weight
r	correlation coefficient
R_{LA}	apparent rate of leaf appearance
R_{P}	apparent rate of primordia initiation
RGR	relative growth rate
SE	Standard error
S.E.M	standard error of means
SLA	specific lamina area
STL	stem length
SWT	pseudostem dry weight
Ta	mean air temperature
Tb	base temperature
TWT	tiller dry weight

CHAPTER 1

GENERAL INTRODUCTION

The main objective of agronomic research is to increase the production of useful plants or parts thereof, especially those for food. In some parts of the world this can still be achieved by bringing more land into cultivation, but in the long run it must be done by increasing the output of the already cultivated areas.

The economic yield (mainly the grain) of cereals represents only a small fraction of the total assimilates fixed by photosynthesis throughout the life of the crop (Donald, 1962). This is because part is lost in respiration and part, notably the roots, is not recovered by the harvesting operations. Nevertheless, the problem of increasing agronomic yield is fundamently the problem of how to increase the total annual photosynthesis per unit area of crop. It follows therefore that the size of the photosynthetic system is an important determinant of crop yield.

The leaves are the main organs of photosynthesis in higher plants, and the area of a leaf is usually assumed to be the size-attribute that best measures its capacity for photosynthesis (Leafe et al., 1978; Gemmell, 1979). The importance of leaf area in controlling plant dry matter production was first recognized by Gregory (1921). It was later stressed by Watson (1958) who concluded that leaf area was the single most important factor determining dry matter production and eventually the yield of agricultural crops. The yield of most crops can be treated as the product of several components, that was first put forward by Balls and Holton

(1914) and Engledow and Wadham (1923). Biscoe and Gallagher (1977) expressed the grain yield (Y) of cereals as:

$$Y = Ne.Ng.Wg$$

where Ne is the number of ears per unit ground area, Ng is the number of grains per ear and Wg is the mean weight per grain at harvest. For analytical purposes yield can be considerd as the product of number of grains per unit ground area (i.e. Ne.Ng) and the mean weight per grain at harvest. In general it is recognized that the number of grains per unit ground area is a major determinant of yield in cereal crops (c.f. for barley Gallagher, Biscoe and Scott, 1975; for wheat Bingham, 1969; and for rice De Dutta and Zarate, 1970). The number of grains is normally determind by the time of anthesis (Bingham, 1971; Gallagher et al., 1975; Duncan, 1975). In an experiment where wheat and barley were subjected to shading for the four weeks before anthesis, Willey and Holliday (1971a) found decreased yield by decreasing both the number of grains per ear and ear number per unit ground area. It is during this period that both number of ears per unit ground area and the number of grains per ear are being determined (Gallagher et al., 1976). It is therefore, speculated that during a period, when ear and grain number are determined, formation of potential grain sites depends on the rates of dry matter production. Experiments on wheat and barley have indicated that during this period there is a competition for assimilates between the rapidly growing stems and ears (Bingham, 1971; Kirby, 1973; Gallagher et al., 1976) and it is likely that

increase in dry matter production by the crop lessens the intensity of competition and allows more spikelets, future grains, to develop. Factors which control crop dry matter production during this period could therefore, be expected to effect the final yield.

During the early part of the crop's life the growth rate of many crops is directly related to the amount of photosynthetically active solar radiation intercepted by their leaf surfaces (Shibles and Weber, 1965; Biscoe and Gallagher, 1977). Furthermore, the total amount of dry matter produced by a number of crops is almost proportional to the total amount of light intercepted by its foliage during the growing season (Duncan, Shaver and Williams, 1973; Monteith, 1977). However, the differences between crops in amount of intercepted radiation are large and have major significance for growth. The differences are the consequences of contrasts in the seasonal pattern of leaf production and death and are conveniently related to the dynamics of leaf area index (Monteith, 1978). Leaf area index is simply the product of leaf area per plant and plant density. Leaf area per plant depends on climatic factors such as temperature, light and daylength (Friend, Helson and Fisher, 1962; Kirby, Appleyard and Fellowes, 1982); on soil factors such as water (Salter and Goode, 1967) and nutrient availability (Novoa and Loomis, 1981; Radin, 1983) and on effects of pests and diseases. Differences in plant density are usually of secondary importance to the yield of arable crops (Monteith, 1978).

The significance of light interception for dry matter production by a crop canopy has stimulated considerable research into the physiology of leaf growth in cereals. In this study an attempt has been made to elucidate the effects of nitrogen supply, seasonal variation in temperature, solar radiation and photoperiod; and plant density on growth and development of leaves of spring barley (Hordeum distichum L. cv. Claret).

The literature review first considers, by reference to published literature, the physiological implications of the effects of environmental variables, nitrogen nutrition and plant density on apical development and leaf growth. The various methods which agronomists and physiologists have used for studying leaf growth are then considered and emphasise the importance of carrying out experiments under as near natural conditions as possible.

The three series of experimental investigations which were carried out to determine the influence of sowing date (and hence the natural variation in temperature, radiation and photoperiod), nitrogen supply and plant density on leaf growth are described in chapter 3, 4 and 5 with a short discussion following results. Chapter 6 discusses the results of the whole series of experiments together, with reference to published literature.

CHAPTER 2

LITERATURE REVIEW

2.1 APICAL DEVELOPMENT : Apical developmental morphology of the cereal apex

In the mature cereal grain (caryopsis) an embryo plant is present. Its shoot apex carries leaf primordia initiated during grain development. Their number is a characteristic of species, varying from two in oats to five or more in maize (Bunting and Drennan, 1966). The shoot apex of barley usually has three or four leaf primordia (Kirby and Appleyard, 1981; Baker and Gallagher, 1983). When sown, following imbibition, additional primordia are initiated at the shoot apex. When the first leaf is emerging, the shoot apex is in the vegetative stage and is about 0.2 mm long and conical in shape (Kirby and Appleyard, 1981). It consists of a meristematic dome and leaf primordia. As in other Gramineae, the primordia of barley are laid down alternatly in two opposite rows around the dome. The earlier formed primordia develop into leaves and the later ones into spikelets. Details of cereal primordia morphology and histogenesis are described by Sharman (1947) and Barnard (1955). A bud develops in the axil of the coleoptile and each of the lower leaves. Usually only a proportion of these buds continue to grow into a tiller; the remainder become dormant. The dome continues to initiate primordia until all the leaves and spikelets are produced.

After a variable number of primordia destined to become leaves have been initiated, there are changes that signal the onset of reproductive development. The transition from leaf to floral development of the shoot apex is accompanied by changes

in its growth rate (Barnard, 1964; Williams, 1964, 1974). The dome continues to initiate primordia and because the primordia are produced faster than they can grow into leaves (Kirby, 1974), their further development is arrested so that a succession of unidentified ridges accumulate on the shoot apex. Morphologically, these ridges are leaf primordia. The primordia at the base of the apex become leaves but the upper part of the small ridges do not grow much more as compared to the rest of the apex. The apex at this stage elongates and another lateral ridge of tissue develops in the region immediately above each arrested primordium - the spikelet primordium. Each spikelet is thus an axillary structure, morphologically equivalent to a tiller bud (Barnard, 1955). Because of the shape and position of these two ridges this stage is known as "double ridge" and marks the begining of "ear initiation". The appearance of double ridges is considered to be an important event in the life of a plant. The apical dome continues to initiate primordia (single ridges) which pass very quickly to the double ridge stage. The size of the apical dome changes systematically with the progress of primordia initiation. Its length and width both increase slowly during leaf initiation and then more rapidly when reproductive development (double ridge formation) starts. The size of the dome is greatest at the time of double ridge formation (Baker, 1979). From then, it becomes smaller until the terminal spikelet is initiated. This pattern has been observed in spring wheat (Kirby, 1974) and in spring barley (Kirby, 1977; Fletcher and Dale, 1977). Double ridge formation

occurs first in the mid-region of the embryo inflorescence (Baker, 1979) and once begun, it spreads rapidly towards the base and tip of the apex. This corresponds to the frequently reported observation that the spikelets in the middle region of the ear are most advanced in development and have the largest grains (Kirby, 1974, 1977), because these are laid down when dome size is greatest. The upper ridge of each double ridge develops further to become a spikelet. In the subsequent stages the spikelet primordia will continue to form and differentiate into various floral structures (Bonnett, 1966).

The spikelet position where double ridges first appear are the first to start initiating florets. Each spikelet primorium rapidly differentiates into the floral parts : first the palea, then lodicules, stamens, and finally carpel (Barnard, 1964). The number of spikelets in wheat cannot increase further once a terminal spikelet has formed (Kirby, 1973; Baker, 1979). In barley, where no terminal or apical spikelet is produced, primordium formation ceases with the initiation of rachis internode elongation (Nicholls and May, 1963). In wheat, the beginning of terminal spikelet formation also coincides with the initiation of rachis internode extension (Holmes, 1973). Hence in barley and wheat, although the production of additional spikelet primordia ceases in a different way in each species, the cessation coincides with the initiation of rachis internode extension. The extension of the rachis internode is regulated by a balance between gibberllin (GA) and an endogenous growth inhibitor "absicin".

Nicholls and May (1964) reported that the concentration of gibberellin-like substances in developing barley inflorescences was highest at the time when extension in the rachis internode began.

In barley, shortly after the cessation of activity of the apical dome some of the last formed primordia will not develop more than ridges on the flank of the dome (Kirby and Faris, 1970). Of the primordia produced, only a proportion survive and grow into potentially fertile florets. A number of the later-initiated primordia at the tip of the shoot apex die at an early stage and make no contribution to the final number of florets. Usually about 30-40% of the maximum number of primordia produced die before ear emergence (Kirby and Faris, 1972; Gallagher and Biscoe, 1978). In addition some spikelets, usually at or adjacent to the collar node, may be poorly developed and may not set grain, thus reducing the potential grain yield (Beveridge, Jarvis and Ridgeman, 1965). Survival of spikelets is related to the number of spikelet primordia initiated. However, the proportion of the spikelet primordia that survive to form grains is less in ears with most spikelet primordia (Appleyard, Kirby and Fellowes, 1982). This may be due to competition for resources in the ear (Kirby and Faris, 1972).

The importance of large ears for high yielding wheat was recognised some 89 years ago (Farrer, 1898). The significance of large ears to yield has been experimentally shown in studies of spring and winter wheats (Pinthus, 1967) , where

differences in yield were due almost entirely to the number of spikelets produced per ear. Donald (1968) advocated this hypothesis and recommended this as a characteristic of a wheat ideotype. The high yield potential in wheat and barley is associated with a higher number of grains per spike or per unit ground area (Cock, 1969; Syme, 1969, 1970; Gallagher et al., 1975; Biscoe and Gallagher, 1977). In view of the importance of grain number in affecting grain yield, there is a need to understand more clearly the genetic, environmental and nutritional influences on the expression of this character. It was proposed by Kirby (1974) that variation in the final number of leaves and spikelets should be analysed in terms of the rates and durations of the processes of primordia initiation.

Leaf primordia are initiated at a slower rate than spikelet primordia. At about the time of the formation of the primordium destined to become the collar a conspicuous increase in the rate of primordia initiation was observed by Kirby (1974) for spring wheat and by Baker (1979) for winter wheat. A similar increase of rates has been observed in both spring and winter wheats grown in controlled environments (Sunderland, 1961; Aspinall and Paleg, 1963; Rawson, 1970; Holmes, 1973). In all of these experiments a linear relationship of primordium number with time was described for both phases. Gallagher (1979) found a gradual increase in the rate of primordia initiation, in winter wheat, with time, contrasting with Kirby's (1974) results for spring wheat which

showed two distinct and constant primordial initiation rates; the slower associated with leaves and the faster with spikelets. However, when Gallagher (1979) plotted total number of primordia against thermal time, two distinct phases of leaf and spikelet initiation were recognised. The likely cause of the increase in rate seems to be enhanced hormone production (Holmes, 1973).

In spring wheat it has been shown that formation of terminal spikelets on tillers occur about 2-3 days after the formation of the terminal spikelet on the main shoot (Stern and Kirby, 1979a; Frank and Bauer, 1982). Tillers synchronize in development with the main shoot and have a shorter apex growth period, but the rate of spikelet initiation increases to compensate for the shorter duration (Stern and Kirby, 1979).

There are differences between cereal genotypes in the numbers of leaf and spikelet primordia which are initiated (Cooper, 1956; Austin and Jones, 1974). Appleyard et al. (1982) found variation in the maximum number of primordia produced in 11 genotypes of spring barley. It was the duration of the period of primordia initiation which was important in determining the total number of primordia. No significant differences in the rate of spikelet primordia initiation were observed. This is in contrast to other work where genetic variation in the rate of spikelet primordia initiation has been shown. Jenkins, Kirby and Roffy (1976) found differences in the rate of primordia initiation in two winter barley varieties and progeny from a cross of these. Rahman, Halloran and Wilson

(1978) found that spikelet number in wheat was under simple genetic control and suggested that the gene determining the number of spikelets does so by determining the rate of spikelet primordia initiation. Differences among cultivars of spring wheat in time taken to double ridge formation and in number of day degrees accumulated (herein referred to as thermal time) to terminal spikelet stage were also reported by Frank and Bauer (1984). Using a stepwise regression analysis technique a close association between the time taken to reach double ridge and grain yield was found. Time taken to double ridge accounted for 57% of the variation in yield for all the cultivars tested. Their result suggested that the longer time peiod a plant has to produce and grow leaves prior to double ridge stage the greater the yield potential. However, the differences among cultivars in their ability to produce more spikelets, either through a faster rate or longer duration of primordia initiation, are strongly influenced by environmental variables, especially temperature.

Barley and wheat are grown successfully in a wide range of environments where the temperature regime during the growth and development of the crop varies considerably. The available information on the influence of such differences in temperature on the apical development of barley and wheat does not present a consistant account. Friend, Fisher and Helson (1963) reported that an increase in temperature from 10 to 30^{o}C caused earlier floral initiation, and the rate of morphological development of floral primordia was more rapid at high temperature. The higher rate of primordia production

at high temperature shortened the interval between floral initiation and anthesis. In later experiments Friend (1965a) reported a decrease in the number of spikelets formed as the temperature increased from 10 to 30°C. On the other hand, no significant differences in spikelet number were found over a similar range of temperature by Lucas (1971), although floral initiation started earlier at intermediate temperature (16 or 20°C) than at extremes (10 or 30°C). Similarly Warrington, Edge and Green (1978) reported that an increase in temperature from 15 to 25°C before the double ridge stage had no affect on grain number, but the same increase in temperature from double ridge to anthesis reduced grain number. They also reported that higher temperature shortened duration of the vegetative and reproductive phase of development. However, Frank and Bauer (1982), for spring wheat grown in controlled environments at 10, 18 and 26°C, reported that as temperature decreased from 26 to 18 or 10°C duration of the vegetative and reproductive phase of apex development was prolonged, resulting in an increase in total number of spikelets formed. In contrast, Mohapatra, Aspinall and Jenner (1983) reported that high temperature (30°C) from germination onward delayed the initiation of double ridges in comparison to low temperature (20°C). The rate of primordia production was reduced at the higher temperature and there was a decrease in the final number of spikelets produced. Halse and Weir (1974) also found a decrease in spikelet number in plants grown in more extreme temperature regimes, both low (10/5°C) and high (26/21°C) day and night temperatures than in plants grown in

moderate temperature regimes (14/9 - 22/17°C day and night temperatures). The apparent inconsistancies in response may be at least partially explained by differences in temperature sensitivity at different photoperiods (Rahman and Wilson, 1977).

2.2 PHYSIOLOGICAL ASPECTS OF LEAF GROWTH AND DEVELOPMENT

Leaf growth and development in cereals has been thoroughly reviewed by Milthorpe (1956) and more recently by Dale and Milthorpe (1983). However, a brief account of leaf growth in relation to environment and nutrition will be given in this section.

2.2.1 Cell division and expansion

During the vegetative growth of barley the main growth process is leaf growth. The formation of a leaf primordium begins by rapid cell division in the outermost cell layers of the apical dome, giving rise to a microscopic protuberance. At its inception the whole of the leaf primordium is meristematic, but soon cell division activity becomes confined to an intercalary meristem near the base of the leaf (Sharman, 1942a; kaufman, 1959). This region becomes divided into two zones through the formation of a band of parenchyma cells, and this coincides with the appearance of ligule. The ligule is formed from the adaxial protoderm (Barnard, 1975) and subsequently the leaf is distinguished as a lamina and sheath. These events mark the beginning of separate development within

the foliar organ, for the upper portion of the meristem is associated with growth of the lamina, while activity in the lower portion leads to the growth of the sheath (Langer, 1979).

Leaf growth may be interpreted in terms of two fundamental processes, cell division and cell extension. Ashby and Wangermann (1950) claimed that in Ipomea the two processes were consecutive, a view which appears to be shared by Langer (1979). He states that cell division in the lamina of a grass ceases when the ligule is differentiated. However, dissection of wheat apices has shown that the ligule is differentiated when the leaf is only about 10 mm long (Baker, 1979). If Langer's statement is strictly correct then most of the lamina growth results from the extension of cells formed very early in the life of the leaf. Sunderland (1960) pointed out that Ashby and Wangermann's conclusion was based on a study of epidermal cells, in which division stops earliest. He demonstrated that in Lupin and Sunflower, cell division and extension were concurrent in other leaf tissues until one-half to three-quarter of final leaf size, depending on the species, so that the two-phases view of the leaf growth was clearly untenable. More relevantly for the present work it is supported by Williams and Rijven (1965) for wheat leaf growth. These workers obtained good estimates of cell number per leaf. They found that cell division went on almost until the leaf reached its final leaf size. More recently, Baker (1979) using their data on cell numbers at a particular leaf length,

observed that when a leaf was the length at which ligule differentiation occurred, only 7.5 % of the final cell number were present. Even at leaf appearance less than 40 % of the final cell number has been differentiated. However, because Williams and Rijven used wheat grown in a controlled environment with a high proportion of fluorescent light, their data may not be applicable to plants grown in the field.

The above discussion shows that production of new cells continues while those already formed are expanding. It seems essential that this should happen, because cell division and extension are two different phases of a continuous process.

Further growth of the leaf continues from cell division and enlargement of the intercalary meristem established above and below the ligule (Sharman, 1942b). This causes the lamina to move up inside the rolled sheaths of the encircling older leaves. Emergence of the lamina is accompanied by several profound changes, for not only do the cells of the exposed portion cease expansion but they also encounter an entirely new environment in which they photosynthesize and transpire. Meristematic activity in the lamina comes to an end when the ligule appeares and this marks the end of elongation and the lamina has now reached its final length, but the sheath continues to grow for a time afterwards (Baker, 1979). The next leaf is meanwhile moving up inside the sheath of this leaf. It is generally held that the growing part of a grass leaf is wholly within the encircling sheath (Sharman, 1942a; Kaufman, 1959; Soper and Mitchell, 1956; Begg and Wright,

1962; Barnard, 1975; Kemp, 1981a). It can be concluded, that the tip of a leaf represents its oldest and the base its youngest portion. The leaf tip is, therefore, physiologically more mature than the base and maturation passes from the tip to the base. Leaf senescence also starts from the tip.

The importance of the division and extension of cells in determining leaf growth rate and final size is clearly evident from the above discussion. However, it is still not entirely certain how much each of these two processes contributes to leaf growth (Auld, Dennett and Elston, 1978). Increase in cell number during the early growth of a leaf is more or less exponential (Williams, 1960; Dale, 1976) but there is at first little concurrent cell extension. At this stage the cells are of the order of 15 μm long and there is a high relative rate of leaf extension, although the leaf is still less than 1 mm long (Williams and Rijven, 1965; Gallagher, 1976). When such cells extend their increase in length it is often up to 200 μm (Brown, 1976). This implies that, although division and extension are concurrent throughout most of the leaf, it is cell extension that contributes most to the increase in leaf size.

2.2.2 Ontogenetic changes in leaf size

In general, the pattern of leaf growth in the Gramineae is such that leaf size continues to increase with leaf position up to the time of stem elongation. For leaves growing after stem elongation, leaf size may continue to increase or be

variable (Percival, 1921; Jewiss, 1966; Wardlaw, 1975; Wilson, 1976). In rye grass, the laminae are progressively longer at higher leaf positions, reaching a maximum at a position several nodes below the flag leaf. Lamina initiated after floral initiation become progressively shorter (Borril, 1959; Edwards, 1967). Gallagher (1979) found a similar trend in barley, lamina length incresing with leaf position, reaching a maximum for those leaves extending at the time of double ridge formation. Leaf length then declined. A similar pattern was observed by Kirby and Eisenberg (1966) in growth rooms and Kirby and Faris (1970) in the field, Kirby (1973) found that in barley the penultimate leaf was the longest. For wheat, Baker (1979) found that the first four or five leaves were of similar length and width, but thereafter length and width both increased at successively higher position up the stem and the flag leaf was the longest. Similar findings for wheat were also reported by Gallagher (1979). Ontogenetic differences in the size of leaves began at about leaf 5. Gallagher (1976) showed that each leaf had a different rate of leaf extension per unit of thermal time during the linear growth phase. There was a linear relationship between the rate of leaf extension in thermal time and final leaf length. He also found that the reciprocal of the duration of the phase of linear growth was linearly related to mean air temperature during linear growth. He concluded from these findings that the differences in final size between leaves of different ontogenetic rank was the result of their differences in extension rate and was not a temperature effect. Since leaf length largely determines leaf

area, it follows that leaf area will be changed with the change in length. The position of the longest leaf on the stem also varies with variation in temperature and daylength (Borril, 1959) and also with the supply of nitrogen (Puckridge, 1963).

2.2.3 Nitrogen nutrition

At least 13 mineral elements are generally recognized as being essential for the growth of most plants. Nitrogen, phosphorus and potassium are usually required in the greatest amount (Ingestad, 1972). The growth of leaves has long been known to be especially sensitive to application of nitrogen, which increases leafiness in many crops. However, the effects of nitrogen on other aspects of plant growth are so much greater so that there is little precise information available on the effects of nitrogen supply on the area of individual leaves. Robson and Deacon (1978) reported that increased nitrogen supply resulted in faster elongation, greater leaf length and area in ryegrass. Baker (1979) compared the effect of two nitrogen levels on the growth of successive leaves on the main shoot of wheat. He found that effect of nitrogen on lower leaves was not significant. For leaf 8 and up to the flag leaf (leaf 12) there was significant differences in final lamina length of the corresponding leaves in the two treatments. The duration of linear growth was similar for the same leaf in each treatment. This would be expected if duration is controlled by temperature which would have been the same in both nitrogen treatments.

Increasing the nitrogen supply does not only increase leaf area but may also modify the succession of leaf size on a tiller. Puckridge (1963) grew wheat plants at 3 levels of nitrogen. He found that at the lowest level of nitrogen, leaf 4 was the largest, but leaf 5 was the largest at the highest level of nitrogen, and the upper leaves were slightly smaller. He concluded that the sequence of leaf sizes was determined by the supply of nitrogen, but he did not study apex development. It is possible that, the needs of the ear and stem for nitrogen are met preferentially and the resulting internal competition for nitrogen between the apical meristem and stem may restrict the growth of the later leaves (Williams, 1960; Kirby, 1973; Rogan and Smith, 1975). This speculative suggestion is however, in contradiction with Halse et al. (1969). While analysing the effects of nitrogen deficiency on the growth and yield of Western Australian wheat grown on a nitrogen deficient sandy soil, these workers found that floral initiation in plants receiving no nitrogen was delayed compared with plants receiving 336 Kg N ha^{-1}. Macdowall (1972a) undertook a comprehensive study of the growth rate of Marquis wheat in relation to nitrogen supply and light intensity. He reported that the optimum nitrogen supply increased as the light intensity increased. At light intensities below 70 Wm^{-2} the optimum nitrogen supply was 42 ppm (in the nutrient solution) and the optimal nitrogen requirement at the highest light intensity used (100 Wm^{-2}) was 210 ppm. The nitrogen rquirement for various crop growth

processes may therefore change with the variation in light environment.

2.2.4 Light intensity and photoperiodic effects

In the early vegetative stage of plant development increases in irradiance may accelerate both plant dry weight and expansion of the leaf surface (Doley, 1978; Ketring, 1979). The greater leaf surface expansion is due to faster production of new leaves and to more rapid expansion of individual leaves. Leaf cell division rate, final cell number and cell size are enhanced under high irradiance (Milthorpe and Newton, 1963; Ludlow and Wilson, 1971). As the barley crop develops and leaf area index increases it would be expected that the optimum light level required for whole plant growth and development would also increase (Pendleton and Weibel, 1965; Willey and Holliday, 1971a; Fischer, 1975). Total plant photosynthesis would also be expected to vary with light intensity and leaf area index (Puckridge, 1970). He has shown that photosynthesis by the wheat crop in the field depends on light intensity and does vary from day to day during crop growth. Whether the rate of plant and leaf growth depends on the rate of photosynthesis has not been established. However, growing leaves are dependent on an imported carbohydrate supply until they reach one-third to half of their final size (Fellows and Greiger, 1974) and one might expect that the rate of growth of young leaves to be directly dependent on light intensity. Kemp (1981b) compared changes in leaf extension rate of wheat with the carbohydrate concentration under

conditions of intense shading, conditions which hardly occur in the field. Shading experiments with wheat (Pendleton and Weibel, 1965; Willey and Holliday, 1971b; Fischer, 1975) have shown that crop growth rate can be reduced by shading, but the intensity and duration of the period of shading used in these experiments is usually in excess of that which occurs with natural fluctuations of light intensity.

For the maintenance of leaf growth of grasses, it is essential that the expanding leaves be well supplied with carbohydrates. Studies with ^{14}C (Williams, 1964; Felippe and Dale, 1972; Ryle and Powell, 1972,1974,1976) have shown that the apical meristem has priority over other meristems for assimilates, especially from the upper leaves. Growing wheat leaves are supplied primarily with assimilates from the leaves immediately below, especially the second leaf below (Patrick, 1972). As the leaf unfolds it becomes progressively more self-sufficient for the metabolites, notably carbon assimilates required for growth.

The leaves of wheat and barley plants grown at low light intensities are longer, thinner, narrower and larger in area than those grown at high light intensities (Newton, 1963; Dale, 1965; Friend, 1966). The increased lamina area is usually associated with increased lamina length. Forde (1966) found a 10 fold difference in lamina length of ryegrass and cocksfoot grown under shading regimes. The observed changes in leaf shape are related to changes in cell size, number and shape (Friend and Pomeroy, 1970). The greater length of leaves

grown at low light is primarily related to increased cell number; cell length shows less variation. Decreased leaf thickness is closely related to shorter cells in the palisade layers, fewer layers of palisade, and reduced size and frequency of spongy measophyll cells under low light conditions (Nobel, Zaragoza and Smith, 1975). Thus, in shaded situations, such as under trees or close to a hedge, grass leaves may be quite large but low in weight. This is well illustrated by an experiment with perennial ryegrass (Langer, 1979) in which a five-fold decrease in light intensity at 20°C caused an increase in leaf size from 15.0 to 24.7 cm^2 but a decline in leaf dry weight from 73.3 to 55.4 mg. Specific lamina area is a very sensitive measure of incident light energy and of differences between sun and shade leaves. Although the physiological details of this response are not entirely clear, it appears that the greater leaf size at low light intensity compensates for reduced net photosynthetic rate per unit leaf area under these conditions.

In many species, increasing the daylength results in an increase in leaf thickness. This is especially marked for succulence where it is often associated with reduction in leaf area (Dale, 1982). In addition to direct effects upon leaf area, photoperiod may also exert effects by affecting the onset of flowering (Whatley and Whatley, 1980). In many species later formed leaves are smaller in plants about to flower than in plants which remain vegetative. That is to say that there is an ontogenetic drift towards smaller leaves as

flowering occurs.

Light quality also affects leaf growth in many species. The ratio of the far red to red light results in greater stem extension and a reduction in area of individual leaves (Dale, 1982). When daylight passes through a crop canopy, there is an enhancement of the far red:red ratio because of absorption of red light by the photosynthetic pigments. The morphological changes observed in plants grown in environments with a high far red:red ratio may therefore indicate a role for photochrome in detection of mutual shading between leaves and the initiation of responses to minimize this effect (Holmes and Smith, 1977).

2.2.5 Temperature effects

Temperature is known to affect leaf growth and appearance (Friend, Helson and Fischer, 1962; Watts, 1973; Gallagher, 1976; Kirby, 1974 ; Baker, 1979), but the wide range of temperatures experienced by a cereal plant during its growing season causes problem in analysing the measurements of leaf growth.

In general, as temperature increases, wheat leaves become narrower, longer and thinner (Friend, 1966). The optimum temperature for maximum leaf length and area has been found to be 20 to 25^{o}C (Friend, 1966; Friend and Pomeroy, 1970), while for breadth and thickness the optimum is 10 to 15^{o}C (Friend, 1966; Chanon, 1971). The changes in leaf size have been previously associated with changes in cell size. Other grasses

respond to temperature in a similar manner to wheat, though in tall fescue changes in leaf dimensions were associated with changes in both cell size and cell number (Robson, 1969). In addition, Robson found that the effects of temperature on sheath size was the same as for lamina size.

The expansion of the leaf surface depends on a number of factors including rate of leaf production and senecence, tillering and the rate and duration of leaf expansion. Leaves are produced more rapidly as the temperature increases to 20 or 30°C (Terry, 1968; Fukai and Silsbury, 1976; Dennett, Elston and Milford, 1979). Once formed, the growth of individual leaves is also usually more rapid between 20 and 30°C (Peet, Ozbun and Wallace, 1977; Auld et al., 1978). The duration of leaf growth, however, often increases with decrease in temperature below 20-25°C (Auld et al., 1978; Dennett et al., 1979). Consequently, the optimum temperature for lamina expansion may not be the same as that for final area. Data for wheat (Friend et al., 1962) show that although optimum temperature for leaf area is close to 20°C, with a marked reduction at higher temperatures, length is much less sensitive to higher temperatures. Leaf breadth and thickness both show lower temperature optima, at about 15°C, with a steady decline in both parameters as temperature rises further.

Increase in temperature produces significant morphological and anatomical changes. Growing grasses at supera-optimal temperatures (35°C) results in short and rigid leaves that are

low in chlorophyll (Darrow, 1939; Duff and Beard, 1974), though in these instances it is possible that water stress may have occured in the high temperature treatments. The consequences of these effects on leaf extension rate are uncertain. Peacock (1975) grew perennial ryegrass plants at 5 and 15°C, then compared the extension rates and found no differences. This would indicate that within the temperature range encountered in the field the temperature would have little effect on leaf extension rate. However Biscoe and Gallagher (1977) and Gallagher (1979), for wheat and barley, found a strong relationship between leaf extension rate and temperature.

2.2.6 Interactions between light and temperature

So far, in dealing with both light and temperature each factor has been concidered in isolation from the other. This pragmetic approach masks the fact that light and temperature may interact in controlling leaf growth. Experiments with ryegrass have shown that the effects of temperature on leaf area, dry weight and specific lamina area vary with light intensity. It is likely that these differences are due to effects on cell size rather than cell number.

These interactions between light and temperature make leaf growth studies in the field and in the semicontrolled environments (such as used in this study and where both factors are never constant) difficult to interpret. In consequence, many workers prefer to use controlled environment

facilities for experiments on leaf growth to ensure constancy of temperature and of light conditions so that the interactions between them can be more easily assessed.

2.2.7 Effects of plant density

Plant density is another very important factor which has a marked effect on the growth and development of individual plants. Most of the studies on plant population have concentrated either upon the growth and yield of the crop, or upon the final ear number, spikelet number per ear and grain size of the plant. There is very little detailed information available upon initiation and growth of leaves, tillers and subsequent growth of spikelet initials at the shoot apex.

The barley plant can adjust through its life cycle to the micro-environmental changes caused by varying plant populations (Kirby, 1967,1969a). The data of Kirby (1967) show that relative growth of total and leaf dry matter, and lamina development as measured by the specific lamina area are strongly influenced by plant density. Increasing plant density reduces leaf number and causes internode elongation to start earlier and at a lower node (Kirby and Faris, 1970). Kirby and Faris also observed an increase in lamina and sheath of lower leaves at high plant density. Lamina width, however, was reduced by increasing plant density.

2.2.8 Effects of water stress

Leaf growth is highly sensitive to water stress. Leaf

enlargement is one of the first growth processes to be affected by a decrease in leaf water potential (Hsiao, 1973). Many experiments in controlled environments have shown that leaf extension rate is slowed by low water potentials but several different forms of response have been reported. For several crop species; wheat (Sands and Correll, 1975), maize (Barlow, Boersma and Young, 1976; Acevedo, Hsiao and Henderson, 1971), and sugarbeet (Lawlor and Milford, 1973), leaf extension rate has been shown to decrease almost linearly with falling water potential. Field studies of Gallagher and Biscoe (1979) also showed that leaf extension rate decreased with decrease in water potential. However, the effect of water stress on the growth and developmental processes of cereal plants is beyond the scope of this study, because the plants were kept well watered and water supply was not a limiting factor.

2.2.9 Conclusions

The conclusion from this section of the review is that environmental variables influence plant growth to a very large degree via their effects on leaf expansion. With the exception of light, environmental influences on photosynthesis appear in general to be less pronounced than those of leaf expansion. Because of the complex nature of the interdependence of and interactions between environmental variables, and because of the effect of plant nutrition and sensitivity of leaf extension to water stress, it becomes more complex to

interpret and explain the effects of these factors in the field or semi-controlled environments.

2.3 PHYSIOLOGICAL ASPECTS OF TILLERING

For cereals, tillering is one of the most important developmental processes, since it helps plant establishment, allows the plant to compensate for low population densities and the effects of pests and diseases, and the tillers make a significant contribution to grain yield (Jewiss, 1972; Kirby and Faris, 1972; Isbell and Morgan, 1982; Marshall and Boyed, 1985). Cereal grain yield can be defined by the following components : number of plants per unit area, number of ear-bearing tillers per plant, number of grains per ear and their mean weight (Darwinkel, 1978; Power and Alessi, 1978). The process of production and survival of tillers would determine the number of grains per unit ground area and hence affect final grain yield (Gallagher et al., 1976). Tillering is therefore, a major yield determining factor (Friend, 1965b).

Tillers arise as axillary buds on the main shoot apex, as a meristematic activity in the sub-hypodermal tissue. In the embryo within the seed, tiller buds are usually visible in the axil of the coleoptile and first leaf primordia (Fletcher and Dale, 1974; Williams, Sharman and Langer, 1975; Kirby and Appleyard, 1981). The tiller buds grow tightly tucked in between the leaf sheath of the subtending leaf. It becomes dome shaped and an encircling ridge of tissue is initiated upon its flanks (Kirby and Appleyard, 1981). This ridge grows

to form the prophyll which is a sheathing structure, very similar to the coleoptile of the main shoot. Tiller buds on dissection, will reveal a shoot apex which is the replica of the main shoot apex, with an apical meristematic dome and leaf primordia. The meristematic dome initiates leaves, axillary buds and then spikelets in exactly the same way as the main shoot. On emergence, the tiller again resembles the parent shoot with its own system of leaves and its own adventitious roots. Although complete in every respect, tillers remain in vascular connection with one another (Langer, 1979). Developing buds and elongating tillers are initially dependent on their subtending leaf and parent shoot for supplies of raw materials for growth (carbohydrates, organic nitrogen, minerals and water), but as each tiller establishes leaf area and develops roots it will become less dependent on its parental shoot for its nutritional requirements. For example, Qiunlan and Sagar (1962) showed that in young wheat plants, ^{14}C-labelled assimilate was translocated from the main shoot to developing primary tillers, and that this declined with time as the tillers became established. Similar observations have been recorded in young plants of Lolium prenne (Marshall and Sagar, 1968; Colvill and Marshall, 1981). During the reproductive phase of development and stem elongation, the development of the inflorescence represents a major sink for carbohydrates and minerals and so the availability of assimilates for tiller development is likely to be reduced, and hence the production of new tillers is greatly restricted (Bunting and Drennan, 1966). It can be stimulated by removal

of the inflorescence or by addition of nitrogen (Leopold, 1949; Aspinall, 1961, 1963; Bunting and Drennan, 1966). The results of detillering experiments in wheat and barley show that the grain yield and total biomass of the main shoot may be greatly increased by the removal of tillers (Kirby and Jones, 1977; Mohamad and Marshall, 1979; Kemp and Whingwiri, 1980), which also suggests that developing tillers compete with the main shoot for assimilates and nutrients and that this can restrict its growth and development (Aspinall, 1961; Kirby, 1973).

The tillers developed in the axil of main shoot leaves are called primary tillers. These tillers have their own leaves which in turn may produce shoots from their axillary buds. These shoots are designated as secondary tillers. Under favourable environmental and nutritional conditions, from the leaves of secondary tillers tertiary tillers are produced and a complicated system of tillers of various hierarchial order develops on the same plant. It is usual to designate each tiller by reference to its position of origin. Thus, the tiller in the coleoptile is designated Tc and tillers in the axils of leaf 1 (L1), L2 and L3 of the main shoot are designated T1, T2 and T3 respectively. Similarly secondary tillers are also refered to by their position of emergence on the primary tillers. The first produced primary tiller may grow almost as large as the main shoot. Tillers produce fewer leaves than tha main shoot (Gallagher, 1976) and this tends to synchronise their development with the development of the parent shoot (Frank and Bauer, 1982), so that ear emergence

and subsequently anthesis takes place throughout the crop within about four days (Kirby and Appleyard, 1984). The growth and emergence of tillers are mostly in phase with one another. A tiller emerges when the third leaf following it has emerged i.e. T1 emerges when leaf 4 on the main shoot is visible.

Usually only a portion of the tiller buds which are formed grow and emerge from the surrounding leaf sheath. The remainder either do not grow beyond the bud stage or do not develop into a functional tiller and die without producing an ear (Kirby and Appleyard, 1984). The mortality of late-appearing tillers usually begins during the reproductive development (Rawson, 1971) and many tillers die without producing an ear (Barley and Naidu, 1964; Aufhammer, 1980). Whether such tillers are wasteful of the plant's resources is not clear (Gallagher and Biscoe, 1978; Russelle, Scild and Olson, 1984; Shanahan et al., 1985). The number of tillers per plant reaches its maximum before ear emergence and then declines rapidly and finally stabelizes with very little change until harvest (Watson, Thorn and French, 1958; Cannel, 1969a; Ali, 1984). At any one time, within the same plant, there is a considerable variation in the size of tillers. Some will be very small, bearing only a few leaves and possibly no adventitious roots as yet, while others are well established and may have produced several daughter tillers. This variation is more evident at maturity. The main shoot and T1 tend to have larger ears with more and heavier grain, followed by successive tillers according to their time of origin. The late

developed tillers have fewer grains per ear than earlier formed tillers (Aspinall, 1961). Therefore, the contribution of late tillers to final grain yield would not be of any significant amount (Cannell, 1969b; Woodward, 1986).

The amount of tillering in cereals as in other graminea is basically a genetic phenomenon. Some varieties produce tillers freely, while others only sparsely (Watson et al., 1958; Thorne, 1962; Laude et al., 1967). However, this genetic potential of tillering in cereals and grasses has been known to be affected by several factors of the environment and no simple control mechanism will suffice. It is difficult to separate the effects of environmental factors such as light, temperature and photoperiod in the natural environments, as changes in one factor are often associated with changes in another factor. From experiments conducted in controlled environments it is clear that increases in both irradiance and temperature increase tiller production (Ryle, 1964; Friend, 1965b; Cannell, 1969b). High irradiance increases the level of available carbohydrates and tiller production is increased, that is, a greater proportion of tiller buds grow out (Aspinall and Palge, 1964). Mitchell (1953, 1955) stated that decreasing light intensity inhibited the development of tillers in cocksfoot. When the temperature is raised, leaf emergence and main shoot development tend to be favoured more than tiller production (Friend, 1965b, 1966), but nevertheless more tillers are produced as the temperature increases up to 25^{o}C. Daylength also influences tillering ; tiller production is favoured by short days (Leopold, 1949; Ryle, 1966a, 1966b;

Langer, 1979). In experiments using natural daylight, short days increased tiller number (Doroshenko and Rasumov, 1929 in Kirby, 1969b; Foster et al., 1932). On the other hand in controlled environment experiments, barley varieties differed in rate and pattern of tillering but, in general, tiller number was greater in long days (Aspinall, 1966; Guitard, 1960). Decreases in tiller number in response to longer days have also been reported by Chinoy (1950) for wheat. But Fairey, Hunt and Stoskopf (1975) in their controlled environment experiment found that tillering in barley was not reduced under short daylengths, as noted in some controlled environment studies with wheat (Williams and Williams, 1968). Changes in light quality may also be important in regulating the growth of tiller buds as in lateral bud outgrowth in tomato (Tucker, 1977) and in ryegrass (Deregibus, Sanchez and Casal, 1983).

There is plenty of information available on the importance of mineral nutrition for tillering in cereals. In both cereals and grasses, tiller production is greatly increased by raising the supply of nitrogen, phosphorus and potassium (Langer, 1966), and limitations of other essential elements would also be expected to have an effect. Of the major elements, nitrogen seems to be the most important. Currently, the most direct effect on tillering that can be achieved by a farmer is by the application of nitrogen fertilizer. Nitrogen stimulates the outgrowth of tiller buds (Barley and Naidu, 1964; Spiertz and de Vos, 1983). The addition of nitrogen, especially when

applied early, increases the number of tillers (Thorne, 1966; Needham and Boyed, 1976), but they have to compete for a diminishing nitrogen supply, whereas nitrogen applied later may have little effect on tiller production though survival of tillers already present may be improved (Bremner, 1969; Laloux and Keane, 1977). This probably explains why both increased (Milbourn, Innes and Holmes, 1963; Power and Alessi, 1978; Abdulgalil, 1976) and decreased (Barley and Naidu, 1964) tiller survival has been reported with higher nitrogen levels. Nitrogen deficit however, reduces tillering due to : (a) retarded appearance of tiller buds (Hewitt, 1963); (b) limited root growth (Briggs, 1978); and (c) small and weak shoots with reduced level of chlorophyll and carotenoids (Briggs, 1978).

Water deficit reduces the number of tillers produced and prolonged dry conditions would cause tillers to die (Wal, Smetink and Maan, 1975; Jones and Kirby, 1977; Musick and Dusek, 1980; Lawlor et al., 1981). In general, tiller production and survival are inversely related to soil water stress (Langer, 1979).

Another factor which greatly affects tiller production and survival is plant density. Generally low plant density increases the number of tillers per plant (Kirby, 1967; Puckridge and Donald, 1967; Kirby and Faris, 1972; Darwinkel, 1978; Colvill and Marshall, 1981; Fraser, Dougherty and Langer, 1982; Ali, 1984). It is considered that some form of interplant competition is operative in reducing tiller number at high plant density. It is likely that competition is

primarily for light, nutrients and water. Competition begins earlier in dense crops, early competition being expressed by the initiation of fewer tiller buds and higher proportion of tiller mortality (Darwinkel, 1978).

2.4 YIELD DETERMINATION OF CEREALS

The grain yield of barley and wheat can be resolved into four major components : the number of plants per unit area, the number of ears per plant, the number of grains per ear and specific grain weight. These components are increasingly interdependent and their development and growth is basically a genetic phenomenon. Within a genotype it is largely controlled by plant density, plant nutrition, water supply and environment. A substantial amount of research work has been done to investigate the implications and effects of the above mentioned factors on the determination of grain yield and this has been reviewed elsewhere. However, a brief account of the effects of plant density, nitrogen supply and environments will be given here.

Number of plants per unit ground area will depend on the number of seeds sown, germinability and vigour of the seeds. The general pattern of response of yield to increasing plant density is that, at very low densities, the dry matter yield is directly proportional to the number of plants per unit area, but later this linear relationship ceases to hold and eventually the dry matter yield reaches a maximum and further increase in the density do not bring about any increase in

yield. This has been designated as "law of final constant yield" by Kira, Ogawa and Schinozaki (1953). Further increase in plant density may have a decreasing effect on yield (Holliday, 1960; Donald, 1963; Kirby, 1967). Reduction in grain yield at high densities is frequently associated with lodging and greater incidence of mildew (Rennie, 1957).

Harper (1964a) suggested that with increase in plant density, "the source- supplying power of the environment comes to dominate the rate at which the member of population grow and ultimately sets the limit to the yield irrespective of the plant density" and thus after a certain maximum limit no further increase in yield per unit area is achieved. The final constant yield probably represents maximum fixation of energy that a crop can possibly achieve from the time of sowing to harvest (Bleasdale, 1966a). Holliday (1960) called this type of yield-density relationship an "asymptotic" relationship, where dry matter yield per unit area increases with increase in density to a maximum level and then becomes relatively constant at higher densities. Here, the reaction of the crop to high density is such that the decrease in weight of individual plants almost compensate for the increased number of plants per unit area. Many workers for example Donald (1951), Warne (1951), Harper (1961), Bleasdale (1966b), Puckridge and Donald (1967) and others have observed this "asymptotic" yield density relationship for dry matter yield or vegetative yield of above ground parts of plants. Holliday (1960) also identified another type of relationship; the "parabolic", where yield per unit area rises to a maximum but

then declines at high densities. This situation seems to be most common for the yield of reproductive parts of plants and in particular for grain yield in cereals. This relationship has also been reported by Lang, Pedleton and Dungan (1956), Bleasdale (1966b), Bruinsma (1966), Cambell and Viets (1967), Kirby (1967), Puckridge and Donald (1967) and Chang (1982).

During the vegetative phase density stress affects the number of tillers per plant and thus the potential number of ears per plant (Evans, Wardlaw and Williams, 1964; Kirby and faris, 1972; Evans, Wardlaw and Fischer, 1975; Harper, 1977; Chang, 1982). The stress of density that is experienced after flower initiation is usually reflected in the size of ears that have already been initiated. The potential size of inflorescence is determined relatively early in post-vegetative phase (Evans et al., 1975; Harper, 1977; Donald, 1981). All of these necessary adjustments take place before the period of grain filling. Therefore, grain size absorbs very little density stress (Harper, 1977) and is cosidered to be the character most stable to the effect of plant density. Quinlan and Sagar (1965) and Chang (1982) have also reported the stability of grain size and relative plasticity of other yield determinants in wheat. However, many other workers have reported an increase in number of ears per unit area with increase in plant densities but a decrease in number of grains per ear and average grain weight (Bockstaele and Maddens, 1966, 1974; Kirby, 1967, 1969a; Willey and Holliday, 1971a; Hojmark, 1975; Evans, 1977; Harris, 1981; Ali, 1984). Jackson and Page (1957)

reported a decrease in grain nitrogen content at high plant density, while Jurick (1979) found an increase in the total uptake of nitrogen and its utilization in dry matter production with increasing plant density.

Willey and Heath (1969) have presented a good review of models of the yield-density relationship. Two sets of models have been found to be particularly useful; the geometric and reciprocal. Warne (1951) and Kira et al. (1953) were the first to put forward the geometric equation, which assumes a linear relationship between the logarithm of yield per plant and the logarithm of plant density or space per plant.

Warne's equation is :

$$\text{Log } W = \log A + b \log (S)$$

$$\text{or} \qquad W = A\,(S)^{b}$$

where, W is the yield per plant, S is the space per plant, A and b are the constants of the equation. Kira et al. (1953) also found a linear relationship between the logarithm of yield per plant and the logarithm of plant density. They proposed the equation :

$$\text{Log } W + a \log P = \log K$$

$$\text{or} \qquad \text{Log } W = \log k - a \log P$$

where, K and a are constants, W is the weight of an individual plant and P is plant density. They termed the constant a as the density index. These equations can be useful where yield at the highest density is still increaseing.

The reciprocal equation is based on the mathemetical relationship between the reciprocal of mean yield per plant and plant density. Schinozoki and Kira (1956) were one of the first to propose a reciprocal equation :

$$W^{-1} = a + B\ P$$

where, W^{-1} is a reciprocal of mean yield per plant, P is plant density and a and B are regression constant and regression coefficient respectively. They observed a linear relationship between the reciprocal of plant yield and the density, which they called the "reciprocal yield law". Other more complicated reciprocal equations have been proposed by many other workers i.e. de Wit and Ennik (1958) refered to by Willey and Heath (1969), de Wit (1960), Holliday (1960), Farazdaghi and Harris (1968), Berry (1967) and Watkinson (1981).

More recently Baker and Briggs (1983) compared these two basic type of yield-density equations for 10 cultivars of spring barley, tested for 3 years at 5 plant densities. They established that the relationship between total shoot weight or grain yield of spring barley and plant density can best be described by a reciprocal equation rather than by a logarithmic equation.

2.5 TECHNIQUES OF EXPERIMENTATION

Evans (1963) has emphasised that, in nature, " plant development may well have become geared to the natural sequence of changes in the environment ". The development of

crop plants in relation to environment has been extensively studied in artificial and controlled environments. For cereals, development has been found to be strongly regulated by temperature (Friend, 1965b; Rahman and Wilson, 1978); by light intensity (Friend, 1962); and by photoperiod (Rawson, 1971; Lucas, 1972).

Before going into the discussion on differences between the effects of natural and controlled environments on plant growth and development, it is necessary to give a definition of what is meant by the term environment. In its widest sense this term means the entire complex of physical, chemical and biological factors met by a plant or any other entity. For the present purpose I shall distinguish: (1) "artificial environments", being those of growth cabinets and the like; (2) "natural environments", these being the environments found in the field; (3) "modified natural environments", being natural environments modified to a large extent by cultural measures such as irrigation, application of plant nutrients and so on. In relating the results of experiments conducted in artificial environments to the conditions found or obtained in the field, it can be questioned, how the artificial environment compares with natural or modified natural conditions, i.e. how the various physical, chemical and biological factors in the controlled and uncontrolled environments compare.

In a natural environment most of the factors are interrelated, so a change in one factor is usually accompanied by a change

in other factors. In an artificial or controlled environment most of the factors can be controlled independently within certain limits. Plants in the field grow under the conditions which are changing continously, in microclimates which are spatially diverse, and in communities in which individuals may interact with one another. In controlled environments on the other hand, plants are usually grown under conditions which are more stable in time, spatially uniform, and often free of marked interactions with other individuals. These major differences are likely to have effects on the physiology of plants. There are also other factors eg. pests, diseases and other organisms of importance in natural environments which may be missing from the controlled environments. In a controlled environment study one tries to control those environmental factors which are considered to be very important in order to study the effects of others. However, there may be some other factors whose effect on plant growth and physiology are not yet very well known.

Most of the work done in controlled environments has been done on plants grown singly, where as in the field plants grow in a community with other plants of the same species and with those of other species (weeds). Plants grown singly or individually may have quite different growth patterns to those of plants grown in a community, which are in competition with each other for environmental factors eg. light, water, CO_2 and nutrients (Watson, 1963). In most of the controlled environment experiments plants are grown in small pots or containers, which may cause some physical constraints to the growth,

development and spread of the root system, while in field conditions there will be no such physical limitations on the root volume.

Growth media used in field and controlled environments differ markedly. The availability of nutrients and water to crop roots in the field will also differ markedly to that in a controlled environment, where their supply can be controlled. There are also more complex interactions. Natural soil fertility conditions may change or modify the response of plants to environments, as they may depend on climate, as in the rate of release of nitrogen from soil organic matter (Russell, 1973). Similarly the profile of soil may have a noticeable effect on the plant performance in the field. These important features of the natural environment are not always reproduced in controlled environments.

In growth rooms, environmental factors such as temperature and light are constant both in time and space and there is often a rapid change from the light to dark period and vice versa. In field conditions there is a seasonal and diurnal variation in these environmental factors and the change from light to dark and from dark to light is a gradual one. It has recently been suggested that plants respond to the rate of change of photoperiod (Baker, Gallagher and Monteith, 1980; kirby et al., 1982), and in any case the quality and intensity of light in controlled environments is a continuing source of uncertainity (Huxley and Summerfield, 1976). In controlled-climate installations, the main fluorescent light source has a

spectral composition which differs greatly from that of natural daylight (Collingbourne, 1966). The maximum light intensity and total light quantity per day are lower in controlled climate rooms than in daylight (compare for example the figures quoted by Williams and Williams (1968) for daylight, where the mean light energy for 8-h day was 176 cal cm^{-2}(1.022 MJ $m^{-2}d^{-1}$) with those of Aspinall (1966) 0.11 cal $cm^{-2}min^{-1}$ (0.306 MJ $m^{-2}d^{-1}$), and Friend et al. (1963) 0.096 cal $cm^{-2}min^{-1}$ (0.267 MJ $m^{-2}d^{-1}$) for controlled climate rooms.

Temperate climates are characterised by seasonal variation in weather variables. During the first half of the calender year daylength, daily mean temperature and light intensity are increasing and soils are getting drier, but in the second half of the year this trend is reversed.

However, despite the obvious importance and relevance of the field experiments to the practical situation, experiments in controlled environments are useful in many situations. The advent of controlled environment facilities has facilitated the investigation of the effect of single environmental factor on the growth and development of plants. These investigations have produced valuable informations on the response of particular physiological processes to different environmental variables (eg. Friend, 1966; Kleinendorst and Brouwer, 1970), but it has proved difficult to extrapolate the results from controlled environments to the field (Evans, 1963). In the field plant response to environmental factors is a very complex phenomenon and poses a problem of how to isolate the

effects of the individual environmental factors. Greatest progress in the agricultural research is likely to be achieved with the two techniques working in parallel, with cross referencing of informations.

In this study it was decided to conduct experiments on spring barley grown in glasshouses in a modified natural environments with no artificial control over temperature, photoperiod and light intensity and greater control over nitrogen and water supply. The measurements of temperature and radiation experienced by the crop were made at plant level. In all experiments the plants were kept well watered and water availablity was not considered a limiting factor. The effect of nitrogen and inter-plant competition were studied by regulating nitrogen supply and plant density as experimental treatments. The effects of natural variation in photoperiod and temperature were studied by varying sowing date as an experimental treatment.

2.6 MAIN OBJECTIVES OF THIS STUDY

The main objectives of this study were:

1. To study the effects of growth media and pot size on growth and development of spring barley.

2. To describe the processes of apex development, leaf appearance and leaf extension in Julian time and in thermal time units.

3. To investigate the effects of nitrogen supply, plant density and environments on leaf appearance and apical development.

4. To study the relationship between leaf extension rate, leaf extension duration and final leaf length and how they are affected by sowing date, nitrogen supply and plant density.

5. To separate the effects of environmental variables from ontogeny and to enable the growth patterns of different main shoot leaves to be compared.

CHAPTER 3

EXPERIMENT 1.

Effects of nitrogen supply and sowing date on growth of the first five main shoot leaves of spring barley

3.1 INTRODUCTION

This experiment was carried out to determine the effects of four nitrogen (N) levels (40, 80, 160 and 320 ppm) and four sowing dates (15 September 1980, 1 March 1981, 28 April 1981 and 1 June 1981), on the growth and development of the first five main shoot leaves of spring barley. The nitrogen levels were chosen so as to cover the whole range of the response curve. The sowing dates were varied so that leaves were growing in contrasting photoperiods and temperatures. The experiments were carried out in perlite so as to be able to precisely control nitrogen supply.

The plants were harvested when 5th leaf stopped growing and growth analysis was carried out. Results for the lamina area and dry weight of main shoot leaves, the remainder of the main shoot together with leaf sheaths herein refered to as pseudostem, tiller number and dry weight, the leaf extension rate and duration of the 5th main shoot leaf and dry weight of the whole plant are presented in this chapter.

3.2 MATERIALS AND METHODS

3.2.1 Cultivation of plants and experimental treatments tested

All the measurements were made on spring barley (cv. Claret) grown from carefully graded seed of high genetic purity. The plants were grown in perlite, a nutrient free medium, using 10 l capacity plastic boxes (23 x 23 cm surface x 23 cm deep), in a glasshouse without any supplementary light and heating.

Seeds were sown at 5.5 cm square spacing and at a depth of 3 cm. The seeds were sown in a 4 x 4 grid arrangment with two seeds at each position to allow for any seeds which failed to germinate. Half strength modified Long Ashton nutrient solution (Appendix I) was used to supply nutrients during germination. At the second leaf stage seedlings were thinned to 16 plants per box (equivalent to a plant population of about 300 plants m^{-2}), and received full strength nutrient solution thereafter. Nitrogen was always supplied as nitrate of sodium at four different amounts i.e. 40 ppm (N1); 80 ppm (N2); 160 ppm (N3) and 320 ppm (N4). The nutrient solution was applied twice a week, but plants were watered daily to replace water lost by evapo-transpiration. Four experiments were sown at different times of the year to study the effects of seasonal variation in temperature, solar radiation and photoperiod. The first two experiments were sown on 15 September, 1980 and 1 March, 1981 at the University College Farm, Aber (54^{o} N) and the later two experiments were sown at Pen-y-Ffridd field station, Bangor on 28 April, 1981 and 1 June, 1981. The two experimental locations are about 7 miles apart from each other but are at the same latitude. Each of the experiments was laid out in randomized complete block design with four blocks. Each treatment was randomally allocated to two boxes within each block.

Although the September experiment was carried out in 1980, for convenience the experiments will be referred to on a calendar basis as follows;

Sowing date 1 = 1 March 1981

Sowing date 2 = 28 April 1981

Sowing date 3 = 1 June 1981

Sowing date 4 = 15 September 1980

3.2.2 Meteorological observations

During all the experiments daily minimum and maximum air temeprature were recorded at 0900 h GMT from a thermometer installed at plant level. A thermograph was also used to record the diurnal variation in air temperature. A tube solarimeter (Monteith pattern supplied by Delta-T Devices, Cambridge, England) connected to a millivolt integrator was installed to measure the total daily solar radiation (0.4 - 2.5 μm wavelength) received by the plants.

Mean daily air temperature (Ta) was calculated as the average of maximum temperature (Tmax) and minimum temperature (Tmin) i.e.

$$Ta = \frac{Tmax + Tmin}{2}$$

Thermal time which is an accumulated daily mean air temperature above a fixed base temperature (Tb) was calculated by the method described by Gallagher (1979) and Baker, Gallagher and Monteith (1980) and a convenient unit to use is ^{o}Cd (day degree centigrade).

$$\text{Thermal time } (^{o}Cd) = \sum_{i=1}^{i=n} (Ta - Tb);\ Ta<Tb$$

where Ta is daily mean air temperature, Tb is a base base temperature and n is the number of days after sowing. There is still uncertainty concerning the choice of base temperature, because in all but a few instances the value of Tb is obtained by extrapolation, usually over serveral degrees. In the literature a wide range of values of Tb for growth and development of various crops have been reported. In general Tb for tropical crops ranged from 8°C to 13 °C (Ong and Baker, 1984) and for temperate cereals Tb ranged from -5°C to 9°C (Robertson, 1968; Angus, Mackenzie, Morton and Schafer, 1981) for different processes. For millet and maize the values of Tb for leaf initiation, appearance and expansion are 10°c to 12°C (Ong, 1983; Russelle, Wilhelm, Olson and Power, 1984). For forage rye the rates of leaf appearance in thermal time units were calculated using Tb of 0°C (Hay and Abass Al-Ani, 1983). For leaf initiation, appearance and expansion in winter wheat and spring barley 0°C was found to be an appropriate value of Tb (Gallagher, 1979; Russell, Ellis, Brown, Milbourn and Hayter, 1982; Bauer, Frank and Black, 1984; Frank and Bauer, 1984). It is not clear whether Tb changes for different stages of plant development. However there is some controversy as to whether or not Tb changes with the date of sowing (Kirby, Appleyard, Fellowes, 1982). Ellis and Russell (1984) carried out a study on spring and winter barley sown in both spring and autum and followed plant development in two seasons. They tested a range of Tb (i.e. -2, 0, +2, +4 and +6°C). They found that Tb calculated using the method of least squares did not differ significantly from 0°C. They also found that there was

a strong correlation between the thermal time sums calculated above base temperature near $0^{o}c$. There are no clear basis on which to prefer one Tb to another and which Tb to use for which sowing. Hence in this study, and following Gallagher (1979), a Tb of $0^{o}c$ was taken for all the sowing dates.

Nevertheless, despite uncertainties over Tb, thermal time is still the most useful and meaningful method of analysis to separate the effect of temperature on the leaf growth in the environments where temperature and other environmental factors vary simultanously. For example, Gallagher and his co-workers have shown that the production of leaf and spikelet primordia, leaf appearance, leaf expansion and the duration of leaf growth, in field grown wheat and barley can best be described in terms of thermal time (Gallagher, 1979; Baker and Gallagher, 1983). Thermal time satisfies practical needs, and is derived from temperature, an easily and widely measured parameter which is routinely available from weather stations and can conveniently be measured on a farm.

Values for the length of daylight were taken from the Smithsonian Tables (List, 1951) assuming that the experimental sites are at 54^{o} N. Photoperiod was calculated as the duration of daylight plus twice the duration of civil twilight. Values for the 1, 5, 9, 13, 17, 21 and 25 days of each month were taken from the Smithsonian Tables and values for the remaining days were calculated by linear interpolation (Appendix II).

3.2.3 Leaf extension measurements

Within each pot ten plants were selected at random and marked for leaf extension measurements. The 5th leaf on the main shoot was chosen for extension measurements because its primordium is believed to be the second to be initiated after germination (assuming that the embryonic apex has three primordia (Kirby, 1977)) and its growth is thought to be little influenced by seed reserves (Williams,1975). The length of the 5th leaf of the main shoot was measured daily commencing the day it emerged in the angle of the 4th leaf and continuing until at least three successive observations showed no measureable increase in length. Measurements were taken of the distance between the tip of the leaf and the point of emergence of the encircling sheath. Mean leaf length of ten plants was calculated for each pot for each day and a linear regression of leaf length (Y) against thermal time (X) was calculated for each pot, including only the points between 10% and 90% of the final length (c.f. Dennett, Auld and Eiston, 1978; Gallagher, 1979). Temperature has been shown to be an important factor influencing leaf extension in several crops (Friend, 1965a; Gallagher, 1976; Baker, 1979; Ong, 1983). In this study, had leaf extension rate been expressed in units of length per unit time (eg. mm d^{-1}) at least part of the variation observed between sowing dates and between leaf positions within a sowing date could be due to variations in temperature experienced. Hence, in order to permit comparisons between sowing dates and leaf positions, leaf extension growth was expressed in thermal time units. The slope of the linear

regression was taken as the mean rate of leaf extension (LER) and was expressed as mm $^{o}Cd^{-1}$. The final length of a leaf is determined by the rate it is extending and the duration which it takes to achieve its maximum length. Leaf extension duration (LED), in thermal time units (^{o}Cd), between the apparent start and end of leaf extension, was calculated by extrapolating the linear regression line to zero leaf length (start of leaf extension in ^{o}Cd after sowing) and final length (end of leaf extension). An example illustrating the method used is given in Table 3.1 and Figure 3.1.

3.2.4 Plant growth analysis

When the 5th main shoot leaf had achieved its maximum length 20 randomly selected plants were harvested from the 2 boxes of each treatment for growth analysis. All plants were separated into the separate laminae of the main shoot, tillers and pseudostem. The area of each fully expanded main shoot lamina (leaf 1 to leaf 5) was measured using automatic area meter, model AAM7 (Hayashi Denkoh Co. Ltd., Tokyo, Japan). In the case of the first experiment (i.e. September sowing) the automatic area meter was not available so lamina area for that experiment was calculated as the product of length and width of the lamina i.e.

$$\text{Lamina area} = \text{length} \cdot \text{width} \cdot K$$

where K is a constant and its value was taken as 0.70 (Richard, 1983). The separate fractions of plant material were

Table 3.1 An example of the method of determining leaf extension rate (LER in $mm\,^{o}Cd^{-1}$) and apparent extension duration (LED in ^{o}Cd) for a particular pot.

Days after sowing	Thermal time after sowing (^{o}Cd)	Leaf length (mm)
40	806.25	10.50
41	823.50	21.75
42	841.25	38.50
43	859.50	52.75
44	878.25	75.90
45	906.25	94.10
46	923.75	115.80
47	941.75	134.50
48	960.25	153.60
49	979.50	171.50
50	997.75	191.30
51	1015.50	200.70
52	1033.50	212.10
53	1048.75	217.50
54	1063.00	220.90
55	1079.00	221.00
56	1095.25	220.50

Final length = 220 mm

10% of final length = 22 mm

90% of final length = 198 mm

Number of data points used for linearregression=9
(42 to 50 days after sowing)

Coefficient of correlation (r) = 0.9981 ***

Coefficient of determination (r^2) = 0.9962

Regression coefficient (LER) = 0.9667

Regression constant = -775.61

Value of thermal time (X_1) at leaf length (Y)

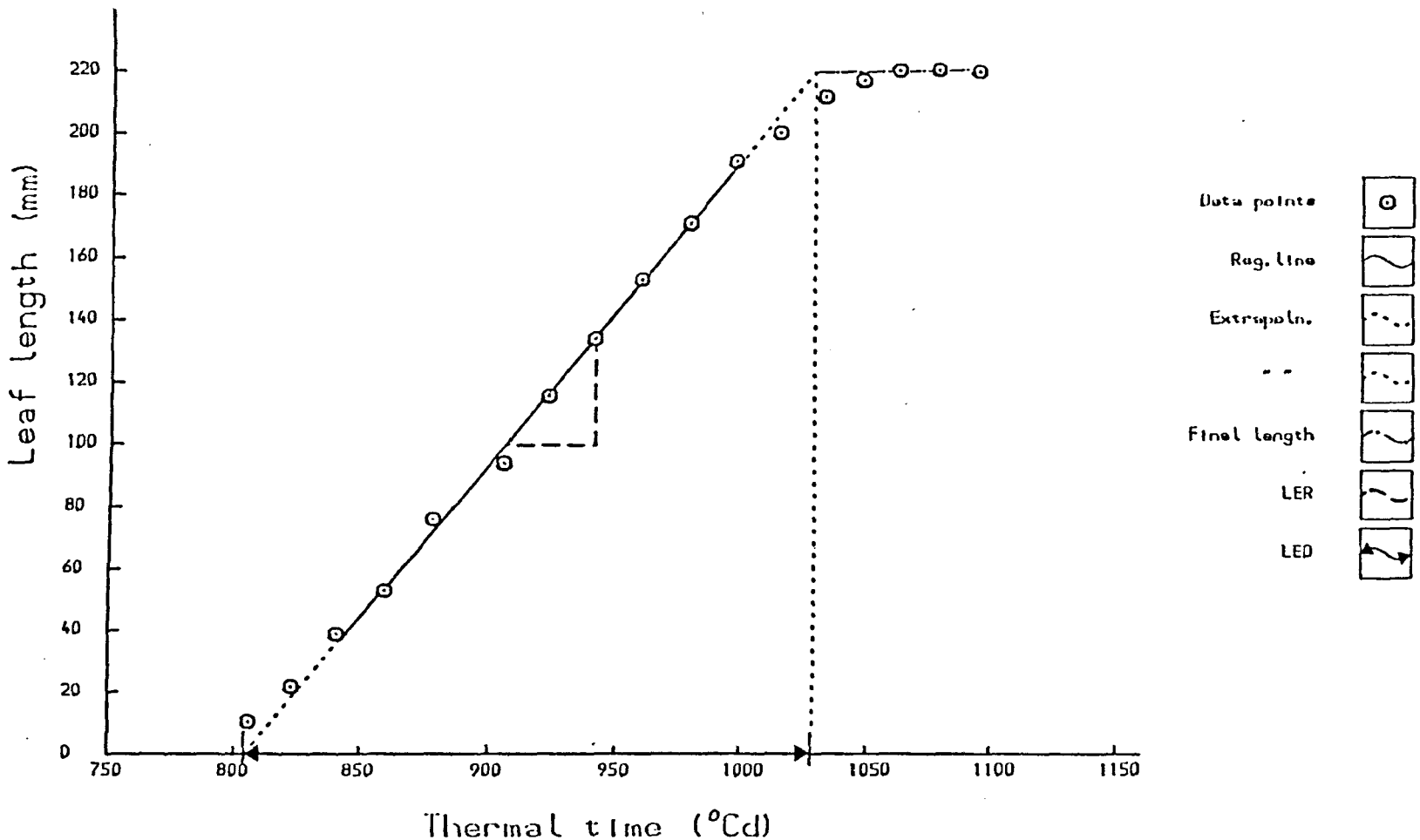
of 0 mm (start of leaf extension) = 802.34 ^{o}Cd

Valueof thermal time(X_2) at leaf length (Y)

of 220mm (final leaf length) = 1029.91 ^{o}Cd

Hence apparent leaf extension duration (LED)(X_2-X_1)
1029.91 - 802.34 = 227.57 ^{o}Cd

Figure 3.1 An example of the method of determining leaf extension rate (LER in mm/°Cd) and apparent extension duration (LED in °Cd).



oven dried for 48 h at 80°C and the dry weight were recorded.

3.2.5 Pests and disease control

Plants were sprayed for pests and diseases with appropriate chemicals as and when was necessary. Aphids and mildew were the main problems encountered but these were immediatly controlled and were not serious during the experiment.

3.3 RESULTS

3.3.1 Environmental conditions during the course of the experiments

3.3.1.1 Water and nutrient supply

Plants were grown in perlite and hence it was possible to have good control over water and nutrient supply. The plants were kept well watered and the nutrient solution used had sufficient phosphorus, potassium and other nutrients to satisfy growth. Hence, the only variable within a sowing date was nitrogen supply. The same nutrient solution and nitrogen levels were used in each experiment and therefore major differences in response between sowing dates must be due to differences in temperature, radiation and photoperiod perceived.

3.3.1.2 Temperature

Average weekly temperatures for each sowing are shown in Figure 3.2. During the March sown experiment mean daily

temperature gradually increased from 18°C to 23°C. During the April and June sown experiments there was little variation in average weekly temperature, it remained within the range of 22 - 24°C. For the September sowing during the first 3 weeks average weekly temperature remained between 21°C and 24°C and after that it fell to 16°C at the time of harvest.

3.3.1.3 Photoperiod

Average weekly photoperiods for each experiment are shown in Figure 3.2. During the March sown experiment photoperiod gradually increased from 12 hd^{-1} to almost 16 hd^{-1}. This trend continued during the April sown experiment, although the increase was not as great (from 16.5 to 18.5 hd^{-1}). For the June sowing photoperiod was almost constant at 18 hd^{-1}. The September sowing experienced a marked decrease in photoperiod from 14 hd^{-1} to 10 hd^{-1}.

3.3.1.4 Solar radiation

Whereas temperature and photoperiod showed consistent trends over time, radiation receipts were more variable. Average weekly solar radiation received by plants during the course of all the sowings is shown in Figure 3.2. For the March sowing solar radiation gradually increased from 3 MJ $m^{-2}d^{-1}$ to 12 MJ $m^{2}d^{-1}$. For the April and June sowings radiation was very eratic and and fluctuated between 7 and 14 MJ $m^{-2}d^{-1}$. For the September sowing the amount of radiation received by the plants was much less than the other sowings and it decreased

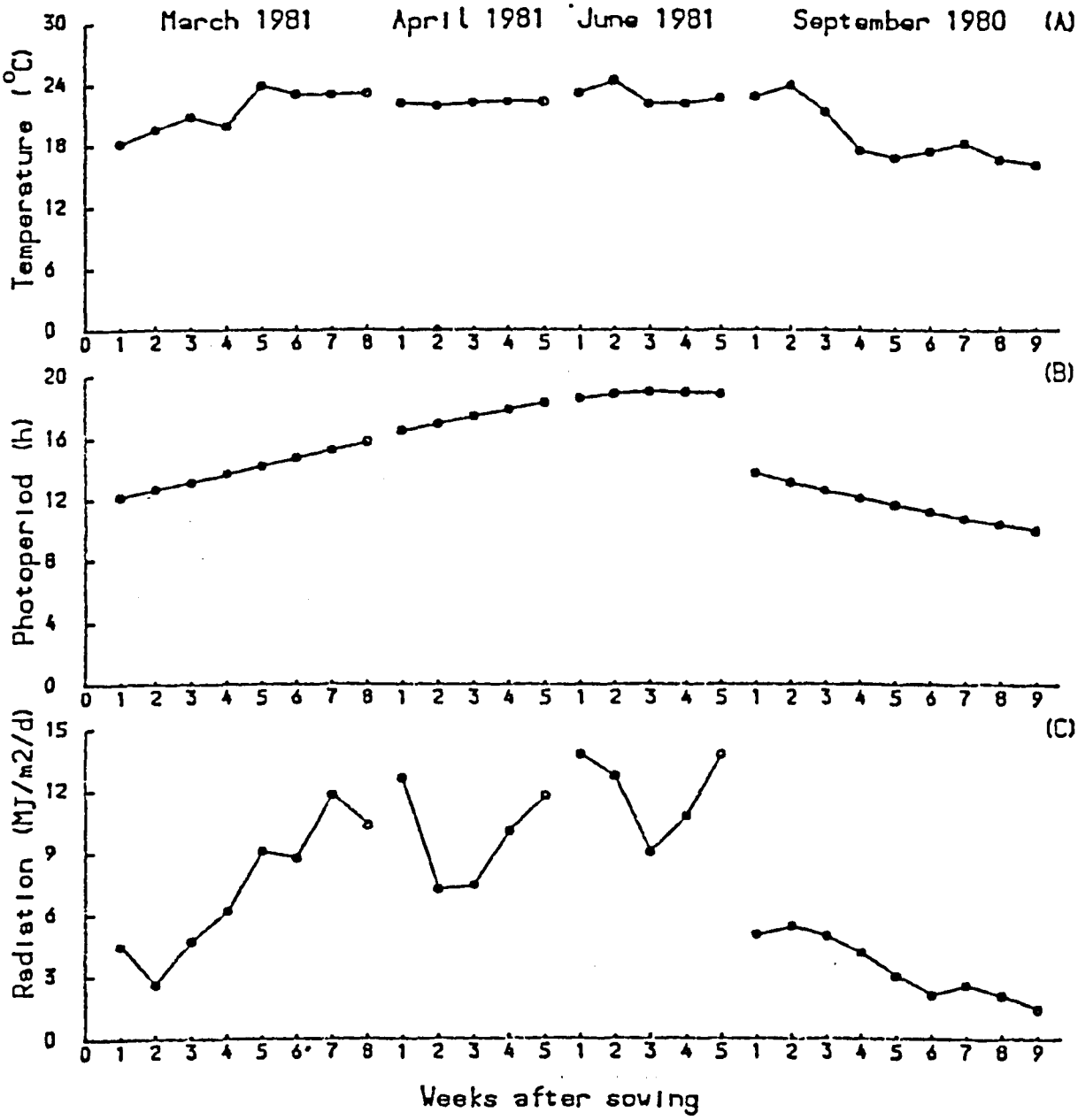


Figure 3.2 Showing average weekly mean air temperature (A), photoperiod (B) and solar radiation experienced by the plants during the course of experiment 1.

gradually from 6 MJ $m^{-2}d^{-1}$ at the beginning of the experiment to about 2 MJ $m^{-2}d^{-1}$ by the end of the experiment.

3.3.1.5 Time taken to different growth stages

The duration both in Julian time (days after sowing) and thermal time (^{o}Cd) taken until the leaf 5 ceased extension growth was very similar for April and June sowings and was much shorter than the other sowings (Table 3.2). The variation in duration appeared to be closely associated with the mean air temperature during the experiment. There was no apparent effect of nitrogen on the time when leaf 5 ceased extension growth.

Table 3.2 Time taken from sowing date to the date when leaf 5 of main shoot ceased extension growth

Sowing date	Date when leaf 5 ceased extension growth	Duration		Mean air temp. (^{o}C)
		Days after sowing	Thermal time (^{o}Cd)	
1.3.81	20.4.81	50	1081	21.63
28.4.81	2.6.81	35	803	22.94
1.6.81	5.7.81	34	807	23.75
15.9.80	12.11.80	58	1145	19.74

3.3.2 Statistical analysis

The data for lamina area, lamina dry weight and specific

lamina area of individual leaves on the main shoot were analysed as a split-split plot design, using a standard statistical package (GENSTAT). In order to determine the effects of sowing date, nitrogen supply and leaf position and interactions between them on leaf growth the data for each character for each of the four sowing dates were pooled together for statistical analysis. Sowing dates were on main plots (as each experiment was an entity in its own right), nitrogen on sub-plots (as the nitrogen treatments were allocated at random within each experiment) and leaf position on sub-sub-plots (as there were 5 leaf positions on the plants within each nitrogen level). An example of the analysis of variance table for one of the sets of data (lamina area) is shown in Table 3.3. Because each block was not the same in each experiment (because they were sown at different times in different locations), sowing date was compared tothe block plus block.sowing date plus residual term in a similar way to a completely randomised design. It could be argued that leaf position is not a random variable, but it was included as one here, in order to determine the effect of nitrogen and sowing date on different leaves. Results for leaf extension rate and duration of the 5th leaf, and dry weight of other plant components recorded in growth analysis were also analysed as a split plot design, with sowing dates on main plots and nitrogen amounts on sub-plots, there being no corresponding sub-sub-plot (leaf position) level in the analyses for these characters. Where significant differences between means occured (at the 5% probability level of the variance ratio),

Table 3.3 An example of analysis of variance table for the data from experiment 1. Data are for lamina area ($cm^2 leaf^{-1}$) at maximum leaf size.

** ANALYSIS OF VARIANCE **

Variate: Main shoot lamina area (cm^2 $leaf^{-1}$)

Source of variation	DF	SS	MS	VR
Sowing date.Block Stratum				
Sowing date	3	5952.45	1984.15	397.13***
Residual	12	59.95	4.99	4.23
Total	15	6012.40	400.82	339.61
Sowing date.Block.Nitrogen Stratum				
Nitrogen	3	1741.45	580.48	109.56***
Sowing date.Nitrogen	9	293.21	32.58	6.15***
Residual	36	190.73	5.29	4.49
Total	48	2225.40	46.36	39.28
Sowing date.Block.Nitrogen.Leaf position Stratum				
Leaf position	4	7657.11	1914.28	1621.91***
Sowing date.Leaf position	12	2964.93	247.08	209.34***
Nitrogen.Leaf position	12	1519.30	126.61	107.27***
Sowing date.Nitrogen.Leaf position	36	319.01	8.86	7.51***
Residual	192	226.61	1.18	
Total	319	20924.77		

*** = Significant at 0.1% level of probability.

Tukey's test was used to determine the significance of the differences between individual means. Values of HSD (honestly significant difference) (Zar, 1984) were calculated using the following formula:

$$HSD = S.E.M * Q (nl,n2),$$

where S.E.M is the standard error of means, the value of Q is obtained from tables of the studentized range for P = 0.05, nl = number of means being compared and n2 = residual degrees of freedom. In the results tables NS indicates not significant difference at the 5 % probability level of the variance ratio.

3.3.3 Main effects and interactions

The significance levels of the main effects and interactions are given in Table 3.4. All main effects, first and second order interactions were significant ($P<0.001$). Therefore in this experiment the effects of sowing date and nitrogen on leaf growth depended on leaf position. A preliminary inspection of the data showed that these factors were affecting leaf growth in a complex way and therefore effects of sowing date, nitrogen supply and leaf position are first presented and briefly discussed in order to describe the general trends within the data.

3.3.3.1 Main effects of sowing date

The main effects of sowing date on leaf growth and other characters are shown in Table 3.5. Although individual sowings

Table 3.4. Significance levels of the main effects of sowing date (SD), nitrogen level (N) and leaf position (LP) and their interactions on the different plant growth parameters recorded.

	Maineffects			Interactions			
	SD	N	LP	SD*N	SD*LP	N*LP	SD*N*LP
PARAMETER							
Lamina area (cm^2 $leaf^{-1}$)	***	***	***	***	***	***	***
Lamina dry weight (mg $leaf^{-1}$)	***	***	***	***	***	***	***
Specific lamina area (mm^2 mg^{-1})	***	NS	***	***	***	***	***
leaf 5 extension rate (mm $^oCd^{-1}$)	***	***	-	***	-	-	-
leaf 5 extension duration (^oCd)	***	***	-	***	-	-	-
Leaf 5 nitrogen content (mg $leaf^{-1}$)	***	***	-	***	-	-	-
Pseudostem dry weight (mg $plant^{-1}$)	***	***	-	***	-	-	-
Main shoot total dry weight (mg $plant^{-1}$)	***	***	-	***	-	-	-
Tiller dry weight (mg $plant^{-1}$)	***	***	-	***	-	-	-
Number of tillers per plant	***	***	-	***	-	-	-
Total plant dry weight (mg $plant^{-1}$)	***	***	-	***	-	-	-

*** = Significant ($P<0.001$)
NS = Not significant ($P>0.05$)
- = Does not occur

Table 3.5 The main effects of sowing date on the various plant growth parameters recorded

Plant growth parameter	Sowing date				HSD
	March	April	June	September	(P=0.05)
[1]Lamina area (cm^2 $leaf^{-1}$)	13.29	5.27	6.98	15.69	1.05
[1]Lamina dry weight (mg $leaf^{-1}$)	39.46	21.84	27.59	36.32	4.11
[1]Specific lamina area (mm^2 mg^{-1})	36.27	22.57	26.68	42.41	3.87
[2]Leaf 5 extension rate (mm $^oCd^{-1}$)	1.32	1.25	0.95	1.32	0.05
[2]Leaf 5 extension duration (^oCd)	208.80	161.79	162.56	227.74	7.11
[2]Leaf 5 nitrogen content (mg $plant^{-1}$)	2.23	1.49	1.02	2.96	0.29
[2]Pseudostem dry weight (mg $plant^{-1}$)	353.00	146.60	254.40	231.00	30.90
[2]Main shoot total dry weight (mg $plant^{-1}$)	546.50	256.60	389.00	410.90	42.74
[2]Tiller dry weight (mg $plant^{-1}$)	141.70	34.50	15.60	126.80	22.25
[2]Number of tillers per plant	1.21	0.97	0.38	1.20	0.34
[2]Total plant dry weight (mg $plant^{-1}$)	688.20	291.10	404.60	537.70	52.97

1 = Data are means of 4 nitrogen levels and 5 leaf positions
2 = Data are means of 4 nitrogen levels

differed significantly from each other, plant response to different sowing times could be grouped into two distinct groups. In general plants from March and September sowings had larger lamina area, greater dry weights, high values of specific lamina area, faster rates of leaf 5 extension and more tillers per plant than plants from April and June sowings. Differences between sowings within these groups (i.e. between March and September sowings and between April and June sowings) were generally smaller than differences between groups.

3.3.3.2 Main effects of nitrogen

Increasing nitrogen supply lead to corresponding and significant ($P<0.001$) increase in almost all of the plant parameters recorded in this experiment with the exception of specific lamina area where nitrogen had no significant effect (Table 3.6). Increasing nitrogen supply from 160 ppm to 320 ppm failed to increase the dry weight of main shoot per plant, above ground total plant weight and pseudostem dry weight.

3.3.3.3 Main effects of leaf position

The data on changes in lamina area, dry weight and specific lamina area in relation to the position of the leaf on the main shoot are presented in Table 3.7. Lamina area and dry weight continued to increase with leaf position on the main shoot, although the increase in lamina area of the 5th leaf over 4th leaf was not statistically significant ($p<0.05$). In

Table 3.6 The main effects of nitrogen supply on the various plant growth parameters recorded.

Plant growth parameter	Nitrogen supply (ppm) 40	80	160	320	HSD (P=0.05)
[1]Lamina area (cm^2 $leaf^{-1}$)	7.36	8.91	11.61	13.38	0.99
[1]Lamina dry weight (mg $leaf^{-1}$)	22.37	27.44	34.41	41.00	2.84
[1]Specific lamina area (mm^2 mg^{-1})	32.20	31.35	32.45	31.93	NS
[2]Leaf 5 extension rate (mm $^oCd^{-1}$)	0.85	1.09	1.31	1.59	0.03
[2]Leaf 5 extension duration (^oCd)	189.71	189.52	197.04	184.62	4.35
[2]Leaf 5 nitrogen content (mg $plant^{-1}$)	0.73	1.21	2.05	2.96	0.21
[2]Pseudostem dry weight (mg $plant^{-1}$)	216.20	247.60	279.90	241.20	33.93
[2]Main shoot total dry weight (mg $plant^{-1}$)	328.50	382.40	450.40	441.80	43.78
[2]Tiller dry weight (mg $plant^{-1}$)	11.30	36.50	11.30	159.50	23.59
[2]Number of tillers per plant	0.34	0.67	1.17	1.58	0.21
[2]Total plant dry weight (mg $plant^{-1}$)	339.80	418.90	561.70	601.30	55.82

1 = Data are the means of 4 nitrogen levels and 5 leaf positions
2 = Data are the means of 4 nitrogen levels
NS = Not significant (P>0.05)

Table 3.7. The main effects of leaf position on lamina area, lamina dry weight and specific lamina area of individual main shoot leaves.

Leaf growth parameter	Leaf position on main shoot					HSD
	1	2	3	4	5	(P=0.05)
Lamina area (cm^2 $leaf^{-1}$)	3.60	5.94	10.97	14.93	16.12	1.82
Lamina dry weight (mg $lamina^{-1}$)	12.40	17.78	31.64	43.67	51.03	1.94
Specific lamina area (mm^2 mg^{-1})	29.91	33.40	33.30	33.17	30.13	1.64

(Data are the means of 4 sowing dates and 4 nitrogen amounts)

the case of specific lamina area there were no significant differences between leaves 2,3 and 4. The specific lamina areas of leaves 1 and 5 were not statistically different but were significantly ($P<0.05$) lower than those of other leaves.

3.3.4 Interactions between nitrogen supply, sowing date and leaf position

All of the two factor interactions (sowing date * nitrogen, sowing date * leaf position and nitrogen * leaf position) for the growth analysis parameters and the three factor interaction (sowing date * nitrogen * leaf position) for the data for individual leaf positions were statistically significant (Table 3.4).

3.3.4.1 Lamina area and dry weight

The effects of nitrogen, sowing date and leaf position on lamina area and lamina dry weight are shown in Figure 3.3. Generally, lamina area was greatest for the March and September sowings and least for the April and June sowings. Lamina area generally increased with leaf position on the main shoot, except for the June sowing, and always increased with the increase in the amount of nitrogen applied. However, the effects of nitrogen and leaf position on lamina area were different for the different sowings. Leaf 5 had the largest lamina area for the March, April and September sowings except at N1 where leaf 4 had a larger area than leaf 5. The variation in lamina area with leaf position was different for

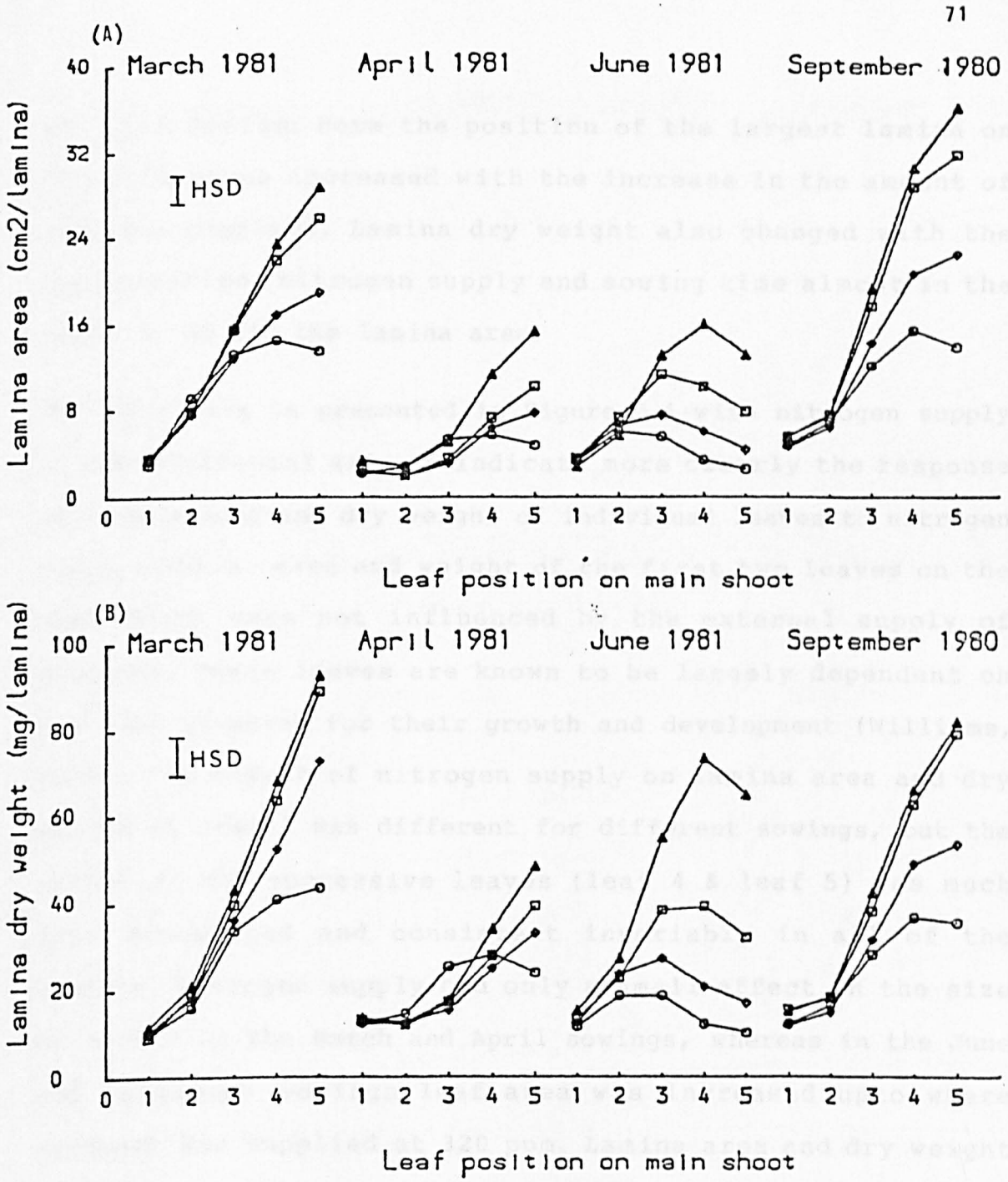


Figure 3.3 Lamina area (A) and lamina dry weight (B) in relation to its position on the main shoot, sowing date and nitrogen supply ; 40 ppm (○), 80 ppm (◇), 160 ppm (□) and 320 ppm (▲). HSD (P=0.05) are to compare means within same sowing date and leaf position.

the June sowing. Here the position of the largest lamina on the main shoot increased with the increase in the amount of nitrogen supplied. Lamina dry weight also changed with the leaf position, nitrogen supply and sowing time almost in the same way as did the lamina area.

The same data is presented in Figure 3.4 with nitrogen supply on the horizontal axis to indicate more clearly the response of lamina area and dry weight of individual leaves to nitrogen supply. Lamina area and weight of the first two leaves on the main shoot were not influenced by the external supply of nitrogen. These leaves are known to be largely dependent on the seed reserves for their growth and development (Williams, 1975). The effect of nitrogen supply on lamina area and dry weight of leaf 3 was different for different sowings, but the effect on the successive leaves (leaf 4 & leaf 5) was much more pronounced and consistent invariably in all of the sowings. Nitrogen supply had only a small effect on the size of leaf 3 in the March and April sowings, whereas in the June and September sowings leaf area was increased upto where nitrogen was supplied at 320 ppm. Lamina area and dry weight of leaves 4 and 5 increased with the nitrogen supply upto 160 ppm for the September and March sowings, and upto 320 ppm for the April and June sowings.

3.3.4.2 Specific lamina area

The results for specific lamina area (SLA) for the first five leaves of the main shoot, four sowing dates and four levels of

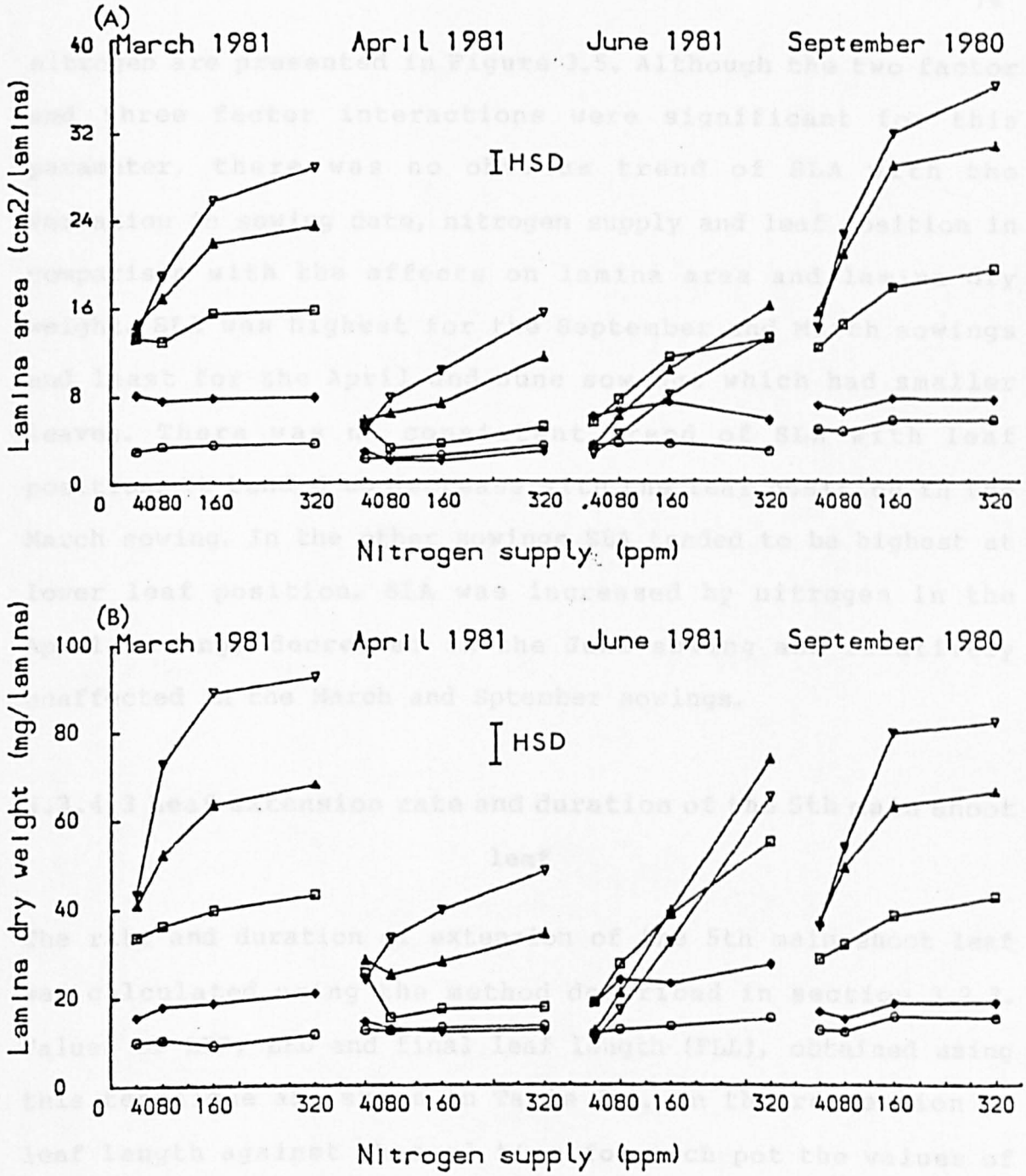


Figure 3.4 Lamina area (A) and lamina dry weight (B) in relation to nitrogen supply, sowing date and its position on the main shoot; leaf 1 (○), leaf 2 (◇), leaf 3 (□), leaf 4 (▲) and leaf 5 (▽). HSD (P=0.05) are to compare means with in same sowing date and leaf position.

nitrogen are presented in Figure 3.5. Although the two factor and three factor interactions were significant for this parameter, there was no obvious trend of SLA with the variation in sowing date, nitrogen supply and leaf position in comparison with the effects on lamina area and lamina dry weight. SLA was highest for the September and March sowings and least for the April and June sowings which had smaller leaves. There was no consistent trend of SLA with leaf position. It tended to decrease with the leaf position in the March sowing. In the other sowings SLA tended to be highest at lower leaf position. SLA was increased by nitrogen in the April sowing, decreased in the June sowing and relatively unaffected in the March and Sptember sowings.

3.3.4.3 Leaf extension rate and duration of the 5th main shoot leaf

The rate and duration of extension of the 5th main shoot leaf was calculated using the method described in section 3.2.3. Values of LER, LED and final leaf length (FLL), obtained using this technique are shown in Table 3.8. In the regression of leaf length against thermal time for each pot the values of the linear correlation coefficients were always significant ($<P<0.001$) and variation in thermal time always accounted for more than 96 % of the variation in leaf length.

In order to determine the effects of sowing date and nitrogen supply on LER and LED analyses of variance were carried out on the values of LER and LED calculated for each pot. Increasing

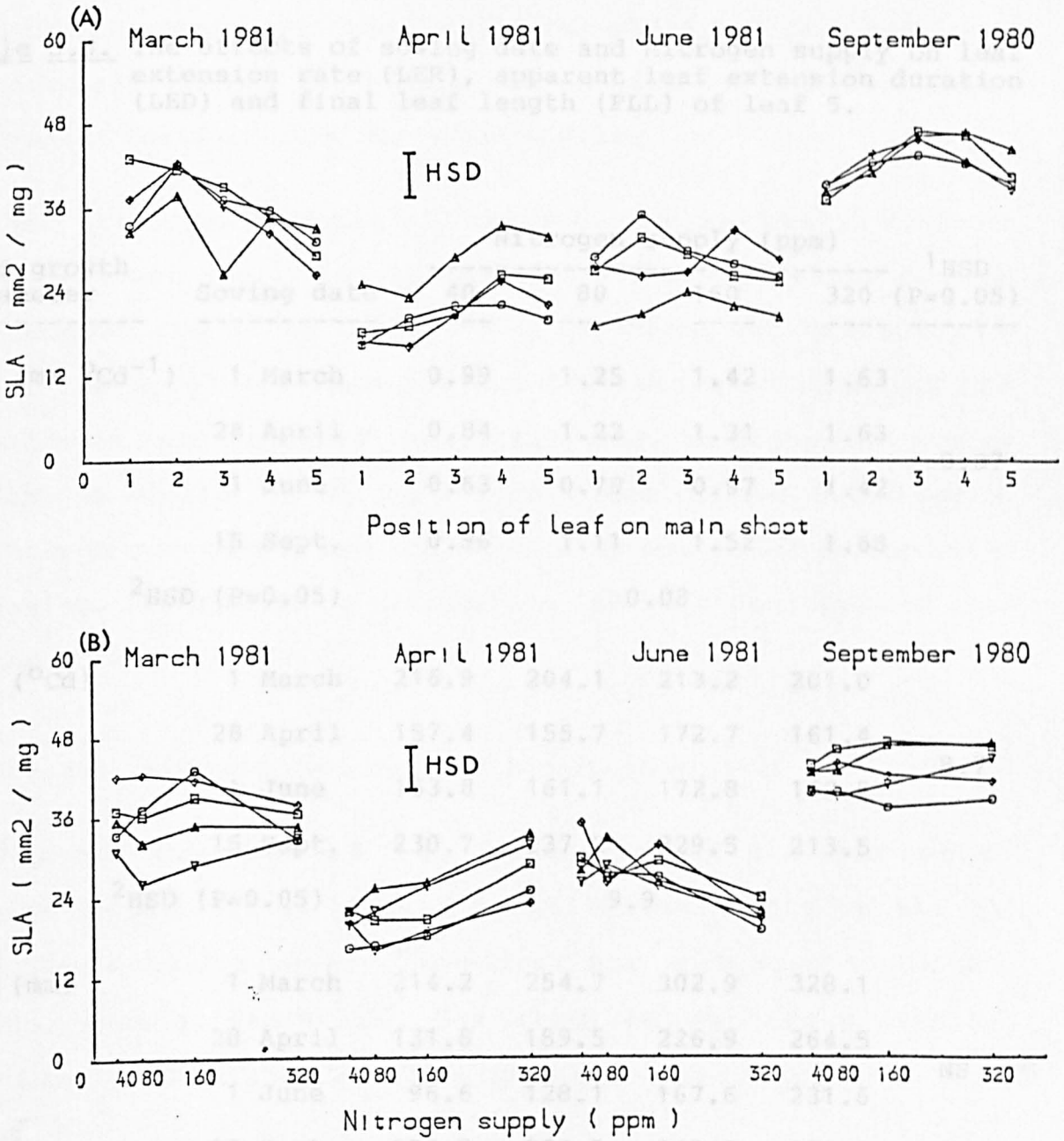


Figure 3.5 Specific lamina area (SLA) in relation to sowing date, nitrogen supply and leaf position on the main shoot.

(A) nitrogen supply; 40 ppm (○), 80 ppm (◇), 160 ppm (□) and 320 ppm (△). HSD (P=0.05) is to compare means within same sowing date and leaf position.

(B) leaf position; leaf 1 (○), leaf 2 (◇), leaf 3 (□), leaf 4 (△) and leaf 5 (▽). HSD (P=0.05) is to compare means witnin same sowing date and level of nitrogen supply.

Table 3.8. The effects of sowing date and nitrogen supply on leaf extension rate (LER), apparent leaf extension duration (LED) and final leaf length (FLL) of leaf 5.

Leaf growth parameter	Sowing date	Nitrogen supply (ppm) 40	80	160	320	[1]HSD (P=0.05)
LER (mm $^{o}Cd^{-1}$)	1 March	0.99	1.25	1.42	1.63	
	28 April	0.84	1.22	1.31	1.63	
	1 June	0.63	0.79	0.97	1.42	0.07
	15 Sept.	0.96	1.11	1.52	1.68	
	[2]HSD (P=0.05)			0.08		
LED (^{o}Cd)	1 March	216.9	204.1	213.2	201.0	
	28 April	157.4	155.7	172.7	161.4	
	1 June	153.8	161.1	172.8	162.5	8.7
	15 Sept.	230.7	237.2	229.5	213.5	
	[2]HSD (P=0.05)			9.9		
FLL (mm)	1 March	214.2	254.7	302.9	328.1	
	28 April	131.8	189.5	226.9	264.5	
	1 June	96.6	128.1	167.6	231.6	NS
	15 Sept.	220.9	262.5	347.9	359.2	

1 = HSD to compare means within same sowing date
2 = HSD to compare means within same nitrogen level
NS = Interaction not significant ($P<0.05$)

nitrogen supply upto the largest amount tested resulted in an increased LER but the effect varied with sowing date, being greater for June than the other sowings.

Leaf extension duration did not show any systematic response to nitrogen supply but it was significantly greater for the September and March sowings than the April and June sowings. For the April and June sowings LED increased upto 160 ppm nitrogen and declined thereafter. For the September sowing LED was similar at 40, 80,160 ppm N, but reduced at 320 ppm N. There was no consistent effect of nitrogen on LED in the March sowing. The effects of nitrogen on LED were much smaller than the effects on LER.

3.3.4.4 Nitrogen content of 5th main shoot leaf

Nitrogen content of 5th main shoot leaf increased significantly ($P<0.05$) with the nitrogen supply in all the sowing dates. However, the effect was much greater for the June sowing (Table 3.9). For March and September nitrogen content were higher than the April and June sowings.

3.3.4.4 Main shoot total dry weight

The results (Figure 3.6a) revealed that, total main shoot dry weight increased upto 160 ppm nitrogen for sowings in March, June and September. At the highest level of nitrogen supply main shoot dry weight was reduced for the March sowing but not for the June and September sowings. Nitrogen supply had no significant effect on main shoot dry weight for the April

Table 3.9. The effects of sowing date and nitrogen supply on the nitrogen content (mg leaf^{-1}) of leaf 5.

Sowing date		Nitrogen supply (ppm) 40	80	160	320	[1]HSD (P=0.05)
1	March	0.98	1.64	2.60	3.68	
28	April	0.69	1.13	1.78	2.34	0.42
1	June	0.25	0.44	0.96	2.41	
15	September	1.02	1.64	2.87	3.37	
[2]HSD (P=0.05)			0.46			

1 = HSD to compare means within the same sowing date

2 = HSD to compare means within same nitrogen level

sowing.

3.3.4.5 Tiller number and dry weight

Data on tiller dry weight and number per plant are presented in Figures 3.6a & 3.6b. It is evident from the data that tiller dry weight and number were markedly increased with the increase in nitrogen supply. The increase being greater for the March and September sowings than the April and June sowings.

3.3.4.6 Plant dry weight

Total dry weight of above ground parts of the plant are shown in Figure 3.6a. The response of total dry weight per plant to different sowing dates and nitrogen supply was similar to that of the individual plant components. It is evident from the results that, with the exception of the April sowing, there was a significant increase in total dry weight, when nitrogen supply was increased. For the April sowing nitrogen supply had no significant effect on total dry weight per plant. For the June and September sowings total plant dry weight increased upto the largest amount of nitrogen tested whereas for the March sowing it did not increase above 160 ppm N.

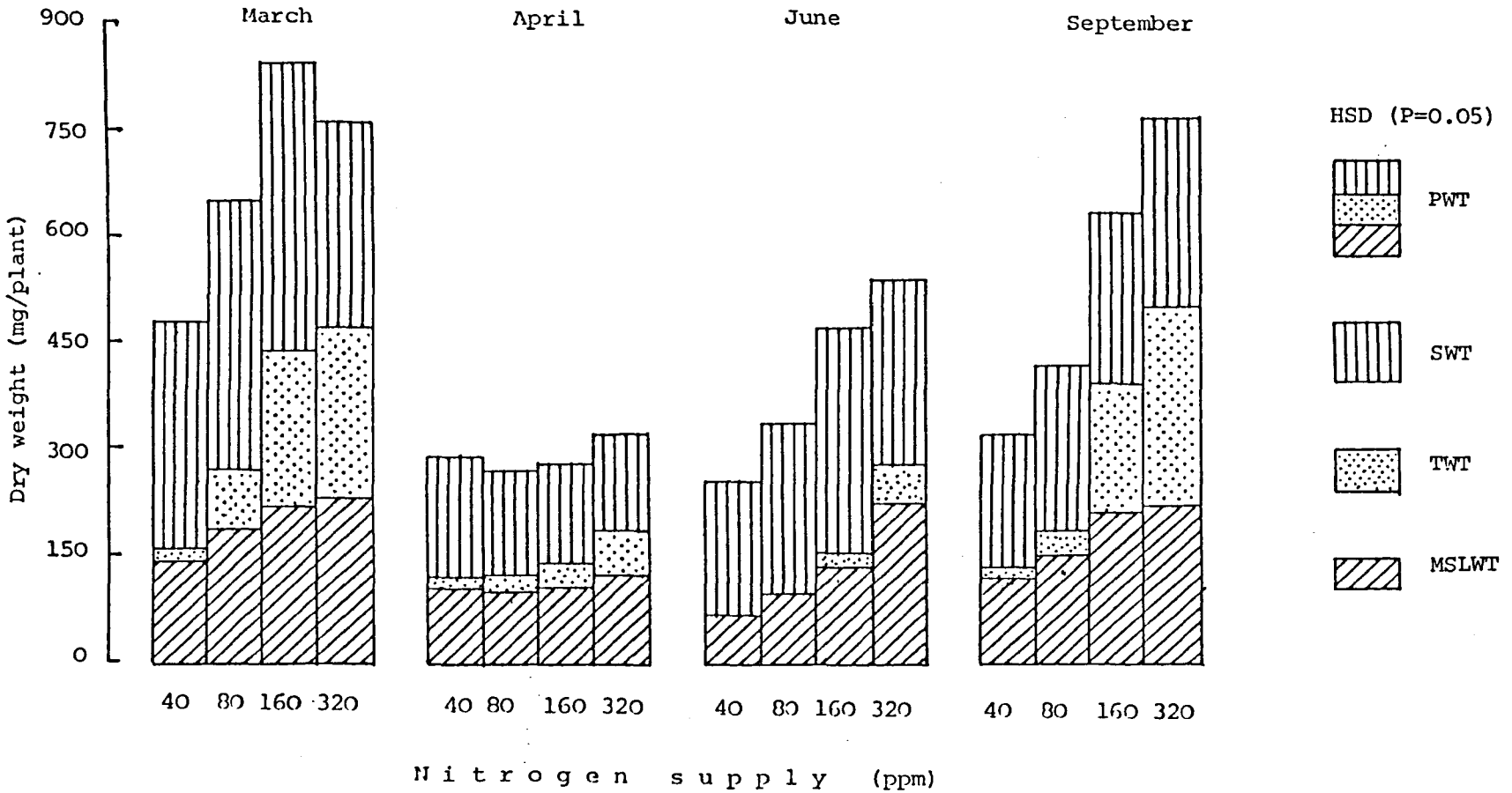


Figure 3.6a The effects of nitrogen supply and sowing date on dry weight of main shoot leaves (MSLWT), dry weight of tillers (TWT), dry weight of pseudostem (SWT) and dry weight of whole plant (PWT). HSD (P=0.05) are to make all possible comparisons for each plant component.

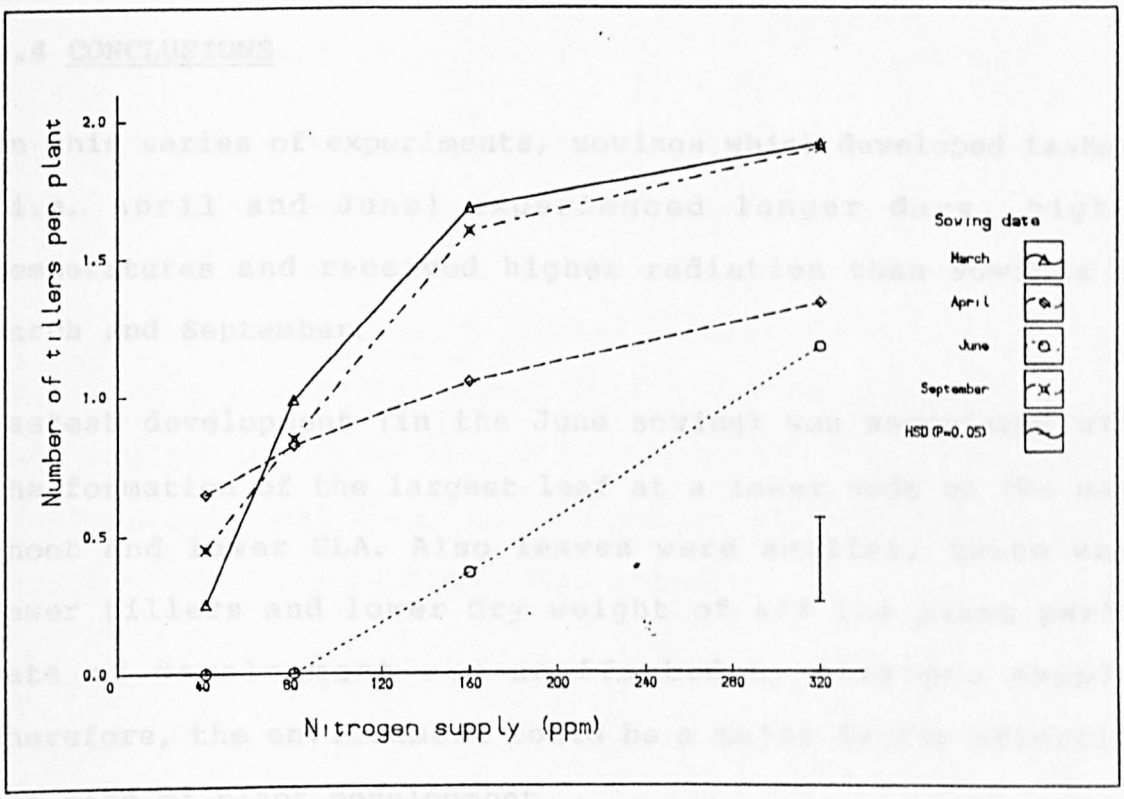


Figure 3.6b The effects of nitrogen supply and sowing date on number of tillers per plant. Vertical bar represent the value of HSD (P=0.05) to make all possible comparisons.

3.4 CONCLUSIONS

In this series of experiments, sowings which developed fastest (i.e. April and June) experienced longer days, higher temperatures and received higher radiation than sowings in March and September.

Fastest development (in the June sowing) was associated with the formation of the largest leaf at a lower node on the main shoot and lower SLA. Also leaves were smaller, there were fewer tillers and lower dry weight of all the plant parts. Rate of development was unaffected by nitrogen supply. Therefore, the environment could be a major factor affecting the rate of plant development.

For the September and March sowings, despite lower temperature, shorter days and lower radiation receipt, the area of leaf 5 was greater due to higher LER and longer LED. This effect was accompanied by a marked increase in SLA, which suggests that the crop could be compensating for lower radiation interception by producing bigger and thinner leaves, so that less dry matter was required to produce unit area of leaf.

Increased nitrogen supply resulted in greater leaf area and leaf and plant dry weight. However the nitrogen effect varied according to sowing date and leaf position. Increasing nitrogen supply increased lamina area due to faster LER. There was only a small effect of nitrogen on LED, which suggests that LER is mainly controlled by nitrogen and environment and

LED by environment only.

Nitrogen had no effect on first 2 leaves, growth of these leaves possibly being dependent on seed reserves. There was evidence of internal plant competition for nitrogen affecting later leaves. In most sowings leaf 5 was biggest at all levels of nitrogen except N0, where leaf 4 was the largest. In the June sowing, which developed fastest, leaf 2 was the largest at N0 whereas leaf 4 was the largest at N4. This could also be due to differences in final leaf number.

The March and September sowings responded to nitrogen upto 160 ppm and the April and June sowings up to 320 ppm, although in April and June plants were small. This suggests that crops which were developing fast had higher nitrogen demand than crops developing more slowly.

CHAPTER 4

EXPERIMENT 2.

Apical development and leaf growth in relation to nitrogen supply and environments

4.1 INTRODUCTION

The results of the previous experiment (Chapter 3) showed a significant effect of nitrogen on the growth and development of leaf 5 of the main shoot and other plant components. The response of main shoot leaves to nitrogen supply varied with their position on the main shoot and with sowing date. Leaf size and dry weight of the first five leaves generally increased with leaf position. However, this trend of increase in leaf size and weight was modified by sowing date. This change in response could have been associated with effects of sowing date on apical development, which is thought to be under photoperiodic control (Allison and Daynard, 1976). Therefore in this experiment, apical development and leaf growth were studied in contrasting photoperiods and varied nitrogen supply to investigate the relationships between apical development and leaf growth. Sowing dates of April, June and September were intentionally chosen, because of the nature of the changes in the environmental variables during these periods, in order to investigate contrasting environments which crops might experience in the field. To find out whether the diffirences in the size of main shoot leaves are due to differences in the rate or duration of leaf extension, leaf extension growth of the first 6 leaves on the main shoot was recorded.

In the first experiment plants were grown in a nutrient free medium (perlite), so that there was good control over nutrient supply. The response of plant growth to nitrogen supply

observed under these conditions could be different to that observed under field conditions. Therefore, in this experiment plants were grown in soil and sand compost, a medium more similar to field conditions.

Plants in the first experiment were harvested when leaf 5 had attained its maximum length, but in this experiment plants were destructively harvested at three growth stages (leaf 5 appearance, leaf 7 appearance and awn emergence) to provide data on the maximum size and weight of all the main shoot leaves and to follow the rate of dry matter production by the above ground plant material over a period of time.

4.2 MATERIALS AND METHODS

4.2.1 Cultivation of plants and experimental treatments tested

4.2.1.1 Plant material

To avoid genotypic differences the variety of spring barley (cv. Claret) grown in the previous experiment was used in this experiment.

4.2.1.2 Growing medium

The experiment was carried out at the University College of North Wales, College Farm, Aber, Gwynedd. Top soil was brought in from a field at College farm and sieved to remove stones. The field had previously grown spring barley and a short term intensively managed ryegrass ley used for silage and grazing. Sieved soil was then throughly mixed with sand to make compost

in a 2:1 (soil:sand) ratio. The compost was then steam sterilized to kill weed seeds before putting in the pots. Analysis of the compost before sterilization showed a substantial amounts of nutrients in it.

Concentration of some nutrients in the compost used in experiment 2

Total N	=	0.4 %
NO_3 - N	=	4 ppm
P	=	3.8 ppm
K	=	83 ppm
pH	=	6.1

The pH of compost was adjusted to pH 7 by adding Ca CO_3 into the compost following the procedure described by M.A.F.F. (1981).

4.2.1.3 Sowing procedure

Plastic containers similar to those used in experiment 1 were used in this experiment. They were filled with the compost after putting about 25 mm layer of perlite in the bottom to avoid possible water logging and to improve drainage. Seeds were sown in the same procedure as in experiment 1 (section 3.2.1) and seedlings were thinned to 16 plants per box (about 300 plants m^{-2}).

4.2.1.4 Details of treatments

There were four nitrogen treatments and three sowing dates.

Nitrogen (as a Sodium nitrate, 16.47% N) was applied at a rate of 0 Kg N ha^{-1}, 25 Kg N ha^{-1}, 50 Kg N ha^{-1} and 100 Kg N ha^{-1}. Nitrogen was applied in one application after crop emergence. Phosphorus and potasium were applied at the same time at a rate of 75 Kg ha^{-1}.

The sowing dates were :

Sowing date 1 = 14 April 1982,

Sowing date 2 = 7 June 1982,

Sowing date 3 = 8 September 1982.

All the three experiments were conducted in an unheated glass house at College Farm, Aber without any supplementary lighting. Plants were watered as and when required to replace evapotranspiration losses and to avoid any possible water stress. The experiments were carried out in a randomized block design with 6 blocks. Each of the treatments was randomly allocated to three pots within each block. One of these pots was harvested at each of the three growth stages (i.e. at leaf 5 appearance, at leaf 7 appearance and at awn emergence).

These harvests were carried out to provide data on the maximum size and weight of all the main shoot leaves and to monitor plant growth rate, tiller production and nitrogen uptake by above ground plant tissue. Root dry weight and nitrogen % were determined but the results were very variable, probably because of problems during root extraction and washing and hence these results are not presented.

4.2.2 Apical development

For each sowing date and nitrogen amount four extra pots were sown to provide plants for apical dissection measurements. Measurements were carried out twice weekly from emergence until when the apex started to die back. On each occasion four plants were sampled from each treatment and the three modal plants were dissected under a stereomicroscope (x40).

Dissection always followed the same procedure. First visible leaf stage was noted and the number of emerged tillers recorded. Visible leaf stage was the number of leaves unfolded plus the number of leaves appearing on main shoot. For example visible leaf stage would be 3+2 for a plant with the first 3 leaves fully expanded and the next 2 appeared but unfolded. A leaf was considered as fully expanded when the ligule and auricle of the leaf was fully developed. The main shoot was identified and tillers were counted. A tiller was defined as emerged when its prophyll extended beyond the ligule of the subtending leaf. Mature leaves were then removed one by one until a leaf of about 30 mm was reached. The plant was then transfered to the dissecting microscope and a needle was then inserted under the leaf margins to break off the young leaves and to expose the shoot apex. All the leaves and primordia present on the main shoot apex were counted; this gave the total number of primordia initiated by the apex. A primordium was considered as present when it bulged beyond an imaginary line extending along the smooth flank of the apical dome

(Kirby, 1977). The apical dome is defined as the part of the apex lying above the most recently initiated primordium. Because there was no visible difference between leaf and spikelet primordia at the time of their initiation, the number of primordia were recorded as the total primordia at the apex. Spikelet development was first apparent when double ridges began to form, by which time several primordia had accumulated at the apex. This event is often refered to as 'floral initiation'. Various stages of apical development are shown in Plates 1, 2 and 3.

For each amount of nitrogen and sowing date, number of primordia was plotted against Julian time (days after sowing), and thermal time (accumulated mean air temperature above a base temperature of $0^{o}C$). An examination of the data showed that during the phase of rapid increase in number of primordia a linear relationship between number of primordia and time could be identified. Hence, linear regression models were fitted to the data for the number of primordia including those values which were greater than the final number of leaves (to exclude leaves) and less than 90% of the maximum number of primordia. These regressions were always significant ($p<0.001$). The mean rate of primordium initiation (R_p) was determined as the slope of the regression and the apparent duration of primordium initiation (D_p) was calculated by dividing the final number of primordia by the mean rate;

$$D_p = \frac{\text{Final number of primordia}}{R_p}$$

EXPLANATION OF SCANNING ELECTRON MICROGRAPHS OF MAIN SHOOT APEX

Plate 1.

(a) The apex, shown in profile view (X250), is classified as 'late vegetative apex'. It consists of meristematic dome and leaf primordia. Arrows indicate the leaf primordia.

(b) The apex, shown in profile view (X100), is classified as 'double ridge stage'. The apex has an elongated cylindrical shape. The stage is so named because a leaf primordium ridge and a spikelet primodium ridge together form a double stucture. In the apex illustrated the primodia at the base of the shoot apex are clearly leaf like; and will form leaves. The upper primordia will develop into spikelets.

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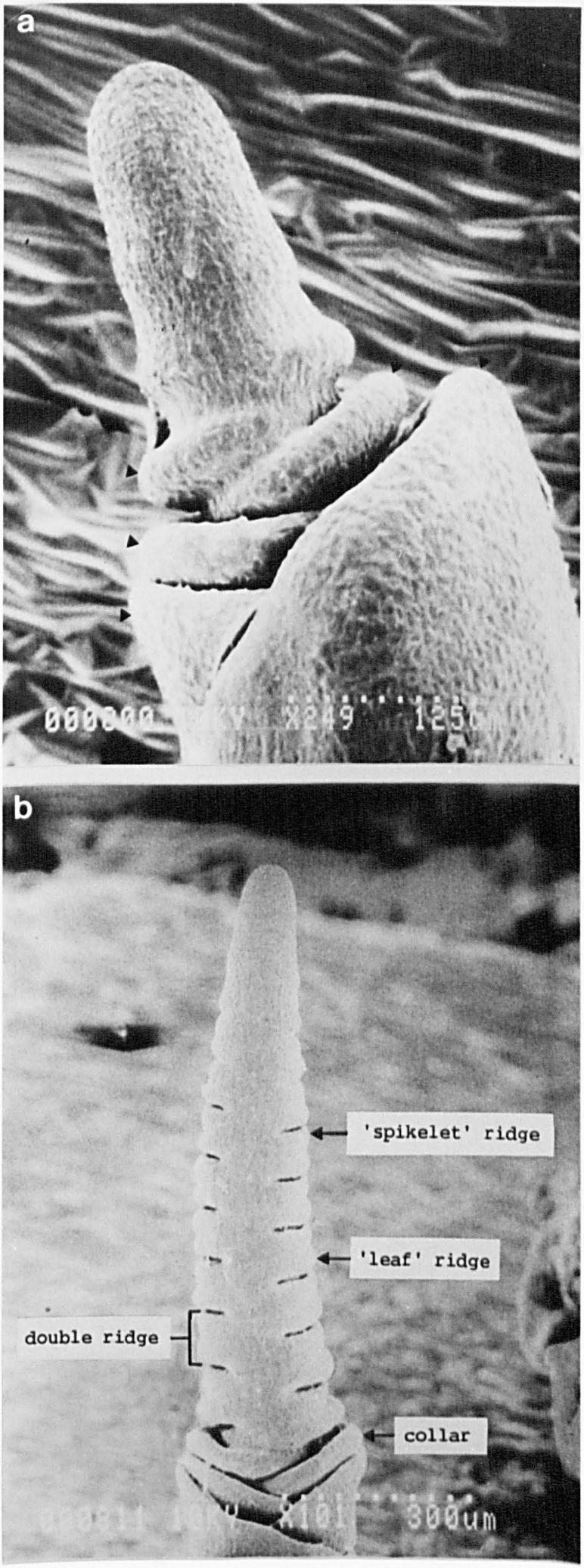
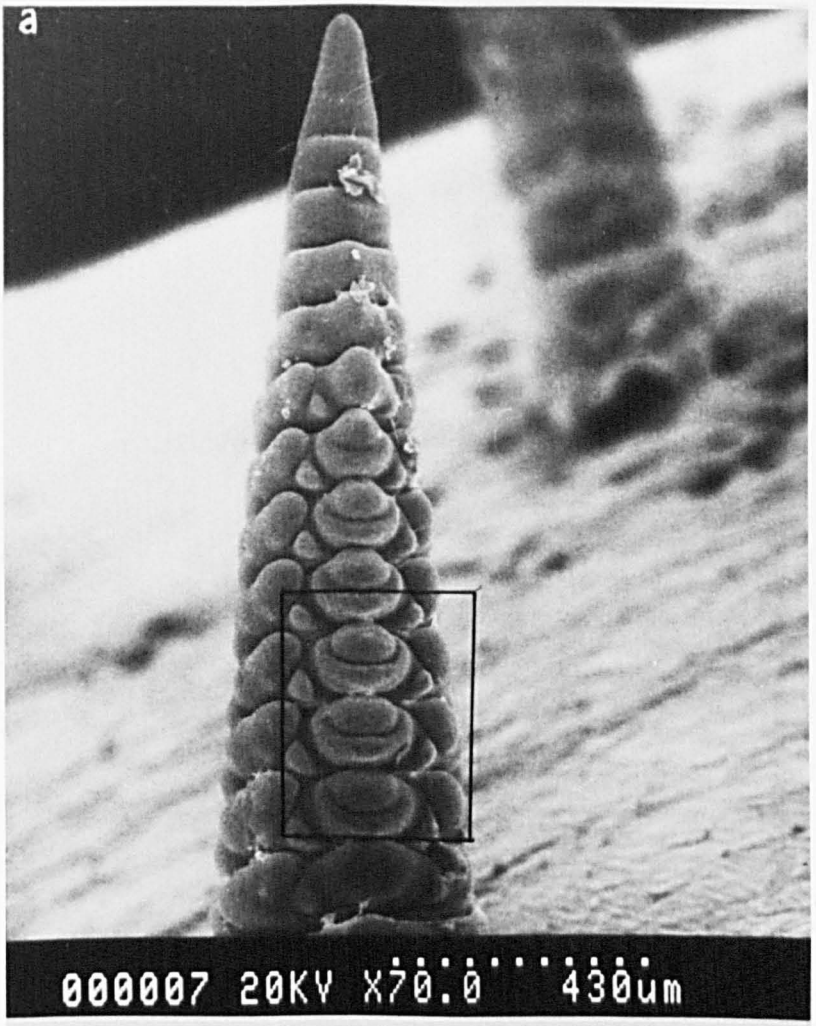

a
b
'spikelet' ridge
'leaf' ridge
double ridge
collar
300um

Plate 2.

(a) The apex, shown in face view (X70), is classified as 'lemma primordium stage'. In the mid-part of the apex, two ranks of lateral spikelets with the median spikelets are well developed. At the tip of the apex, the primordia are younger and less well developed and the dome is still meristematic.

(b) In the marked area on plate 2 (a) (X300). 'Floret meristem' of the median spikelet is the most prominent structure (1); lemma is seen as a crescent-shaped structure, which extends around behind the floret meristem (2); the glumes are now easily distinguished and are situated on the lower right and left flanks of the lemma primordium (3); the lateral spikelet primordia are also clearly differentiated (4).

contd...


a
000007 20KV X70.0 430um

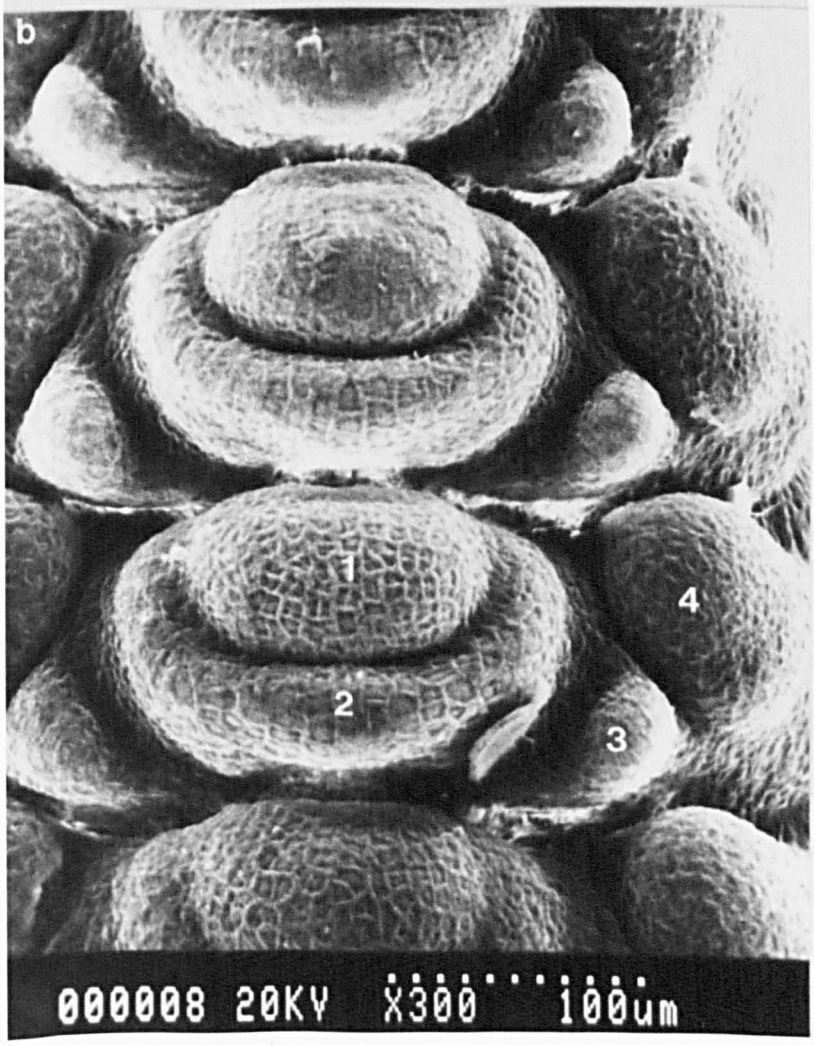
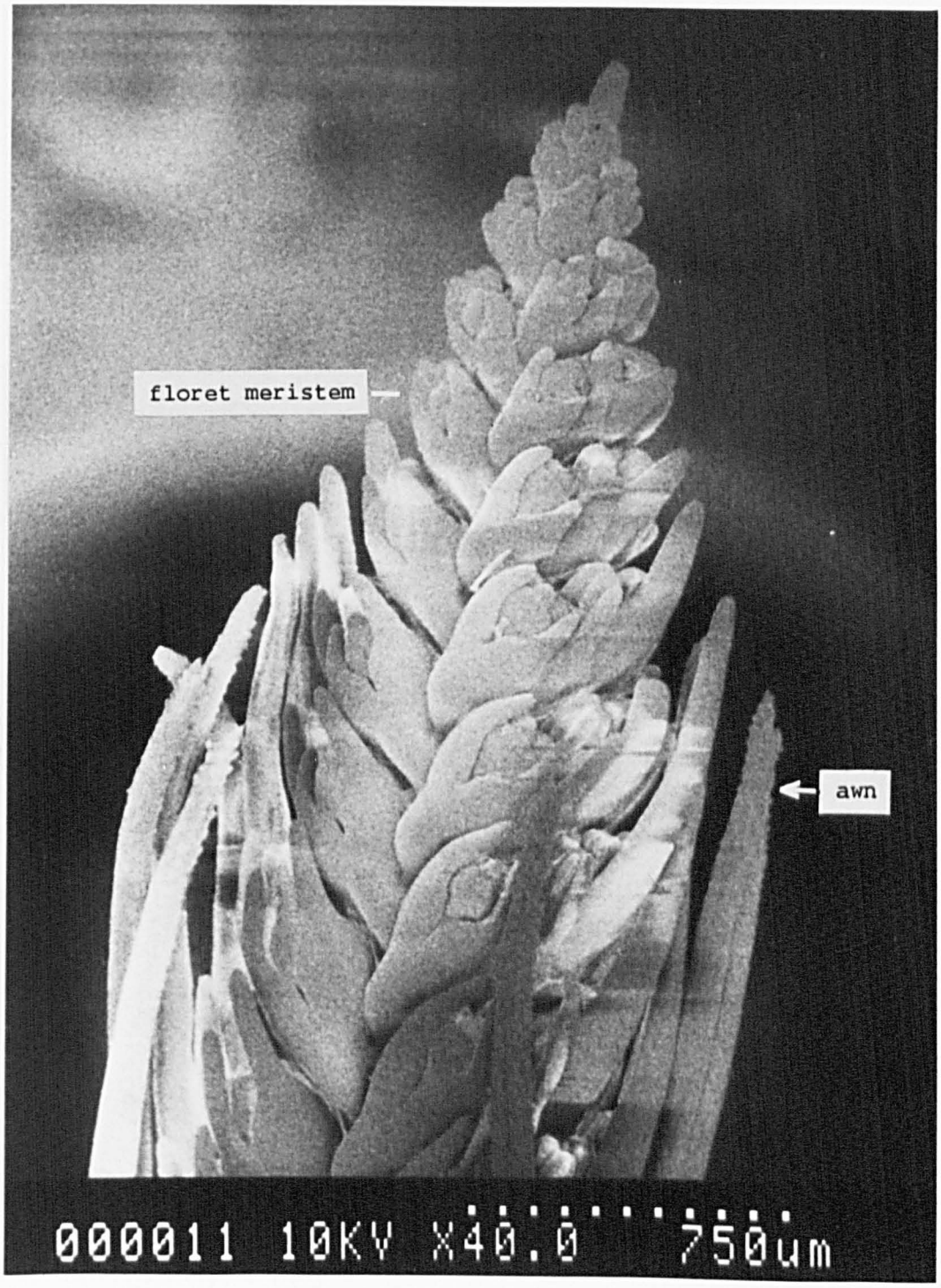

b
1
2
3
4
000008 20KV X300 100um

Plate 3.

The apex, shown in profile view (X40), is classified as 'awn primordium stage'. The awn primordia, which grow from the tip of the lemma, and curve over the floret meristem within the median spikelet are well developed. At the tip of the 'ear' the meristematic dome has ceased activity and is relatively small. The foleret meristem at the tip are less well developed and the last formed ones may not develop any further. In two-row barley and as is shown in this picture, the lateral spikelets are seen in embryo form. The necessary floral structues are formed but they do not develop fully and so these spikelets are sterile.


floret meristem
awn
000011 10KV X40.0 750um

The number of leaves appeared on the main shoot were also plotted against Julian time and thermal time. This revealed a significant linear relationship between number of leaves appeared and Julian and thermal time. Therefore linear regression analyses were carried out on the number of leaves appeared against time in days after sowing and accumulated day degrees. The slopes of these regression lines were taken as the mean rates of leaf appaearance (R_{LA}) and the apparent durations of leaf appearance (D_{LA}) were calculated by dividing final number of leaves on main shoot by mean rate of leaf appearance;

$$D_{LA} = \frac{\text{Final number of leaves}}{R_{LA}}$$

For both leaf appearance and primordia initiation rates, and durations were calculated in time and thermal time units.

4.2.3 Leaf extension measurements

Leaf extension measurements were made on the first six leaves of the main shoot. Measurements were started soon after emergence and were carried out daily on five randomly selected plants for each nitrogen amount, sowing date and block. The length of leaf was measured as the length between the tip of the leaf and soil surface. This technique was maintained for all the leaves studied and during all the three sowings. Extension measurements for a particular leaf continued until at least three successive observations showed no measureable

increase in length. Mean leaf length was calculated from the five plants sampled in each pot. A linear regression of leaf length against thermal time (above base temperature of $0^{o}C$) was carried out as described in Experiment 1 (section 3.2.3) to determine the mean rate of leaf extension (LER) for each leaf in each pot.

Some problems were encountered with the final leaf length data. Final leaf length was measured by two methods ;

1. Growth analysis :- During growth analysis the length of the lamina and sheath of each fully expanded leaf was measured. The total of these two components provided data on actual leaf length.

2. Linear measurements :- The length of the leaf was measured from soil level to the tip of leaf.

There was a reasonable agreement between these two methods for the first 3 leaves. For later leaves linear measurements tended to over estimate true leaf length (Table 4.1) as they included some stem elongation. This error in technique was corrected in a later experiment (Chapter 5). For the purpose of calculating apparent leaf extension duration (LED) final true leaf lengths (measured during growth analyis) were divided by the calculated rate of leaf extension (from the linear measurements). For these leaves calculated LER are greater than expected and hence LED less than expected.

Table 4.2 Leaf length (mm) of first 6 leaves on main shoot as measured during growth analysis time (length of lamina+sheath) and linear measurements (apparent length from soil surface). Data are means of 4 nitrogen levels and 6 blocks

Sowing date	leaf position	Method of measurement	
		Growth analysis	Linear
April 82	L1	121	119
	L2	215	216
	L3	311	304
	L4	372	411
	L5	374	514
	L6	322	471
June 82	L1	123	120
	L2	242	248
	L3	370	389
	L4	439	487
	L5	445	587
	L6	429	581
September 82	L1	129	120
	L2	242	250
	L3	368	390
	L4	495	534
	L5	546	632
	L6	533	663

4.2.4 Plant growth analysis

Growth analysis of above ground material was carried out at three growth stages (leaf 5 appearance, leaf 7 appearance and awn emergence) to provide data for all main shoot leaves and other plant components. At each growth stage 10 randomly selected plants were harvested from each treatment and block using the extra pots established for this purpose. Plants were seperated into their components and the following parameters were recorded;

1. lamina and sheath length of fully expanded main shoot leaves,
2. lamina area and dry weight of fully expanded main shoot leaves,
3. specific lamina area of individual main shoot leaves,
4. nitrogen content of of first 6 main shoot leaves,
5. tiller number,
6. main shoot total dry weight,
7. tiller dry weight,
8. total plant dry weight,
9. tiller contribution to total plant dry weight,
10. nitrogen concentration in above ground plant tissue,
11. nitrogen uptake by above ground plant tissue,
12. relative growth rate,

Length of lamina and sheath of fully expanded main shoot leaves were measured with a rule. Area of each main shoot lamina and tiller laminae were measured using an electronic

planimeter (section 3.2.4). Mean relative growth rate (RGR) for each treatment and block was calculated by the method described by Harper (1980) ;

$$RGR = \frac{\log_e W2 - \log_e W1}{t2 - t1}$$

Where W2 is plant dry weight at time t2 and W1 is plant dry weight at time t1.

Above ground plant material was dried at 80°C for 24 hours and was milled for nitrogen estimation. Kjeldahl procedure was followed to estimate nitrogen in the plant tissue (A.O.A.C., 1942). Nitrogen content for leaves and whole plant were calculated by the following formula ;

$$\text{Nitrogen content} = \frac{\text{Dry weight (mg)} * \text{nitrogen \%}}{100} \text{ mg N}$$

Data on other parameters studied were collected by the procedures described in section 3.2.4.

4.2.5 Meteorological observations

During all the sowings maximum and minimum air temperature in the glass house were recorded daily at 0900 h GMT. Mean air temperature was calculated using the method described in section 3.2.2. Data on photoperiod and solar radiation were collected by the method described in section 3.2.2.

4.2.6 Pests and disease control

Pests and diseases were not a serious problem during the course of experiment. Aphids and powdery mildew were the problems which occured, but their incidence did not vary systematically with sowing date. The plants were sprayed with appropriate chemicals as and when was necessary.

4.3 RESULTS

4.3.1 Environmental conditions during the course of the experiment

4.3.1.1 Temperature

Average weekly air temperature for each sowing are presented in Figure 4.2. During the April sowing mean air temperature fell from 18°C to 14°C by the third week after sowing. Thereafter it gradually increased to 24°C by the end of the experiment. During the June sowing there was little variation in mean temperature and it remained within the range 20°C - 23°C. For the September sowing the temperature was initially quite high (21°C) but then it gradually fell to 11°C by the end of the experiment.

4.3.1.2 Photoperiod

Mean weekly photoperiods for each of the sowings are shown in Figure 4.2. The data show a typical seasonal trend in photoperiod. During the April sowing photoperiod gradually increased from 15 h to 18 h. During the June sowing

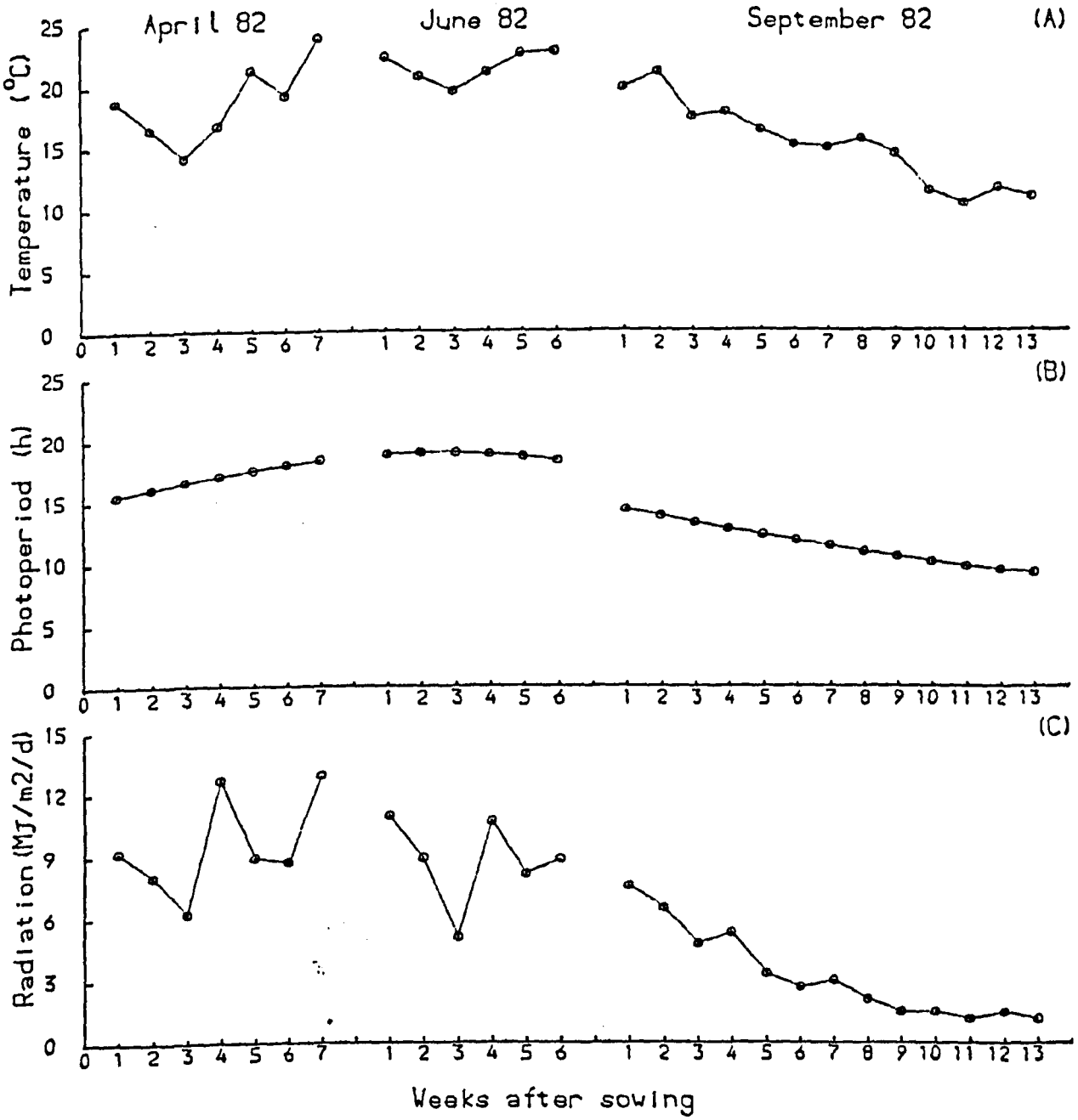


Figure 4.1 Showing weekly mean air temperature (A), photoperiod (B) and solar radiation (C) experienced by the plants during the course of experiment 2.

photoperiod was almost constant at 18 h. For the September sowing there was a marked decrease in photoperiod from 18 h at the begning of the experiment to 9 h by the end of the experiment.

4.3.1.3 Radiation

Mean weekly solar radiation received by the plants during the course of all the sowings is shown in Figure 4.2. For the April and June sowings solar radiation varied between 6 MJ $m^{-2}d^{-1}$ and 12 MJ $m^{-2}d^{-1}$. For the September sowing solar radiation decreased from 7.5 MJ $m^{-2}d^{-1}$ at the begining of the experiment to less than 2 MJ $m^{-2}d^{-1}$ by the end of the experiment. The April and June sowings received similar amount of radiation approximately twice that received by the September sowing due to brighter and longer days.

4.3.1.4 Crop development

Effect of delaying sowing on crop development is shown in Table 4.2. The time taken to reach comparable developmental stages was always least for the June sowing and longest for the September sowing. For the early stages of development there was little difference in time taken between the April and September sowings. However there was a marked diffrence between these sowings in the length of the phase when leaf 5 ceased extension growth to awn emergence, which was 6 days in the April sowing and 41 days in the September sowing. This is attributed to the shorter days, lower temperatures and less

radiation receipt experienced by the September sowing and the fact that the September sowing had one more leaf than the April and June sowings.

Table4.2 The effect of sowing date on the crop development in experiment 2

	Sowing date					
	April		June		September	
	DAS	At	DAS	At	DAS	At
Growth stages						
Germination	5	94.50	4	94.37	5	95.50
Double ridge	15	262.37	13	283.37	17	337.25
When leaf 3 ceased extension	28	463.12	23	483.49	30	564.25
When leaf 5 ceased extension	40	707.37	32	677.74	45	749.75
Awn emergence	46	840.49	39	833.49	86	1328.00
Mean air temperature (^{o}C)	18.27		21.37		15.44	
Mean daylength (h)	16.93		18.78		11.54	
Mean radiation ($MJ\ m^{-2}d^{-2}$)	9.30		8.37		3.23	

DAS = Days after sowing

At = Thermal time (^{o}Cd)

4.3.2 Statistical analysis

It was not possible to use ANOVA procedure to determine the effects of nitrogen and sowing date on apical development as the plants used for the apical dissection were taken from the extra pots established outside the main experiment. Instead the data for the rate of primirdia initiation and rate of leaf appearance were compared by testing the homogeneity of regression coefficients using the method described by Zar (1984). Apparent durations of leaf appearance and primordia initiation were derived from final numbers of leaves and primordia, and rate of leaf appearance and primordia initiation (section 4.2.2), and the data presented are mean values of durations without statistical comparison.

Results for rate and apparent duration of leaf extension, final leaf length, maximum lamina area, dry weight and specific lamina area of individual main shoot leaves were analysed as a split-split plot design using the method adopted in Experiment 1 (section 2.3.2). Sowing dates were on main plots, nitrogen treatments on sub-plots and leaf position on sub-sub plots

Plant growth analysis was carried out at different growth stages to examine the rate of change from one time period to another and to see effect of treatments on the growth pattern of the plants. Therefore, it was important to determine the interaction effect between treatments and stages of observation. However that cannot be done if the analysis of variance is obtained separately for each stage of observation.

Hence, data from all stages of observation were combined to obtain a single analysis of variance. The analysis of variance was accomplished by considering time or stage of observation as an additional factor in the experiment and treating it as if it were a sub-sub plot or the smallest experimental unit. Thus, the format of the pooled analysis of variance for growth analysis measurements over time for this experiment is similar to that for standard split-split plot design with sowing date on main plots, nitrogen level on sub-plots and time of harvest (growth stage) on sub-sub plots. Where the interactions between treatment and harvest were significant, the comparisons were made only between treatments within the same harvest.

A summary of the significance level of the main effects and interactions is presented in Table 4.3. Where significant differences between the means occurred ($p<0.05$) Tukey's test was used to determine the significance of the difference between individual pairs of the means (section 2.3.2).

4.3.3 Apical development

A significant effect of sowing date on primordia initiation and leaf appearance was observed. The effect of nitrogen was very small and not statistically significant ($p>0.05$). The effects of sowing date on primordia initiation and leaf appearance are therefore presented as the means of the four nitrogen levels and three replicate plants in Tables 4.4 and 4.5 respectively. In both sets of data values of the linear

Table 4.3 Summary of the significance levels of the main effects of sowing date (SD), nitrogen amount (N), leaf position (LP), growth stage (H) and their interactions on plant growth parameters recorded during experiment 2

PARAMETERS	Main effects				Interactions						
	SD	N	LP	H	SD*N	SD*LP	SD*H	N*LP	N*H	SD*N*LP	SD*N*H
Leaf extension measurements											
Main shoot leaf extension rate (mm $^{o}Cd^{-1}$)	***	**	***	-	NS	***	-	***	-	*	-
Main shoot leaf extension duration (^{o}Cd)	***	NS	***	-	***	***	-	NS	-	*	-
Main shoot leaf length (mm leaf $^{-1}$)	***	*	***	-	**	***	-	***	-	***	-
Main shoot lamina area (cm^2 $leaf^{-1}$)	***	***	***	-	NS	***	-	***	-	***	-
Main shoot lamina dry weight (mg $leaf^{-1}$)	***	***	***	-	NS	***	-	***	-	***	-
Main shoot specific lamina area (mm^2 mg^{-1})	***	NS	***	-	NS	***	-	NS	-	***	-
Main shoot lamina:sheath ratio	***	***	***	-	NS	***	-	NS	-	NS	-
Main shoot leaf nitrogen content (mg $leaf^{-1}$)	***	***	***	-	*	***	-	NS	-	NS	-
Growth analysis measurements											
Main shoot lamina area (cm^2 $plant^{-1}$)	***	***	-	***	NS	-	***	-	***	-	NS
Main shoot lamina dry weight (mg $leaf^{-1}$)	***	***	-	***	*	-	***	-	***	-	***
Main shoot specific lamina area (mm^2 mg^{-1})	***	NS	-	***	NS	-	***	-	***	-	***
Main shoot total dry weight (mg $plant^{-1}$)	***	NS	-	***	NS	-	***	-	*	-	***
Tiller dry weight (mg $plant^{-1}$)	***	***	-	***	**	-	***	-	***	-	***
Total plant dry weight (mg $plant^{-1}$)	***	***	-	***	**	-	***	-	***	-	***
Tiller contribution to plant dry weight (%)	***	***	-	***	**	-	***	-	***	-	***
Tiller number / plant	***	***	-	***	NS	-	***	-	***	-	*
Nitrogen concentration in plant tissue (%)	***	***	-	***	NS	-	***	-	***	-	**
Nitrogen uptake by plant (mg $plant^{-1}$)	***	***	-	***	***	-	***	-	***	-	***
Relative growth rate (mg g^{-1} d^{-1})	***	***	-	***	***	-	***	-	NS	-	***

*** = Significant (P<0.001)
** = Significant (P<0.01)
* = Significant (P<0.05)
NS = Not significant (p>0.05)

correlation coefficient were significantly higher when thermal time was the independent variable.

4.3.3.1 Primordia initiation and Julian time

The rate of primordia initiation was fastest for the June sowing and slowest for the April sowing (Table 4.4). The difference between the April and September sowings was very small. Plants sown in September continued to initiate primordia for a considerably longer period of time than the other sowings and hence had a greater maximum number of primordia. Duration of primordia initiation was shortest for the June sowing but this sowing had the fastest rate of initiation so that the difference in maximum number of primordia between June and April sowings was very small.

4.3.3.2 Primordia initiation and thermal time

The effects of sowing date on rate of primordia initiation in thermal time units were not consistent with the effects on rate of primordia initiation in Julian time units. Rate was greatest for the April sowing and was similar to that for the June sowing. The durations of primordia initiation for the April and June sowings were also very similar and hence the maximum number of primordia were very similar. The September sowing had the slowest rate of primordia initiation but also the longest duration so that this sowing had about 34% more primordia than the other two sowings.

Table 4.4 Mean rate of primordia initiation (R_p), apparent duration of primordia initiation (D_p) and mean number of primordia in relation to Julian time (days after sowing) and thermal time (^oCd) for different sowing dates together with their appropriate correlation coefficient (r).

		Sowing date		
		April	June	September
Julian time	Rp (±SE)	1.425 (±0.105)	1.717 (±0.171)	1.520 (±0.056)
	Dp	22.49	17.95	29.29
	r	0.991	0.987	0.994
Thermal time	Rp (±SE)	0.093 (±0.005)	0.092 (±0.007)	0.083 (±0.002)
	Dp	334.62	333.91	516.2
	r	0.996	0.991	0.995
Maxixmum number of primordia		32.05	30.82	43.00

SE = Standard error of means

(Data are means of 3 replicate plants and 4 levels of nitrogen)

4.3.3.3 Leaf appearance and Julian time

The data presented in Table 4.5 show that rate of leaf appearance was fastest for the April sowing and slowest for the September sowing. The April and June sowings both had 7 leaves and rates and durations of leaf appearace for these sowings were very similar. The September sowing had a slower rate of leaf appearance but a longer duration and there were 8 leaves on the main shoot.

4.3.3.4 Leaf appearance and thermal time

The effect of sowing date on leaf appearance rate and duration in thermal time units was very similar to the effects when leaf appearance was measured in Julian time units (Table 4.5).

4.3.4 Leaf extension and leaf nitrogen content of first 6 main shoot leaves

Leaf length was measured from the soil surface, hence for leaves higher than leaf 4, this included some internode extension. For these leaves the leaf extension rates (LER) presented are therefore apparent LER because they include some stem extension. They are greater than the true LER. Final leaf length (FLL) was derived from the actual final length of lamina and sheath. This was used to calculate the apparent durations of leaf extension (LED) which are therefore less than expected for leaves 4, 5 and 6.

The statistical significance of the effects of sowing date,

Table 4.5 Mean rate of leaf appearance (R_1), apparent duration of leaf appearance (D_1) and final number of leaves on main shoot in relation to Julian time and thermal time for different sowing dates with their appropriate correlation coefficient (r).

	Sowing date		
	April	June	September
Julian time			
R_1 (leaves d^{-1}) (±SE)	0.173 (±0.003)	0.169 (±0.004)	0.105 (±0.003)
D_1 (days)	40.3	41.2	76.3
r	0.981	0.978	0.986
Thermal time			
R_1 (leaves $^oCd^{-1}$) (±SE)	0.0097 (±0.0002)	0.0089 (±0.0003)	0.0063 (±0.0001)
D_1 (^oCd)	723.1	783.9	1267.8
r	0.988	0.991	0.990
Final leaf number	7	7	8

SE = Standard error of means

(Data are means of 3 replicate plants and 4 levels of nitrogen)

nitrogen and leaf position on leaf extension and leaf nitrogen content (LN) are shown in Table 4.3. All the main effects, some first order interactions and the second order interactions (sowing date * nitrogen amount * leaf position) were statistically significant ($p<0.05$). Therefore the effects of sowing date and nitrogen on leaf growth depended upon leaf position on the main shoot. Under these circumstances a discussion of main effects is not strictly valid, but this was done here in order to aid clarity. Therefore the main effects and first order interactions, where significant, are presented. The data on main effects are presented in Table 4.6 to illustrate the general trends associated with these factors. First order interactions (sowing date * leaf position, nitrogen amount * leaf position and sowing date * nitrogen amount) for LER, LED and FLL are shown in Tables 4.7, 4.8 and 4.9 and for LN in Tables 4.10 and 4.11 respectively.

4.3.4.1 Main effects of sowing date

Leaf length consistently increased with the delayed sowing but there were no consistent effects on LER and LED. LER was greater for June and September sowings than April sowing. The differences in LED were smaller than the differences in LER.

4.3.4.2 Main effects of nitrogen application

Leaf extension rate and final leaf length increased as the amount of applied nitrogen increased, but there was no significant effect of nitrogen on leaf extension duration. LN

Table 4.6 Main effects of sowing date, nitrogen amount and leaf position on leaf extension rate (LER), leaf extension duration (LED), final leaf length (FLL) and leaf nitrogen content (LN) of main shoot leaves.

PARAMETERS	LER (mm $^{o}Cd^{-1}$)	LED (^{o}Cd)	FLL (mm)	LN (mgleaf^{-1})
[1]Sowing date				
April	1.642	171.03	286.21	1.61
June	2.003	164.89	341.69	1.95
September	1.914	192.51	385.61	2.35
HSD (P=0.05)	0.042	4.20	6.15	0.35
[2]Nitrogen amount (Kg N ha^{-1})				
0	1.818	176.40	323.36	1.82
25	1.848	175.26	335.76	1.89
50	1.865	176.81	340.45	2.00
100	1.881	176.12	342.79	2.16
HSD (P=0.05)	0.045	NS	8.73	0.10
[3]Leaf position				
L1	1.130	110.66	124.58	0.69
L2	1.531	153.58	233.39	1.19
L3	1.991	178.35	349.35	2.25
L4	2.257	193.56	435.73	2.50
L5	1.998	228.00	455.39	2.71
L6	2.221	192.72	428.58	2.48
HSD (P=0.05)	0.045	4.79	6.77	0.19

NS = Not significant (P>0.05)
1 = Data are means of 4 nitrogen amounts and 6 leaf positions
2 = Data are means of 3 sowing dates and 6 leaf positions
3 = Data are means of 3 sowing dates and 4 nitrogen amounts

were greater in the September sowing and the difference between the April and June sowings was not significant.

4.3.4.3 Main effects of leaf position

Leaf extension rate, extension duration, final leaf length and leaf nitrogen content increased with leaf position up to leaf 4. Leaf 6 had a similar rate, duration and final leaf length to leaf 4. Final leaf length of leaf 5 was significantly greater than that of the other leaves due to a greater leaf extension duration. Leaf nitrogen content increased with the leaf position up to leaf 5 and the nitrogen content of leaf 6 were similar to leaf 4.

4.3.4.4 Sowing date and leaf position interaction

It is evident from the results shown in Table 4.7 that, leaf length increased with leaf position up to leaf 5 and leaf 6 was smaller than leaf 5. The differences between individual leaves varied with sowing date. The effect of sowing date on leaves above leaf 4 was greater than the effect on lower leaves. Leaf 4 and higher leaves were longest for the September sowing and shortest for the April sowing. These differences in final leaf length were associated with similar trends in LER and LED. Sowing date had no significant effect on leaf extension of leaf 1. For leaves 2 and 3 the June and September sowings had faster LER but a shorter LED so that their final length was reduced in comparison to the April sowing.

Table 4.7 The effects of sowing date and leaf position on leaf extension rate (LER), leaf extension duration (LED) and final leaf length (FLL) of main shoot leaves.

PARAMETERS	LER (mm $^{o}Cd^{-1}$)			LED(^{o}Cd)			FLL (mm)		
Sowing date	April	June	September	April	June	September	April	June	September
Leaf position									
L1	1.102	1.166	1.121	110.33	106.48	115.17	121.39	123.28	129.08
L2	1.308	1.619	1.665	165.49	149.91	145.35	215.87	242.23	242.08
L3	1.563	2.331	2.078	199.65	158.79	176.60	311.53	369.76	366.77
L4	2.184	2.368	2.219	170.97	186.14	223.57	372.48	439.39	495.31
L5	1.740	2.184	2.070	214.84	204.97	264.19	373.75	445.87	546.56
L6	1.954	2.347	2.331	164.91	183.07	230.18	322.25	429.64	533.85
(1)HSD (P=0.05)		0.069			7.31			10.42	
(2)HSD (P=0.05)		0.077			8.31			11.71	

(1) = HSD to compare means within same leaf position
(2) = HSD to compare means within same sowing date
(Data are means of 4 nitrogen amounts)

4.3.4.5 Nitrogen and leaf position interaction

The effect of nitrogen on the first four leaves was not statistically significant (Table 4.8). Nitrogen increased the length of leaf 5 and leaf 6 due to the effects on leaf extension rate. Nitrogen had no significant effect on leaf extension duration. Leaf nitrogen content of first 3 leaves were not statistically affected by the external nitrogen supply (Table 4.10). Leaf 4 was the first leaf to show some response to nitrogen at the highest amount of nitrogen applied.

4.3.4.6 Sowing date and nitrogen interaction

The effect of nitrogen on final leaf length varied with sowing date (Table 4.9). Nitrogen had no significant effect on leaf extension of the September and June sowings, but for the April sowing leaf length increased with nitrogen supply and this effect was brought about by small effect on leaf extension rate and duration. Leaf nitrogen content increased with the increase in nitrogen supply in all the sowings, but pattern of response varied with sowing date (Table 4.11).

4.3.4.7 Sowing date, nitrogen and leaf position interaction

The effects of sowing date, nitrogen and leaf position on final leaf length, leaf extension rate and leaf extension duration area shown in Figures 4.3, 4.4 and 4.5. The general

Table 4.8 The effects of nitrogen application and leaf position on leaf extension rate (LER) leaf extension duration (LED) and final leaf length (FFL) of main shoot leaves.

PARAMETERS	LER (mm oCd-1)				LED (oCd)				FLL (mm)			
Nitrogen amount (Kg N ha-1)	0	25	50	100	0	25	50	100	0	25	50	100
Leaf position												
L1	1.125	1.131	1.128	1.136	111.86	108.45	110.65	111.68	125.07	122.28	124.47	126.52
L2	1.539	1.545	1.513	1.525	154.07	151.22	156.18	152.88	236.64	232.19	233.62	231.12
L3	2.006	1.989	1.982	1.987	179.19	177.35	179.50	177.35	354.39	347.52	348.64	346.86
L4	2.213	2.265	2.251	2.298	197.03	192.11	194.91	190.18	436.21	434.75	436.08	435.87
L5	1.942	1.987	2.019	2.045	224.04	227.68	230.89	229.39	437.90	453.15	463.16	467.36
L6	2.084	2.170	2.295	2.294	192.19	194.76	188.72	195.22	403.94	424.67	436.72	448.99
(1)HSD (P=0.05)			0.085				8.76				13.92	
(2)HSD (P=0.05)			0.089				9.59				13.52	

(1) = HSD to compare maens within same leaf position

(2) = HSD to compare means within same nitrogen amount

(Data are means of 3 sowing dates)

Table 4.9 The effects of sowing date and nitrogen application on leaf extension rate (LER), leaf extension duration (LED) and final leaf length (FLL) of main shoot leaves.

PARAMETERS	LER (mm $^{o}Cd^{-1}$)			LED(^{o}Cd)			FLL (mm)		
Sowing date	April	June	September	April	June	September	April	June	September
Nitrogen amount (Kg N ha^{-1})									
0	1.o65	1.939	1.911	164.86	169.11	195.21	268.81	338.19	390.08
25	1.647	1.985	1.912	169.37	164.11	192.30	284.09	336.53	386.66
50	1.643	2.036	1.915	177.32	162.42	190.69	296.84	343.14	381.36
100	1.673	2.050	1.919	172.58	163.93	191.84	295.10	348.91	384.34
(1)HSD (P=0.05)		NS			6.69			13.21	
(2)HSD (P=0.05)		NS			6.89			15.12	

NS = Not significant (P>0.05)
(1) = HSD to compare means within same nitrogen amount.
(2) = HSD to compare means within same sowing date.

Table 4.10 The effects of nitrogen amount and leaf position on nitrogen content of main shoot leaves.

Leaf position	Nitrogen amount (Kg N ha^{-1})			
	0	25	50	100
L1	0.65	0.66	0.66	0.77
L2	1.15	1.15	1.20	1.22
L3	2.15	2.20	2.31	2.33
L4	2.32	2.39	2.50	2.80
L5	2.45	2.48	2.79	3.10
L6	2.22	2.44	2.55	2.71
(1) HSD (P=0.05)		0.39		
(2) HSD (P=0.05)		0.34		

(1) = HSD to compare means within the same level of nitrogen amounts
(2) = HSD to compare means within the same sowing date
(Data are means of 3 sowing dates)

Table 4.11 The effects of sowing date and nitrogen supply on leaf nitrogen content of main shoot leaves.

Nitrogen amount (Kg N ha^{-1})	Sowing date		
	April	June	September
0	1.56	1.79	2.12
25	1.44	1.83	2.39
50	1.58	2.05	2.37
100	1.86	2.11	2.50
(1) HSD (P=0.05)		0.18	
(2) HSD (P=0.05)		0.37	

(1) = HSD to compare means within same sowing date
(2) = HSD to compare means within same nitrogen amount
(Data are means of 6 leaf positions)

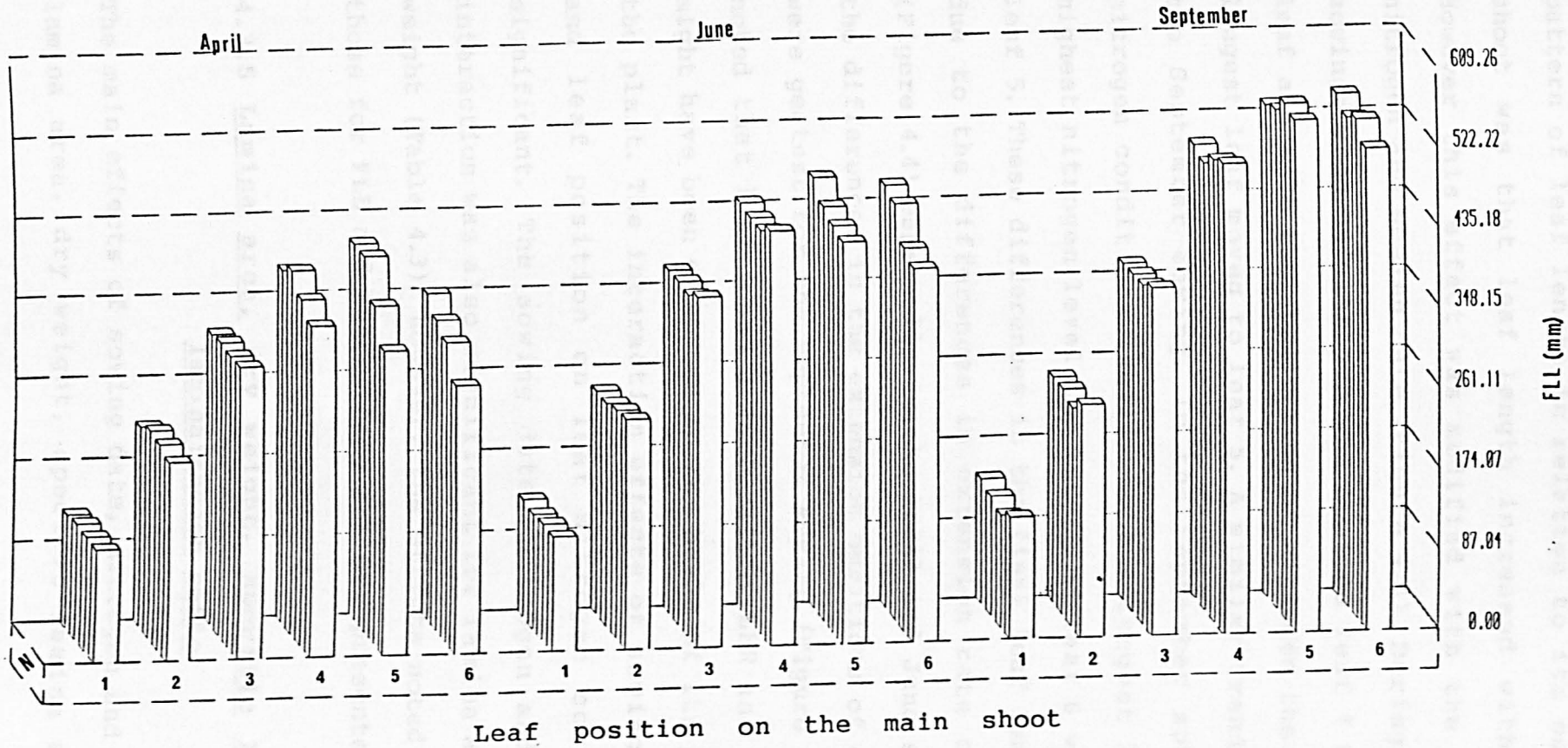


Figure 4.2 Effects of sowing date, nitrogen supply and leaf position on final leaf length (FLL) of first 6 main shoot leaves.

pattern of leaf length in relation to its position on main shoot was that leaf length increased with its position. However this effect was modified with the application of nitrogen and sowing date (Figure 4.3). During April and June sowings when no nitrogen was applied leaf 4 was the longest leaf and with the application of nitrogen the position of the longest leaf moved to leaf 5. A similar trend was evident in the September sowing. In the September sowing under low nitrogen conditions leaf 5 was the longest leaf and at the highest nitrogen level the length of leaf 6 was greater than leaf 5. These differences in the final leaf length were mainly due to the differences in extension rate of these leaves (Figure 4.4) especially in the April and June sowings. However the differences in the extension durations of different leaves were geatest for the September sowing (Figure 4.5) It was also noted that leaf 5 had a much slower LER and longer LED than might have been expected on the basis of its position within the plant. The interaction effects of sowing date, nitrogen and leaf position on leaf nitrogen content were not significant. The sowing date, nitrogen and leaf position interaction was also significant for lamina area, lamina dry weight (Table 4.3). However, the effects noted were similar to those for FLL and hence these are not presented here.

4.3.5 Lamina area, dry weight, specific lamina area and lamina:sheath ratio

The main effects of sowing date, nitrogen and leaf position on lamina area, dry weight, specific lamina area and lamina

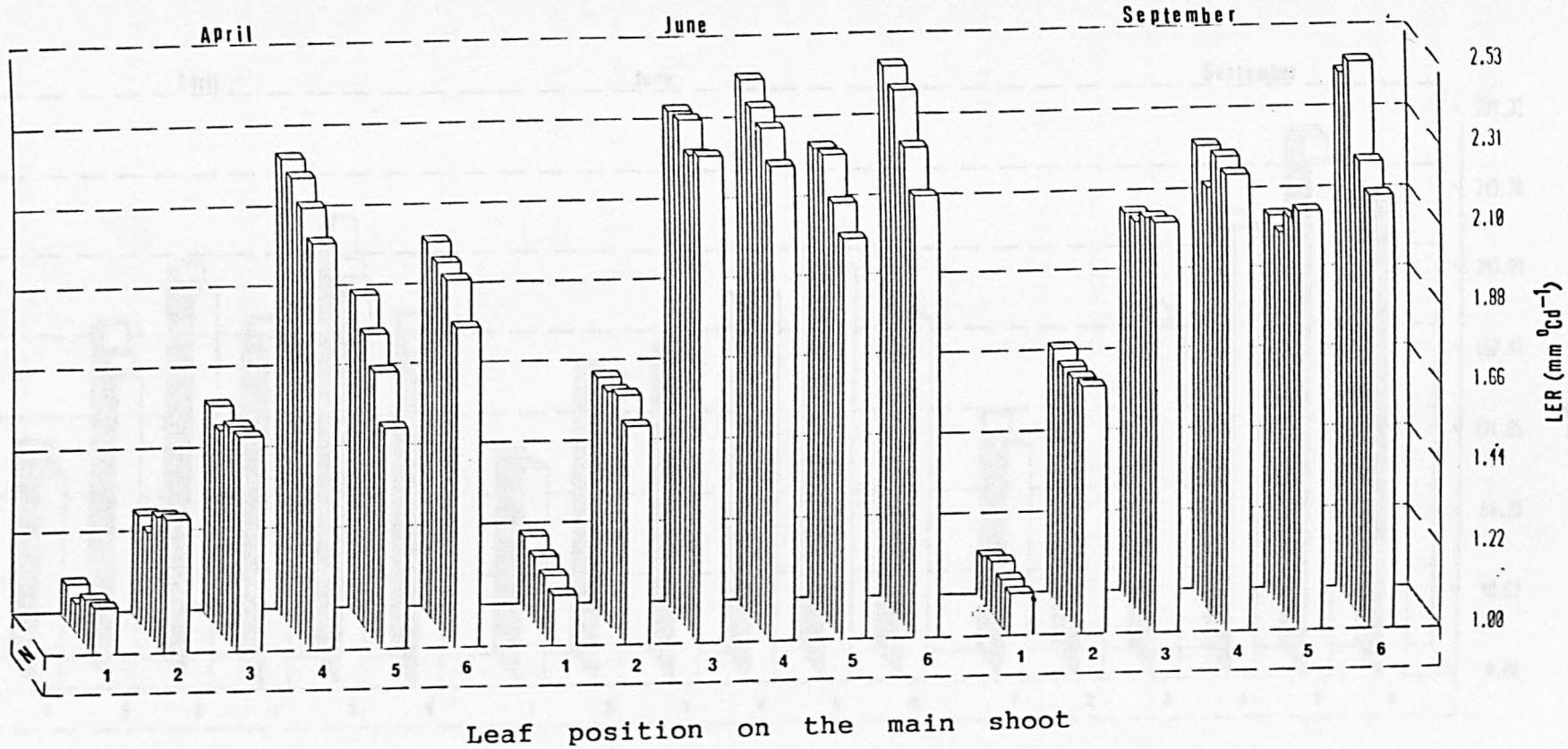


Figure 4.3 Effects of sowing date, nitrogen supply and leaf position on leaf extension rate (LER) of first 6 main shoot leaves.

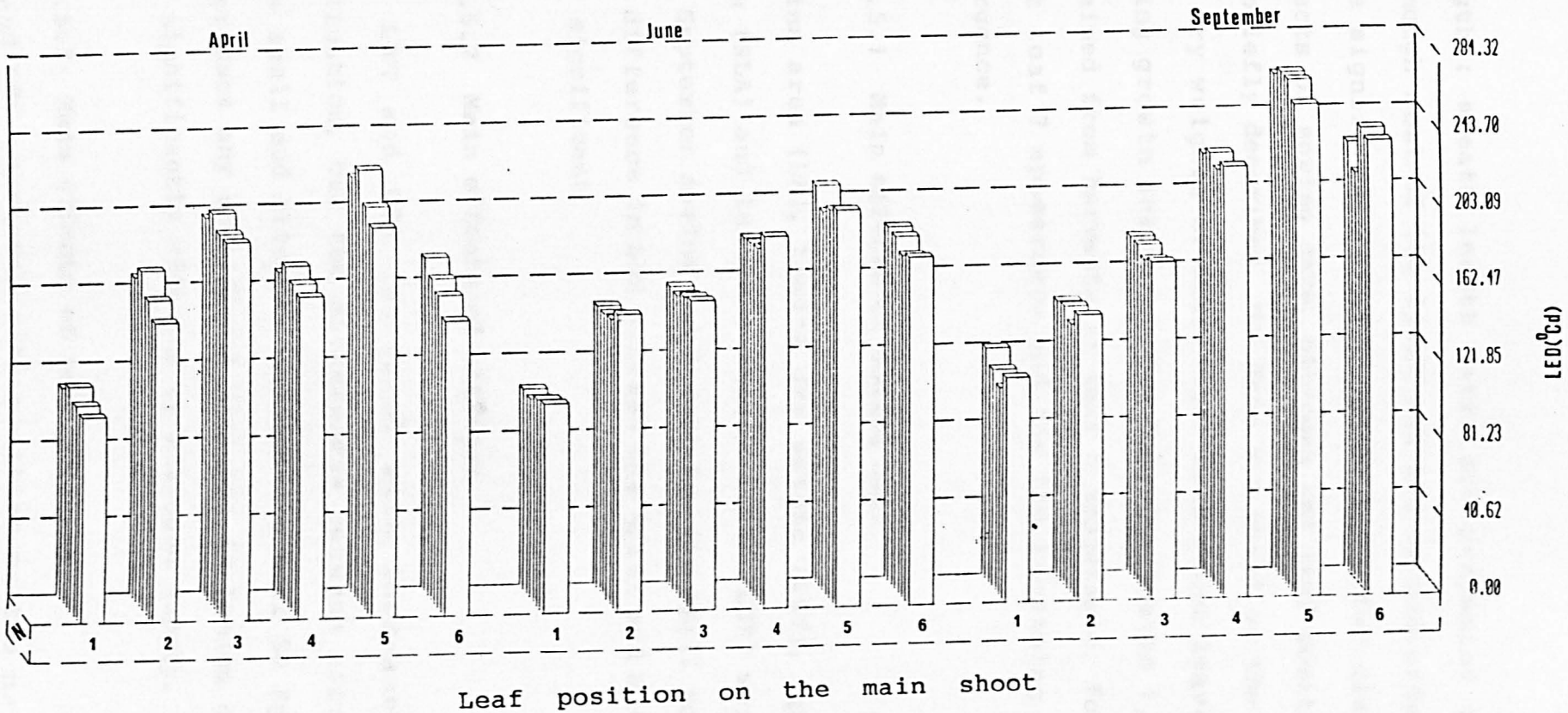


Figure 4.4 Effects of nitrogen supply, sowing date and leaf position on leaf extension duration (LED) of first 6 main shoot leaves.

length : sheath length ratio are presented in Table 4.12. Although most of the first and the second order interaction were significant ($p<0.05$) (Table 4.3), for clarity the main effects of sowing date, nitrogen and leaf position will first be briefly described. The data are based on the maximum sizes and dry weights of individual main shoot leaves as recorded during growth analysis. The data for leaves 1, 2 and 3 were obtained from harvests at leaf 5 appearance, for leaves 4 and 5 at leaf 7 appearance and for the remaining leaves at awn emergence.

4.3.5.1 Main effects of sowing date

Lamina area (LA), lamina dry weight (LWT), specific lamina area (SLA) and lamina : sheath ratio (LSR) were highest for the September sowing and lowest for the April sowing. However, the difference in LSR between the April and June sowings was not significant.

4.3.5.2 Main effects of nitrogen

LA, LWT and LSR increased with increase in nitrogen application, but the differences between nitrogen amounts were small and nitrogen applications over 50 Kg N ha^{-1} failed to produce any significant increase in lamina growth. SLA was not significantly affected by nitrogen supply.

4.3.5.3 Main effects of leaf position

LA and LWT increased with position on the main shoot up to

Table 4.12 Main effects of sowing date, nitrogen amount and leaf position on lamina area (LA), lamina dry weight (LWT), specific lamina area (SLA) and lamina length:sheath length ratio (LSR) of the individual main shoot leaves. Data are based on the maximum size and wieght of the fully expanded leaves.

PARAMETER	LA (cm^2)	LWT (mg)	SLA (mm^2mg^{-1})	LSR
[1]Sowing date				
April	9.98	39.35	23.68	1.97
June	12.79	44.34	27.19	2.00
September	19.98	60.35	33.70	2.47
HSD (P=0.05)	0.59	0.97	1.14	0.05
[2]Nitrogen amount (Kg N ha^{-1})				
0	13.39	44.73	28.16	2.09
25	13.87	47.20	27.97	2.09
50	14.57	49.14	28.32	2.19
100	15.16	50.98	28.29	2.22
HSD (P=0.05)	0.72	1.65	NS	0.08
[3]Leaf position				
L1	5.03	15.10	33.51	2.65
L2	9.21	24.77	37.34	2.74
L3	16.54	46.11	35.90	2.58
L4	20.92	73.34	28.89	2.72
L5	23.52	83.61	28.21	2.62
L6	22.96	86.26	25.79	2.30
L7	11.79	40.81	26.39	1.20
L8	4.02	14.10	9.49	0.37
HSD (P=0.05)	0.75	2.26	1.09	0.14

NS = Not significant (P=0.05)
1 = Data are means of 8 leaves and 4 nitrogen amounts
2 = Data are means of 8 leaves and 3 sowing dates
3 = Data are means of 4 nitrogen amounts and 3 sowing dates

leaf 6 and then decreased rapidly. The flag leaf was similar in size and weight to leaf 1. The difference in LA between leaf 5 and 6 was not significant, but LWT of leaf 6 was significantly greater than that of other leaves. SLA was greatest in leaf 2 and then it decreased with leaf position. The effect of leaf position on LSR was significant. Leaves 1-5 had very similar LSR which were greater than those of the upper leaves. The contribution of leaf lamina to leaf length decreased above leaf 5 and it was lowest for the flag leaf.

4.3.5.4 First order interactions

The sowing date and nitrogen interaction was generally not statistically significant ($P<0.05$). However, for most parameters the interaction between sowing date and leaf position and nitrogen and leaf position were significant ($P<0.01$). Hence the effects of sowing date and nitrogen depended on leaf position, whereas nitrogen and sowing date effects were independent.

4.3.5.4.1 Sowing date and leaf position interaction

LA in relation to its position on the main shoot changed during different sowings (Table 4.13). For the April and June sowings LA increased with leaf position up to leaf 5 and then decreased. In the September sowing leaf 6 was the largest leaf. For the June sowing the difference between leaf 5 and 6 was not significant.

Table 4.13 The effect of sowing date and leaf position on main shoot lamina area (cm^2 $leaf^{-1}$).

Leaf position	Sowing date		
	April	June	September
L1	5.11	4.89	5.10
L2	8.62	9.66	9.35
L3	14.18	17.47	17.96
L4	16.84	21.62	24.29
L5	19.12	22.58	28.86
L6	12.41	20.96	35.51
L7	3.59	5.15	26.65
L8	0.00	0.00	12.07
(1)HSD (P=0.05)		1.09	
(2)HSD (P=0.05)		1.29	

(1) = HSD to compare means within same leaf position
(2) = HSD to compare means within same sowing date
(Data are means of 4 nitrogen amounts)

The effect of sowing date on LWT was very similar to its effects on LA. Sowing date had little effect on the dry weight of leaves 1-5 but a large effect on leaf 6 and leaf 7 (Table 4.14). The effect of delaying sowing was to change the position of the largest leaf on the main shoot. For the April sowing leaf 5 had the largest dry weight, but for the June and September sowings it was the leaf 6 which had the greatest LWT.

No systematic trend in the response of SLA to sowing date and leaf position could be easily identified (Table 4.15). In general it appeared that plants sown in September had higher SLA'S for the leaves above leaf 3 than the other two sowings. SLA tended to be highest for leaf 2 and then declined with the increase in leaf position.

LSR decreased with leaf position on the main shoot and was lowest for the flag leaf in all the sowings (Table 4.16). There was a significant ($P<0.05$) effect of sowing date on a particular leaf but this effect was very eratic on the first 4 leaves. Leaves higher than leaf 4 showed a definite trend in response to sowing date. LSR for these leaves were significantly the highest for the September sowing and lowest for the April sowing.

4.3.5.4.2 Nitrogen and leaf position interaction

The interaction between nitrogen and leaf position for SLA and LSR was not significant ($P>0.05$) (Table 4.3). Therefore, only the interactions for LA and LWT are presented.

Table 4.14 The effects of sowing date and leaf position on main shoot lamina dry weight (mg leaf^{-1}).

Leaf position	Sowing date		
	April	June	September
L1	16.53	13.83	14.93
L2	25.65	23.77	24.88
L3	45.93	44.55	47.84
L4	76.22	76.13	67.67
L5	80.82	82.06	87.94
L6	55.01	91.90	111.87
L7	14.61	22.48	85.35
L8	0.00	0.00	42.30
(1)HSD (P=0.05)		2.96	
(2)HSD (P=0.05)		3.92	

(1) = HSD to compare means within same leaf position.
(2) = HSD to compare means within same sowing date.
(Data are means of 4 nitrogen amount)

Table 4.15 The effect of sowing date and leaf position on main shoot specific lamina area (mm^2 mg^{-1}).

Leaf position	Sowing date		
	April	June	September
L1	30.94	35.37	34.21
L2	33.79	40.63	37.59
L3	30.92	39.22	37.56
L4	22.20	28.47	36.01
L5	24.32	27.50	32.81
L6	22.62	22.96	31.79
L7	24.63	23.34	31.20
L8	0.00	0.00	28.46
(1)HSD (P=0.05)		1.72	
(2)HSD (P=0.05)		1.89	

(1) = HSD to compare means within same leaf position
(2) = HSD to compare means within same sowing date
(Data are means of 4 nitrogen amounts)

Table 4.16 The effects of sowing date and leaf position on main shoot lamina length:sheath length ratio.

Leaf position	Sowing date		
	April	June	September
L1	2.02	2.42	2.51
L2	2.81	2.56	2.83
L3	2.67	2.44	2.61
L4	2.58	2.99	2.59
L5	2.45	2.52	2.88
L6	1.65	2.32	2.92
L7	0.55	0.76	2.31
L8	0.00	0.00	1.10
(1)HSD (P=0.05)		0.17	
(2)HSD (P=0.05)		0.23	

(1) = HSD to compare means within same leaf position
(2) = HSD to compare means within same sowing date
(Data are means of 4 nitrogen amounts)

The effects of nitrogen amount and leaf position on LA and LWT are presented in Tables 4.17 and 4.18. There was no significant effect of nitrogen on the LA of the first 4 leaves. Leaf 5 was the first leaf to show some response to nitrogen. The effect of nitrogen on leaves 6 and 7 was very significant and the LA of individual leaves increased significantly with increase in nitrogen amount above 25 Kg N ha^{-1}.

The effect of leaf position on LA within each nitrogen amount was significant ($P<0.05$), but the position of the largest leaf changed with the change in nitrogen supply. As the amount of nitrogen applied increased from 0 to 100 Kg N ha^{-1}, the position of the largest leaf on the main shoot changed from L4 to L6.

The effect of nitrogen on LWT of individual main shoot leaves was very similar to that for LA (Table 4.18).

4.3.6 Plant size and dry weight at different growth stages

4.3.6.1 Sowing date and time of harvest interaction

The effect of sowing date on various plant growth parameters, recorded at different growth stages, are shown in Table 4.19. The effect of delaying sowing from April to September was to increase main shoot lamina area, dry weight and specific lamina area at all harvests, although the effect was greater at awn emergence. Delaying sowing was also associated with

Table 4.17 The effects of nitrogen application and leaf position on main shoot lamina area (cm^2 $leaf^{-1}$).

Leaf position	Nitrogen amount (Kg N ha^{-1})			
	0	25	50	100
L1	4.98	4.94	5.04	5.18
L2	8.96	9.18	9.42	9.29
L3	16.56	16.62	16.36	16.60
L4	21.35	20.94	20.98	20.41
L5	21.26	23.39	24.50	24.93
L6	20.39	21.66	23.73	26.08
L7	10.23	10.48	12.49	13.98
L8	3.45	3.76	4.06	4.81
(1)HSD (P=0.05)			1.37	
(2)HSD (P=0.05)			1.49	

(1) = HSD to compare means within same leaf position
(2) = HSD to compare means within same nitrogen amount
(Data are means of 3 sowing dates)

Table 4.18 The effects of nitrogen amount and leaf position on main shoot lamina dry weight (mg leaf^{-1}).

Leaf position	Nitrogen amount (Kg N ha^{-1})			
	0	25	50	100
L1	15.07	14.99	14.84	15.49
L2	24.75	24.79	24.80	24.72
L3	46.77	45.90	45.97	45.80
L4	75.56	73.33	72.55	71.93
L5	74.83	82.96	88.08	88.55
L6	73.66	84.08	90.27	97.03
L7	34.53	38.36	42.71	47.65
L8	12.68	13.22	13.86	16.65
(1)HSD (P=0.05)		3.91		
(2)HSD (P=0.05)		4.52		

(1) = HSD to compare means within same leaf position
(2)SD = HSD to compare means within same nitrogen amount
(Data are means of 3 sowing date)

Table 4.19 The effects of sowing date on plant growth parameters recorded at different growth stages during experiment 2.

Growth stages	Leaf 5 appearance			Leaf 7 appearance			Awn emergence			HSD* (P=0.05)
Sowing date	April	June	September	April	June	September	April	June	September	
PARAMETER										
Main shoot lamina area (cm^2 $plant^{-1}$)	40.5	44.7	50.6	71.3	83.2	107.4	73.3	105.1	155.4	6.3
Main shoot lamina dry weight (mg $plant^{-1}$)	129.7	116.1	138.3	293.4	288.9	300.6	312.3	417.5	442.5	14.3
Main shoot specific lamina area (mm^2 mg^{-1})	31.3	38.5	36.6	24.4	28.8	35.7	23.5	25.3	35.1	2.2
Main shoot total dry weight (mg $plant^{-1}$)	179.8	173.3	191.5	593.9	516.6	536.0	780.8	923.1	1071.5	45.1
Tiller dry weight (mg $plant^{-1}$)	27.5	14.7	50.5	189.2	181.5	237.8	417.1	847.7	2116.8	94.1
Total plant dry weight (mg $plant^{-1}$)	207.3	187.9	242.0	783.1	698.1	773.8	1197.9	1770.7	3188.3	110.9
Tiller contribution to plant dry weight (%)	13.1	7.7	20.7	23.3	25.7	30.6	34.4	46.2	66.1	3.5
Number of tillers per plant	1.2	0.8	1.4	1.4	1.9	2.3	1.7	2.7	3.4	0.3
Nitrogen concentration in plant tissue (%)	4.4	4.7	5.1	1.8	3.5	2.7	1.6	2.3	1.4	0.3
Nitrogen uptake by plant (mg $plant^{-1}$)	9.2	8.9	12.3	14.3	24.4	21.1	18.8	42.1	45.4	3.1
Relative growth rate (mg g^{-1} d^{-1})	190.3	227.5	210.9	110.2	145.7	61.2	71.9	130.2	34.5	12.7

* HSD to compare means within same growth stage
(Data are means of 4 nitrogen amounts)

increased tiller number and dry weight per plant, especially at leaf 7 appearance and at awn emergence. So that tillers made a greater contribution to total plant dry weight. Relative growth rate was unaffected by sowing date during the first harvest period. During the 2nd and 3rd harvest period relative growth rate was significantly affected by sowing date, being highest for June sowing and lowest for September sowing. The results also show that plant size and dry weight increased significantly ($P<0.05$) with the development of the plant in all the sowings. Specific lamina area, nitrogen % in dry matter and relative growth rate decreased significantly ($P<0.05$) with the age of the plant in all the sowing dates.

4.3.6.2 Nitrogen and time of harvest interaction

The effects of nitrogen on the various growth analysis parameters, recorded at different growth stages, are shown in Table 4.20. Generally, nitrogen had little effect on growth at leaf 5 appearance, small effect at leaf 7 appearance and a large effect at awn emergence. The effects of nitrogen on + tiller number and dry weight were greater than the effects of nitrogen on main shoot lamina area and dry weight, so that at the highest level of nitrogen, tillers made a greater contribution to total plant dry weight. Nitrogen % in dry matter and total nitrogen uptake increased up to the highest amount of nitrogen tested at all the harvests. Relative growth rate was unaffected by nitrogen during 1st and 2nd harvest periods, but increased by nitrogen during period from 7th leaf stage to awn emergence.

Table 4.20 The effects of nitrogen application on plant growth parameters recorded at different growth stages during experiment 2.

Growth stages	Leaf 5 appearance				Leaf 7 appearance				Awn emergence				HSD* (P=0.05)
Nitrogen amount (Kg N ha-1)	0	25	50	100	0	25	50	100	0	25	50	100	
PARAMETERS													
Main shoot lamina area (cm^2 $plant^{-1}$)	43.1	45.6	46.1	46.5	78.1	86.7	91.3	92.9	104.1	108.2	113.3	119.4	6.3
Main shoot lamina dry weight (mg $plant^{-1}$)	124.6	127.2	129.9	130.3	275.9	289.3	305.4	306.6	351.3	385.9	402.4	423.6	17.2
Main shoot specific lamnia area (mm^2 mg^{-1})	34.7	35.9	35.6	35.7	28.2	30.0	29.9	30.4	28.9	27.6	27.7	27.7	2.3
Main shoot total dry weight (mg $plant^{-1}$)	177.5	180.1	183.4	185.1	560.8	544.0	555.1	535.4	893.4	935.0	938.9	933.2	46.9
Tiller dry weight (mg $plant^{-1}$)	25.3	31.1	33.5	33.6	147.9	179.5	241.6	242.4	897.2	1009.5	1210.6	1391.4	105.6
Total plant dry weight (mg $plant^{-1}$)	202.8	211.3	216.9	218.6	708.8	723.5	796.6	777.8	1790.6	1944.5	2149.5	2324.6	130.2
Tiller contribution to plant dry weight(%)	11.8	14.1	14.7	14.8	20.4	24.5	30.3	31.0	43.7	46.5	50.8	54.7	3.4
Number of tiller per plant	1.0	1.2	1.2	2.2	1.4	1.7	2.1	2.2	2.2	2.4	2.7	3.1	0.4
Nitrogen concentration in plant tissue(%)	4.3	4.7	4.9	5.1	2.0	2.5	2.8	3.3	1.5	1.6	1.9	2.2	0.3
Nitrogen uptake by plant (mg $plant^{-1}$)	8.8	9.9	10.7	11.1	14.4	17.6	22.2	25.4	25.1	28.5	38.5	49.6	3.9
Relative growth rate (mg g^{-1} d^{-1})	207.8	209.4	210.4	210.8	104.6	103.1	108.9	106.4	71.2	78.8	77.2	88.2	13.3

* HSD to compare means within same growth stage
(Data are means of 3 sowing dates)

4.3.6.3 Sowing date and nitrogen interaction

There was little effect of nitrogen on plant growth up until awn emergence. Hence Table 4.21 shows the effect of nitrogen on various growth parameters at this stage of plant growth. Generally, almost all the growth parameters were affected by nitrogen application in all the sowings, although the effect was greater during June and September sowings. The effect of nitrogen on tiller number and dry weight was greater than the effects on other parameters, so that contribution of tillers to total plant dry weight, at awn emergence, was greater at the highest nitrogen tested. Nitrogen % in dry matter and total nitrogen uptake increased significantly ($P<0.05$) with the increse in the amount of nitrogen applied. The effect of nitrogen on specific lamina area at H3 was not significant ($P<0.05$) and the effect on relative growth rate was not consistent in all the sowings.

4.4 CONCLUSIONS

1. The results of this experiment were broadly very similar to experiment 1, but the response to nitrogen was much smaller. In experiment 1 plants were grown in perlite (a nutrient free medium), while in experiment 2 plants were grown in soil+sand which contained some organic matter and other essential elements. Therefore a smallar response to nitrogen was expected.

Table 4.21 The effects of sowing date and nitrogen application on plant growth parameters recorded at awn emergence stage in experiment 2.

Sowing date	April				June				September				HSD*
Nitrogen amount (Kg N ha^{-1})	0	25	50	100	0	25	50	100	0	25	50	100	(P=0.05)
PARAMETERS													
Main shoot lamina area (cm^2 $plant^{-1}$)	66.6	72.8	76.9	77.0	98.4	103.7	105.6	112.7	147.4	148.2	157.4	168.5	9.3
Main shoot lamina dry weight (mg $plant^{-1}$)	274.0	311.2	329.8	334.2	359.8	407.1	434.1	469.2	420.2	439.2	443.2	467.6	25.5
Main shoot specific lamina area (mm^2 mg^{-1})	24.4	23.4	23.3	23.1	27.3	25.5	24.3	24.0	35.1	33.9	35.5	36.1	NS
Main shoot total dry weight (mg $plant^{-1}$)	757.3	809.4	791.8	764.9	846.4	897.4	963.7	984.7	1076.5	1098.3	1061.2	1050.0	69.7
Tiller dry weight (mg $plant^{-1}$)	314.5	445.1	445.6	463.2	558.8	617.9	907.3	1306.7	1818.2	1965.6	2278.8	2404.5	156.8
Total plant dry weight (mg $plant^{-1}$)	1071.8	1254.5	1237.4	1228.0	1405.2	1515.3	1871.1	2291.4	2894.7	3063.9	3340.0	3454.4	193.3
Tiller contribution to plant dry weight (%)	28.8	35.2	35.9	37.6	39.5	40.4	48.2	56.9	62.8	63.8	68.2	69.6	5.0
Number of tiller per plant	1.4	1.8	1.9	1.9	2.3	2.3	2.5	3.5	2.9	3.0	3.6	3.9	0.5
Nitrogen concentration in plant tissue (%)	1.2	1.3	1.7	2.0	2.1	2.1	2.4	2.7	1.1	1.2	1.4	1.8	0.5
Nitrogen uptake by plant (mg $plant^{-1}$)	12.5	17.0	21.6	24.1	30.2	32.0	44.9	61.1	32.4	36.6	48.8	63.6	5.9
Relative growth rate (mg g^{-1} d^{-1})	77.0	88.1	59.3	63.0	104.2	114.0	137.9	164.7	32.3	34.3	34.5	36.8	19.8

* HSD to compare means within sowing date
NS = Not significant (P>0.05)

2. Plant development in terms of time taken to various growth stages, leaf appearance and initiation of primordia were little influenced by the nitrogen supply but were strongly influenced by sowing date. As in experiment 1 fastest development was found in the June sowing, due to warmer temperatures, longer days and higher radiation receipts.

3. Leaf growth was strongly influenced by sowing date and to a smaller extent by nitrogen supply. Change of leaf size with leaf position was affected by both sowing date and nitrogen supply. In the April and the June sowing at zero nitrogen leaf 4 was the longest leaf and where nitrogen was supplied leaf 5 was the longest. The same trend was present in the September sowing but leaf 5 was the largest leaf at zero nitrogen and leaf 6 was the largest where nitrogen was applied. Addition of nitrogen and delaying sowing resulted in the largest leaf occurring higher up the plant. It is suggested that these effects are due to (i) reduced internal competition for nitrogen at higher supply of nitrogen (ii) more number of leaves in delayed sowing.

   The variation in the sizes of the leaves was mainly due to differences in their LER, similar trends were noted in experiment 1. The relationship between FLL and LER and LED are discussed further and in more detail in section 6.4.1. The LER for leaf 5 was lower than expected. This could be due to the fact that it was extending at the time of stem extension.

4. Delaying sowing was associated with greater leaf area, leaf

dry weight and higher SLA of individual leaves, possibly to compensate for low light availability. There were more tillers and also bigger plants at each growth stage.

5. The effects of sowing date and nitrogen on the first 3 leaves were small and the effects increased with leaf position and with time. A similar trend was found in experiment 1.

6. Relative growth rate decreased with time in all the sowings and the biggest decrease was observed in the September sowing. It was more affected by sowing date than nitrogen supply. It was highest in the June sowing and the lowest in the September sowing. The effect of sowing date was more pronounced in the later part of plant development.

CHAPTER 5

EXPERIMENT 3

The effects of plant density and nitrogen supply on apical development, leaf growth and yield of spring barley.

5.1 INTRODUCTION

In the previous experiments leaf growth and development of spring barley was significantly affected by the time of sowing and application of nitrogen fertilizer (Chapters 3 and 4). However, the observations during these experiments were made on plants grown at the same plant density i.e 300 plants m^{-2} and plants were equidistant from each other. In this experiment, therefore, it was decided to include plant density as a factor to study the effect of plant density on apical development, leaf growth and economic yield. During the previous experiments, reported in chapters 3 and 4, plants were destructively harvested at different growth stages and measurements were restricted to the phases before awn emergence. In this experiment plants were taken to maturity and yield analysis was carried out.

The previous experiments were carried out in relatively small pots. In this experiment plants were grown in large tanks filled with soil and sand compost, to provide more space for root development and to closer simulate field conditions. The experiment was sown in March which is the recommended time of sowing for spring barley and is comparable to one of the sowings used in the previous experiment. Threee plant densities (150, 300 and 600 plants m^{-2}) and two ammounts of nitrogen (0 and 100 kg ha^{-1}) were tested.

The experiment was laid out in a 'Dutch' type glasshouse with no supplementary heating or lighting to provide plants with environmental conditions which were much closer to the

conditions found in the field.

5.2 MATERIALS AND METHODS

5.2.1 Cultivation of plants and experimental treatments tested

5.2.1.1 Plant material

The variety of spring barley (Claret) grown in previous experiments (reported in Chapters 3 and 4) was also used in this experiment.

5.2.1.2 Growing medium

Field soil was collected from the same field as in experiment 2, brought to the glasshouse and broken down by a soil shredder. Stones were removed. The soil was then mixed with sand (2:1 soil sand ratio) using a concrete mixer. The plants were grown in large tanks, hereafter refered to as plots, which were 1m * 1m surface * 1m deep. This was done to provide plants with a greater volume available for root development and to create conditions which were more closer to those found in the field. The compost was steam sterilized to kill weed seeds before putting into the plots. The pH of the compost was adjusted to pH 7 with lime. A uniform amount of P and K (75 kg ha^{-1}) was cultivated into each plot before sowing.

5.2.1.3 Details of treatments and experimental design

Three plant densities (150, 300 and 600 plants m^{-2}) and two

amounts of nitrogen (0 and 100 Kg N ha^{-1}) were tested in this experiment.

The experiment was laid out in a Randomized Complete Block Design with 3 blocks and all combinations of plant density and nitrogen amount (3*2) were randomly allocated to each block. For apical dissection measurements extra plants of each of the treatments were grown in spare single plots in the same glass house. A limited number of plots were avaiable in the glasshouse and it was not possible to have extra replicated plots of each treatment to provide plants for apical dissection measurements. Plants were watered daily to avoid occurence of any water stress.

5.2.1.4 Sowing method

Seeds were sown on 17 March, 1983 at 8, 6 and 4 cm square spacings and 3 cm depth to achieve plant densities of about 150,300 and 600 plants m^{-2}. Two seeds were sown at each position to allow for any seeds which failed to germinate. At the second leaf stage seedlings were thinned to the required plant densities and nitrogen (as sodium nitrate) was applied by hand.

5.2.2 Apical development

Main stem apical development was recorded twice weekly on three plants of each treatment. The methods of sampling, dissection and calculations adopted in Experiment 2 (section 4.2.2) were also used during this experiment.

5.2.3 Leaf extension measurements

Extension growth of the first 6 main shoot leaves was recorded daily on 10 randomly selected plants for each treatment. The method used for measuring leaf length is described in section 4.2.3. In experiment 2 it was found that the apparent length of leaves above leaf 3 on the main shoot (when measured from the soil surface) also inculeded some internode elongation. To exclude this effect in this experiment actual stem elongation (distance from base of plant to shoot apex) was recorded during dissection measurements and lengths of leaf 4 and above were adjusted accordingly. Adjusted leaf length (ADLL) was calculated by taking the stem length (STL) away from the observed leaf length (OLL).

$$ADLL = OLL - STL$$

These adjusted leaf lengths were found to be very similar to the actual leaf lengths recorded in growth analysis.

For each plot the mean leaf length of 10 plants was determined and LER and LED were calculated by the methods described in sections 3.2.3 and 4.2.3.

5.2.4 Plant growth analysis

To provide data on the maximum area and dry weight of individual main shoot leaves and to follow plant growth 10 plants were harvested from each plot at three growth stages ; appearance of leaf 5, leaf 7 and awn emergence. Details of the

method adopted for growth analysis are given in sections 3.2.4 and 4.2.4. The following parameters were recorded during growth analysis;

1. lengths of lamina and sheath of fully expanded main shoot leaves,
2. lamina area and dry weight of fully expanded main shoot leaves,
3. total lamina area of main shoot leaves,
4. specific lamina area of fully expanded leaves,
5. number of tillers,
6. main shoot total dry weight,
7. tiller dry weight,
8. plant dry weight,
9. tiller contribution to plant dry weight,
10. nitrogen concentration in plant tissue,
11. nitrogen uptake by plant,
12. nitrogen content of first 6 main shoot leaves,
13. relative growth rate.

The methods used to record and caculate the above parameters are described in sections 3.2.4 and 4.2.4.

5.2.5 Yield analysis

At maturity plants from a fixed area of 50 * 25 cm were harvested from each plot. The number of plant shoots and ears was determined. The ears and straw were separated and then dried at 80^{o}C overnight. The grains were threshed out and

counted using a Tecator electronic seed counter and then dried to detrmine grain dry weight. Specific grain weight (i.e. mean grain weight) was calculated by dividing total grain weight of the sample by the total number of grains per sample. Number of grains per ear was calculated by dividing the total number of grains present in a sample by the number of ears in that sample. Grain yield was calculated both on a per plant and per hectare basis and expressed as g $plant^{-1}$ and Kg ha^{-1} respectively. To calculate the total number of grains per plant, number of grains per ear was multiplied by the number of ears per plant. Above ground biomass was calculated from the total weight of grain and straw. The percentage of ear bearing shoots was calculated by the following formula ;

$$\% \text{ of ear bearing shoots} = \frac{\text{Number of ears}}{\text{Maximum number of shoots (recorded duringgrowth analysis)}} * 100$$

Harvest index (HI) was calculated by the following method and was expressed on percentage basis ;

$$HI = \frac{\text{Grain dry weight}}{\text{Above ground biomass}} * 100$$

In order to minimise edge effects samples for apical dissection, growth analysis and yield were not taken from outside rows or rows adjacent to previously harvested areas.

5.2.6 Meteorological observations

Air temperature, photoperiod and solar radiation were recorded and calculated by the methods described in section 3.2.2.

5.2.7 Pests and disease control

No serious disease problem occured during this wxperiment, except a small incidence of powdery mildew which was immediatly controlled using a fungicide spray of an appropriate fungicide.

5.3 RESULTS

5.3.1 Environmental conditions during the course of the experiment

Data for average weekly mean air temperature, photoperiod and solar radiation are presented in Figure 5.1. The results show that all the weather variables recorded gradually increased during the course of the experiment. Mean air temperature increased from 12^{o}C at the beginning of the experiment to 24^{o}C by the end of the experiment. During the experiment photoperiod gradually increased from 13h to 18h. The amount of solar radiation recieved by the plants was variable, but the underlining trend was that of an increase with time. Solar radiation increased from 3 $MJm^{-2}d^{-1}$ to 12 $MJm^{-2}d^{-1}$ by the end of the experiment.

5.3.2 Time to various growth stages

Plant development in the early part of the experiment was not affected by plant density and effects were only apparent at the time of stem elongation (Table 5.1). At high plant density stem elongation started 5 days earlier than low density. The

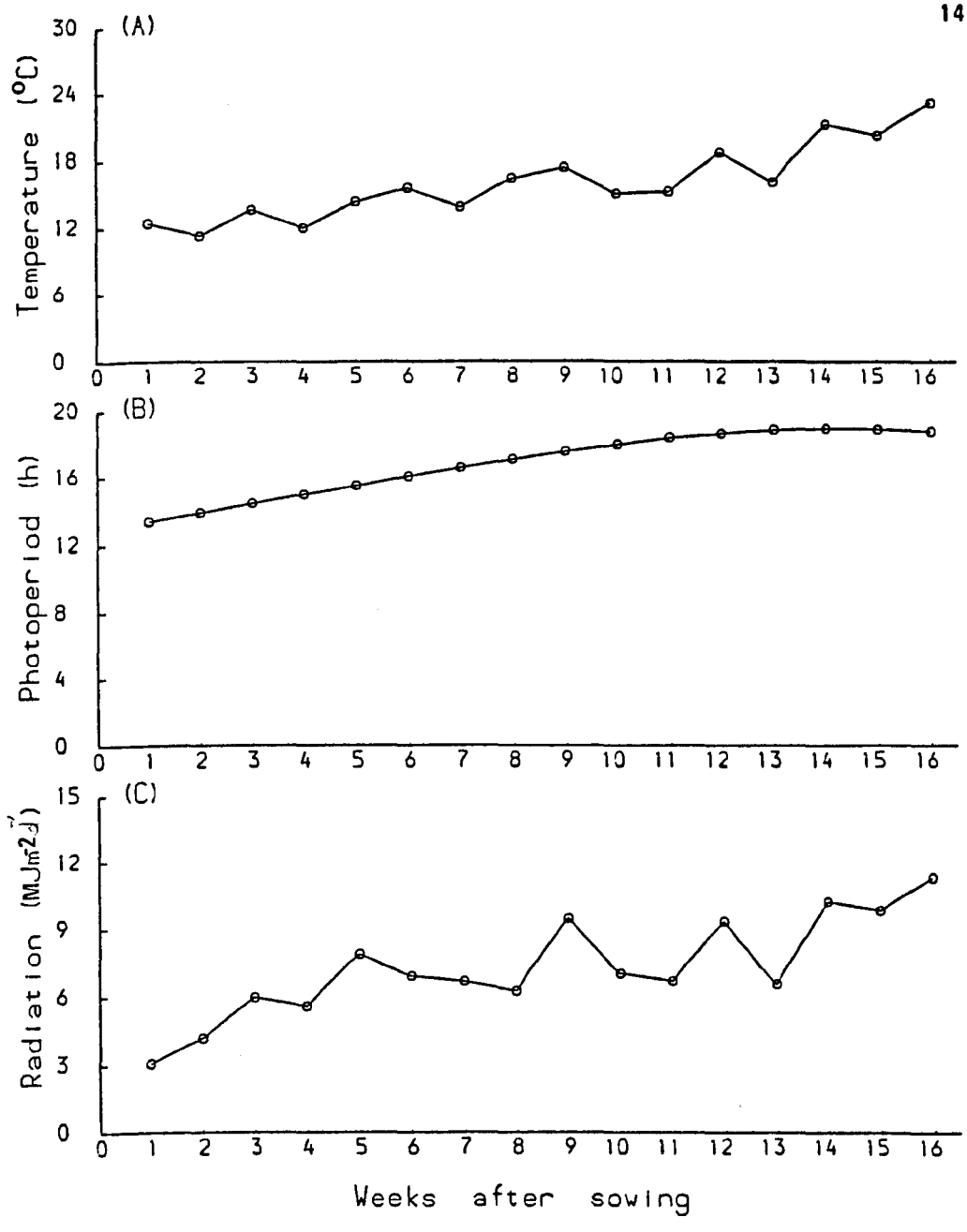


Figure 5.1 Showing weekly mean air temperature (A), photoperiod (B) and solar radiation (C) experienced by the plants during the course of experiment 3.

time at which leaf 5 ceased extension growth was delayed by 2 days at high plant density, but awn emergence occurred at more or less the same time in all the plant densities. If temperature or daylength were the only factors controlling controlling plant development then in this experiment all three plant densities should have attained the various growth stages at the same time. Such trends were not evident which suggests that other factors must be important. Nevertheless there is no doubt that temperature is important. The time taken to different growth stages in this experiment was longer than the time taken to reach corresponding growth stages in other experiments. This was associated with lower temperatures during this experiment.

Table 5.1 The effect of plant density on the time taken to from sowing date to various growth stages

	Plant density (Plants m^{-2})					
	150		300		600	
	DAS	At	DAS	At	DAS	At
Growth stages						
Germination	8	102.0	8	102.0	8	102.0
Double ridge	27	331.7	27	331.7	27	331.7
When leaf 3 cesed extension	34	432.5	34	432.5	35	446.5
Stem elongation	41	541.7	39	507.9	36	461.0
When leaf 5 ceased extension	50	674.5	52	708.5	54	738.5
Awn emergwnce	70	996.8	68	965.5	69	981.0
Mean air temperature	13.65^{o}C					

DAS = days after sowing; At = thermal time above Tb 0oC

5.3.3 Statiatical analysis

Since apical development and leaf appearance were recorded on spare plants grown outside the main experiment it was not possible to use an ANOVA procedure to determine the effects of plant density and nitrogen on these parameters. The data for the rates of primordia initiation and leaf appearance were compared by the method adapted in Chapter 4 (section 4.3.2). It was not possible to apply any appropriate statistical procedure to compare apparent durations of these processes and final number of primordia and leaves, so the data presented for these parameters are the mean values without statistical comparison.

The data on leaf extension parameters recorded during this experiment were analysed as a split-plot design; plant density and nitrogen amounts being on main plots and leaf position on sub-plots.

Plant growth analysis was carried out at different growth stages and the data on plant growth parameters were analysed using an ANOVA procedure considering plant density and nitrogen amounts on main plots and time of growth analysis on sub-plots. However, where the interactions between treatments and harvests were significant the comparisons were made between treatments within the same harvest.

The data on yield and its components were analysed using the standard ANOVA procedure for a randomized block design.

A summary of the significance levels of the main effects and interactions is presented in Table 5.2. Where the effects of treatments were found to be significant ($P<0.05$) the means were compared using Tukey's test. It is interesting to note that in this experiment nitrogen affected fewer parameters than in the earlier experiments (Chapters 3 and 4). The interactions between nitrogen * plant density and nitrogen * leaf position was also in virtually all cases not significant. Leaf position had a large and significant effect, and the effects of density varied with leaf position. Most of the second order interactions were not statistically significant and these are not discussed further. All the HSD's presented in the results tables are calculated at the 5% probabilty level.

5.3.4 Apical development

In experiment 2 (section 4.3.3) a significant ($P<0.05$) linear relationship was found between thermal time and both the number of primordia initiated at the shoot apex and the number of leaves appeared on the main shoot. In this experiment it was therefore decided to calculate the rates and apparent durations of primordia initiation and leaf apprearance in thermal time units only.

5.3.4.1 Primordia initiation

The data on the effects of plant density and nitrogen amount on primordia initiation are presented in Table 5.3. The results show that the maximum number of primordia initiated on

Table 5.1 Summary of the significance levels of the main effects of plant density (D), nitrogen amount (N), leaf position (LP) and harvest (H) and their interactions on plant parameters recorded during Experiment 3.

PARAMETER	Main effects				Interactions						
	D	N	LP	H	D*N	D*LP	D*H	N*LP	N*H	D*N*LP	D*N*H
Leaf extension parameters											
Main shoot leaf extension rate (mm $^{o}Cd^{-1}$)	NS	NS	***	-	NS	NS	-	NS	-	**	-
Main shoot leaf extension duration (^{o}Cd)	NS	NS	***	-	NS	NS	-	NS	-	**	-
Main shoot leaf length (mm $leaf^{-1}$)	NS	NS	***	-	NS	***	-	NS	-	NS	-
Main shoot lamina area (cm^2 $leaf^{-1}$)	NS	**	***	-	NS	***	-	***	-	*	-
Main shoot lamina dry weight (mg $leaf^{-1}$)	***	***	***	-	*	***	-	***	-	**	-
Main shoot specific lamina area (mm^2 mg^{-1})	*	NS	***	-	NS	**	-	NS	-	NS	-
Main shoot lamina:sheath ratio	NS	NS	***	-	NS	**	-	NS	-	NS	-
Growth analysis measurements											
Main shoot lamina area (cm^2 $plant^{-1}$)	NS	NS	-	***	NS	-	**	-	***	-	NS
Main shoot lamina dry weight (mg $plant^{-1}$)	***	***	-	***	NS	-	***	-	***	-	NS
Main shoot specific lamina area (mm^2 mg^{-1})	***	NS	-	**	NS	-	NS	-	NS	-	NS
Main shoot total dry weight (mg $plant^{-1}$)	***	NS	-	***	NS	-	***	*	*	-	NS
Tiller dry weight (mg $plant^{-1}$)	***	NS	-	***	NS	-	***	-	NS	-	NS
Total plant dry weight (mg $plant^{-1}$)	***	NS	-	***	NS	-	***	-	*	-	NS
Tiller contribution to plant dry weight (%)	***	NS	-	***	NS	-	***	-	*	-	NS
Nitrogen concentration in plant tissue (%)	NS	***	-	***	NS	-	NS	-	***	-	*
Nitrogen uptake by plant (mg $plant^{-1}$)	***	***	-	***	NS	-	***	-	***	-	**
Relative growth rate (mg mg^{-1} d^{-1})	***	*	-	***	NS	-	***	-	NS	-	NS
Yield and yield components											
Total number of shoots /plant at final harvest	***	NS	-	-	NS	-	-	-	-	-	-
Number of ears /plant	***	NS	-	-	NS	-	-	-	-	-	-
Percentage of ear bearing shoots	*	*	-	-	NS	-	-	-	-	-	-
Number of grains /ear	***	*	-	-	NS	-	-	-	-	-	-
Number of grains /plant	***	NS	-	-	NS	-	-	-	-	-	-
Specific grain weight (mg $grain^{-1}$)	NS	NS	-	-	NS	-	-	-	-	-	-
Grain yield (g $plant^{-1}$)	***	NS	-	-	NS	-	-	-	-	-	-
Grain yield (t ha^{-1})	NS	NS	-	-	NS	-	-	-	-	-	-
Harvest index (%)	NS	NS	-	-	NS	-	-	-	-	-	-
Nitrogen concentration in grain (%)	NS	NS	-	-	NS	-	-	-	-	-	-
Nitrogen uptake by grains (mg $plant^{-1}$)	***	NS	-	-	NS	-	-	-	-	-	-
Nitrogen uptake by grains (Kg ha^{-1})	NS	NS	-	-	NS	-	-	-	-	-	-

*** = Significant (P<0.001)
** = Significant (P<0.01)
* = Significant (P<0.05)
NS = Not significant (P>0.05)
- = Does not occur

Table 5.3 The effects of plant density and nitrogen amount on primordia initiation on main shoot apex

PARAMETER	Rate of primordia initiation (numbers $^{o}Cd^{-1}$) ± SE		Primordia initiation duration (^{o}Cd)		Maximum number of primordia	
Nitrogen amount (Kg N ha^{-1})	0	100	0	100	0	100
Plant density (plants m^{-2})						
150	0.107±0.005	0.105±0.005	400.65	415.90	42.87	43.67
300	0.103±0.007	0.102±0.005	388.35	411.18	40.00	41.94
600	0.101±0.006	0.103±0.006	374.95	375.05	37.87	38.63

SE = Standard error

the apex of the main shoot was decreased by plant density due to reductions in both the rate and duration of primordia initiation. The effect of nitrogen was very small and not significant.

5.3.4.2 Leaf appearance

The number of leaves on the main shoot was decreased by about 12% with the increase in plant density (Table 5.4). This decrease in number was associated with a decrease in the apparent duration of leaf appearance. The effect of nitrogen on leaf appearance and leaf number was very small and not significant.

5.3.5 Leaf extension of first 6 main shoot leaves

The main effects of plant density, nitrogen amount and leaf position on LER, LED and FLL of the first 6 main shoot leaves are shown in Table 5.5. Not all the first order and second order interactions were significant ($P<0.05$). Therefore the main effects of treatments and their interactions where significant are described.

5.3.5.1 Main effects of plant density, nitrogen amount and leaf position

There was no significant ($P>0.05$) effect of plant density and nitrogen amount on the leaf extension parameters recorded in this experiment (Table 5.5), but there was a significant effect

Table 5.4 The effects of plant density and nitrogen amount on leaf appearance on main shoot.

PARAMETER	Rate of leaf appearance (number $^{o}Cd^{-1}$) ± SE		Leaf appearance duration (^{o}Cd)		Final number of leaves	
Nitrogen amount (Kg N ha^{-1})	0	100	0	100	0	100
Plant density (plants m^{-2})						
150	0.0097±0.001	0.0097±0.001	836.9	851.2	8.13	8.53
300	0.0094±0.001	0.0097±0.002	850.9	820.5	8.00	8.00
600	0.0094±0.001	0.0094±0.002	790.3	784.3	7.13	7.37

SE = Standard error

Table 5.5 Main effects of plant density, nitrogen amount and leaf position on the rate of leaf extension (LER), duration of leaf extension (LED) and final leaf length (FLL) of main shoot leaves.

PARAMETER	LER ($mm\,^oCd^{-1}$)	LED (^oCd)	FLL (mm)
[1]Plant density (plants m^{-2})			
150	1.779	206.1	341.6
300	1.671	207.5	342.6
600	1.749	214.3	362.3
HSD (P=0.05)	NS	NS	NS
[2]Nitrogen amount (Kg N ha^{-1})			
0	1.724	201.2	344.1
100	1.742	217.5	353.7
HSD (P=0.05)	NS	NS	NS
[3]Leaf position			
L1	0.903	138.1	120.3
L2	1.291	160.4	206.5
L3	1.728	181.9	309.6
L4	2.276	201.8	451.4
L5	2.546	213.1	512.7
L6	1.654	360.4	492.9
HSD (P=0.05)	0.318	59.8	19.5

NS = Not significant (P>0.05)
1 = Data are means of 2 nitrogen amounts and 6 leaf positions
2 = Data are maens of 3 plant densities and 6 leaf positions
3 = Data are means of 3 plant densities and 2 nitrogen amounts

of leaf position. The results show that, leaf length increased significantly with the point of insertion on the main shoot upto leaf 5. This increase in length was mainly brought about by an increased rate of leaf extension. Above leaf 5 LER and FLL decreased, but LED was increased.

5.3.5.2 First order interactions

The first order interactions between nitrogen and plant density and nitrogen and leaf position were not significant ($P>0.05$). Therefore only data for the plant density and leaf position interaction are presented (Table 5.6).

The results in Table 5.6 show that, there was no effect of plant density on the lengths of leaves 1 and 5. However, the lengths of leaves 2,3 and 4 increased significantly ($P<0.05$) with the increase in plant density mainly due to a longer LED. This trend was reversed in leaf 6, Leaf length being reduced at the high density mainly (but not solely) due to decrease in LED.

5.3.6 Lamina area, dry weight, specific lamina area and lamina length:sheath length ratio

Leaf extension measurements were restricted to the first 6 leaves on the main shoot. In growth analysis data were collected for all the leaves on the main shoot. The main effects of plant density, nitrogen and leaf position on LA, LWT, SLA and LSR are presented in Table 5.7.

Table 5.6 The effects of plant density and leaf position on leaf extension rate (LER), leaf extension duratio (LED) and final leaf length (FLL) of main shoot leaves.

PARAMETER	LER (mm oCd-1)			LED (oCd)			FLL (mm)		
Plant density (plants m-2)	150	300	600	150	300	600	150	300	600
Leaf position									
L1	0.990	0.890	0.829	121.6	143.1	149.0	116.0	121.2	123.8
L2	1.295	1.263	1.316	143.5	161.0	176.6	185.4	202.1	232.1
L3	1.809	1.644	1.730	152.0	180.8	212.9	269.5	292.5	366.6
L4	2.387	2.214	2.225	183.9	204.1	217.5	435.6	445.8	472.9
L5	2.427	2.445	2.768	220.2	210.0	209.3	517.5	508.8	511.8
L6	1.767	1.569	1.626	415.6	345.9	319.9	525.4	485.4	467.8
(1)HSD (P=0.05)		NS			NS			32.6	
(2)HSD (P=0.05)		NS			NS			27.6	

(1) = HSD to compare means within same leaf position
(2) = HSD to compare means within same plant density
NS = Not significant (P>0.05)

5.3.6.1 Main effects of plant density, nitogen supply and leaf position

The results (Table 5.7) show that LA, LWT and LSR decreased with increasing plant density. SLA increased with the increase in plant density.

LA and LWT of individual leaves increased significantly ($P<0.05$) with nitrogen supply. The effect of nitrogen on SLA and LSR was not significant ($P>0.05$).

The results also show that LA, LWT, SLA and LSR changed significantly ($P<0.05$) with the position of the leaf on the main shoot. LA and LWT increased with leaf position up to leaf 6 and then decreased. The differences in SLA between the lower leaves were very small, but these leaves had high SLA than upper leaves. The LSR decreased with the position of the leaf on the main shoot. For leaves 1 to 7 lamina length was greater than sheath length. For leaf 8 the data are misleading because not all densities had 8 leaves. Hence for these leaves it is important to consider the density and leaf position interaction.

5.3.6.2 First order interactions

i) Plant density and nitrogen interaction

The interaction between plant density and nitrogen amount for LA, SLA and LSR was not significant ($P>0.05$). For LWT, the

Table 5.7 Main effects of plant density, nitrogen amount and leaf position on lamina area (LA), lamina dry weight (LWT), specific lamina area (SLA) and lamina length: sheath length ratio (LSR) of main shoot leaves.

PARAMETER	LA (cm2 leaf-1)	LWT (mg leaf-1)	SLA (mm2 mg-1)	LSR
[1]Plant density (plants m-2)				
150	19.17	64.29	30.18	2.80
300	18.31	57.06	32.00	2.60
600	16.71	44.65	35.33	2.27
HSD (P=0.05)	NS	4.03	4.05	0.33
[2]Nitrogen amount (Kg N ha-1)				
0	16.73	51.08	32.33	2.50
100	19.39	59.59	32.61	2.62
HSD (P=0.05)	1.87	2.69	NS	NS
[3]Leaf position				
L1	4.43	14.47	30.91	3.87
L2	7.55	21.42	35.41	3.76
L3	13.13	34.36	38.29	2.58
L4	22.19	62.38	35.60	2.32
L5	32.30	88.17	37.37	2.77
L6	33.74	103.87	32.73	2.65
L7	24.20	88.46	27.77	1.82
L8	6.95	29.55	21.69	0.71
HSD (P=0.05)	2.43	7.06	4.44	0.39

NS = Not significant (P>0.05)
1 = Data are means of 2 nitrogen amounts and 8 leaf position
2 = Data are means of 3 plant densities and 8 leaf position
3 = Data are means of 3 plant densities and 2 nitrogen amounts

effect of nitrogen increased as plant density increased (Table 5.8).

ii) Plant density and leaf position interaction

The effect of plant density on LA, LWT, SLA and LSR depended on the leaf position. Plant density affected the areas of individual leaves and the position on the main shoot of the largest leaf. The results (Table 5.9) show that LA of leaves 1 to 4 increased with plant density. Density had no effect on leaf 5 and above leaf 5 this effect was reversed, leaf area decreasing as density increased. At the lowest density leaf 6 had the largest area, at the highest density leaf 5 had the largest area.

The effect of plant density on LWT of the first 4 leaves was not significant ($P<0.05$) and leaf 5 was the first leaf to show some response to plant density. The effect of plant density was much geater on leaves higher than leaf 5. LWT of upper leaves decreased significantly ($P<0.05$) as the plant density increased.

SLA of leaves 1 to 7 consistently increased with the increase in plant density. In leaf 8 this trend was reversed.

LSR was generally decreased by increase in plant density.

iii Nitrogen and leaf position interaction

The results presented in Table 5.2 show that the interaction between nitrogen and leaf position for SLA and LSR was not

Table 5.8 The effects of plant density and nitrogen amount on lamina area (LA), lamina dry weight (LWT), specific lamina area (SLA) and lamina length:sheath length ratio (LSR) of main shoot leaves.

PARAMETER	LA (cm^2 $leaf^{-1}$)		LWT (mg $leaf^{-1}$)		SLA (mm^2 $leaf^{-1}$)		LSR	
Nitrogen amount (Kg N ha^{-1})	0	100	0	100	0	100	0	100
Plant density (plants m^{-2})								
150	18.70	19.69	62.36	66.23	30.01	30.35	2.81	2.79
300	15.70	20.92	50.48	63.64	30.76	33.24	2.52	2.68
600	15.80	17.61	40.40	48.90	36.22	34.24	2.18	2.37
(1)HSD(P=0.05)	NS		4.66		NS		NS	
(2)HSD(P=0.05)	NS		4.66		NS		NS	

(1) = HSD to compare means within the same plant density
(2) = HSD to compare means within the same nitrogen amount
NS = Not significant (P>0.05)
(Data are means of 8 leaf positions)

Table 5.9 The effects of plant density and leaf position on lamina area (LA), lamina dry weight (LWT), specific lamina area (SLA) and lamina length:sheath length ratio (LSR) of main shoot leaves.

PARAMETER	LA (cm^2 $leaf^{-1}$)			LWT (mg $leaf^{-1}$)			SLA (mm^2 mg^{-1})			LSR		
Plant density (plants m^{-2})	150	300	600	150	300	600	150	300	600	150	300	600
Leaf position												
L1	4.36	4.37	4.55	15.23	14.87	13.32	28.91	29.50	34.31	4.28	3.87	3.47
L2	7.03	7.47	8.16	21.62	21.97	20.67	32.59	34.05	39.59	4.36	3.89	3.02
L3	12.08	12.43	14.88	34.48	32.75	35.85	35.13	37.98	41.75	2.92	2.67	2.16
L4	19.95	21.56	25.08	63.55	60.43	63.17	31.37	35.65	39.76	2.35	2.17	2.45
L5	32.05	31.53	33.32	97.08	89.87	77.55	33.06	35.35	43.70	2.53	2.81	2.95
L6	36.13	33.84	31.25	119.03	103.38	89.18	30.41	32.60	35.18	2.82	2.70	2.42
L7	30.53	27.17	14.89	116.70	99.45	49.23	26.07	27.03	30.22	2.26	2.05	1.16
L8	11.27	8.08	1.52	46.63	33.77	8.25	23.92	23.84	17.31	0.92	0.66	0.56
(1)HSD (P=0.05)		3.94			9.49			6.61				0.58
(2)HSD (P=0.05)		4.21			12.23			7.68				0.69

(1) = HSD to compare means within same leaf position
(2) = HSD to compare means within same plant densityy
(Data are the means of 2 nitrogen levels)

significant (P>0.05). Nitrogen had no effect on LA and LWT of the first five leaves. LA and LWT of leaves above leaf 5 was increased significantly by nitrogen (Table 5.10)

5.3.7 Growth analysis : Plant size and dry weight at different growth stages

To monitor plant growth over time, growth analysis was carried out at leaf 5, leaf 7 and awn emergence stages. The interaction between plant density and nitrogen and the second order interaction (density * nitrogen * harvest) for most of the parameters recorded were not significant (Table 5.2). Thus the effects plant density did not depend upon nitrogen supply. Therefore, main effects and first order interactions, where significant , will be described in the following sections.

5.3.7.1 Main effects of plant density

The data on the effects of plant density on plant growth parameters recorded during the growth analyses are presented in Table 5.11. All parameters recorded during growth analysis except SLA were decreased by increasing plant density. Total dry weight of above ground plant material decreased significantly (P<0.05) as the density of plants increased, and this decrease in plant dry weight was mainly associated with the decrease in tiller number and dry weight per plant. The contribution of tillers to total plant dry weight was 3 times

Table 5.10 The effects of nitrogen amount and leaf position on lamina area (LA), lamina dry weight (LWT), specific lamina area (SLA) and lamina length:sheath length ratio (LSR) of main shoot leaves.

PARAMETERS	LA (cm^2 $leaf^{-1}$)		LWT (mg $leaf^{-1}$)		SLA (mm^2 mg^{-1})		LSR	
Nitrogen amount (Kg N ha^{-1})	0	100	0	100	0	100	0	100
Leaf position								
L1	4.32	4.54	14.30	14.64	30.49	31.32	3.88	3.87
L2	7.53	7.58	21.64	21.19	34.91	35.91	3.72	3.79
L3	13.12	13.14	33.31	35.41	39.43	37.15	2.57	2.59
L4	21.74	22.65	61.29	63.48	35.48	35.71	2.35	2.29
L5	30.98	33.62	85.71	90.62	36.92	37.82	2.72	2.81
L6	30.72	36.76	96.36	111.38	32.21	33.25	2.54	2.75
L7	20.57	27.83	74.66	102.27	28.40	27.15	1.64	2.01
L8	4.91	9.00	21.38	37.72	20.79	22.58	0.61	0.82
(1)HSD (P=0.05)	2.68		6.44		NS		NS	
(2)HSD (P=0.05)	2.60		9.99		NS		NS	

(1) = HSD to compare means within same leaf position
(2) = HSD to compare means within same nitrogen amount
NS = Not significant (P>0.05)
(Data are the means of 3 plant densities)

Table 5.11 Main effects of plant density on different plant growth parameters recorded during experiment 3.

Plant density (plants m-2)	150	300	600	HSD (P=0.05)
PARAMETER				
Main shoot lamina area (cm^2 $plant^{-1}$)	92.50	85.70	83.90	NS
Main shoot lamina dry weight (mg $plant^{-1}$)	292.40	259.50	215.60	16.10
Main shoot specific lamina area (mm^2 mg^{-1})	32.01	33.07	38.73	3.69
Main shoot total dry weight (mg $plant^{-1}$)	711.00	636.30	530.40	51.90
Tiller dry weight (mg $plant^{-1}$)	1482	755	151	252
Total plant dry weight (mg $plant^{-1}$)	2193	1391	681	275
Tiller contribution to plant dry weight (%)	47.10	36.92	15.70	7.03
Tiller number / plant	3.33	2.21	1.14	0.42
Nitrogen concentration in plant tissue (%)	3.59	3.50	3.39	NS
Nitrogen uptake by plant (mg $plant^{-1}$)	49.92	34.22	16.88	7.09
Relative growth rate (mg g^{-1} d^{-1})	118.80	109.00	93.40	4.40

NS = Not significant (P>0.05)
(Data are the means of 2 nitrogen levels and 3 harvests)

higher at low plant density than at high plant density. Relative growth rate at the high plant density was significantly lower than at the low plant density. Specific lamina area increased as plant density increased.

5.3.7.2 Main effects of nitrogen amount

Application of nitrogen increased most of the parameters recorded but the increase was rarely statistically significant (Table 5.12)

5.3.7.3 Main effects of time of harvest (growth stage)

Most of the plant growth parameters reported in Table 5.13 increased significantly ($P<0.05$) with the age of the plant. SLA, nitrogen % in the dry matter and relative growth rate decreased significanty ($P<0.05$) as the plants grew older.

5.3.7.4 Plant density and harvest interaction

The effect of plant density on various plant growth parameters, recorded at different growth stages, are shown in Table 5.14. Generally, plant density had little effect on growth at leaf 5 appearance, a large effect at leaf 7 appearance and greatest effect at awn emergence. The effects of plant density on tiller number and dry weight were greater than the effects on main shoot lamina area and dry weight, so that at the highest density tillers made a small contribution to total plant dry weight. Specific lamina area and nitrogen % in the dry matter were not affected by plant density at all

Table 5.12 Main effects of nitrogen amount on different plant growth parameters recorded during experiment 3.

Nitrogen amount (Kg N ha^{-1})	0	100	HSD (P=0.05)
PARAMETERS			
Main shoot lamina area (cm^2 $leaf^{-1}$)	83.8	91.0	NS
Main shoot lamina dry weight (mg $leaf^{-1}$)	243.2	268.5	10.8
Main shoot specific lamina area (mm^2 mg^{-1})	34.75	34.46	NS
Main shoot total dry weight (mg $plant^{-1}$)	610.9	640.9	NS
Tiller dry weight (mg $plant^{-1}$)	734	854	NS
Total plant dry weight (mg $plant^{-1}$)	1345	1499	NS
Tiller contribution to plant dry weight (%)	31.78	34.71	NS
Tiller number / plant	2.16	2.29	NS
Nitrogen concentration in plant tissue (%)	3.26	3.74	0.21
Nitrogen uptake by plant (mg $plant^{-1}$)	26.68	40.66	4.73
Relative growth rate (mg g^{-1} d^{-1})	105.2	108.9	2.9

NS = Not significant (P>0.05)
(Data are the means of 3 plant densities and 3 harvests)

Table 5.13 Main effects of time of growth analysis on different plant growth parameters recorded during experiment 3.

Time of growth analysis	Leaf 5 appearance	Leaf 7 appearance	Awn emergence	HSD (P=0.05)
PARAMETER				
Main shoot lamina area (cm^2 $leaf^{-1}$)	31.9	91.5	138.6	6.5
Main shoot lamina dry weight (mg $leaf^{-1}$)	94.7	255.7	417.1	11.9
Main shoot specific lamina area (mm^2 mg^{-1})	33.9	35.9	33.9	1.7
Main shoot total dry weight (mg $plant^{-1}$)	138.6	424.4	1314.6	40.6
Tiller dry weight (mg $plant^{-1}$)	16	331	2041	204
Total plant dry weight (mg $plant^{-1}$)	154	755	3356	222
Tiller contribution to plant dry weight (%)	9.73	40.04	49.95	3.98
Tiller number / plant	1.17	2.62	2.89	0.30
Nitrogen concentration in plant tissue (%)	4.99	3.59	1.93	0.21
Nitrogen uptake by plant (mg $plant^{-1}$)	7.70	27.49	65.83	5.20
Relative growth rate (mg g^{-1} d^{-1})	148.0	97.0	76.2	5.9

(Data are the means of 3 plant densities and 2 nitrogen amounts)

Table 5.14 The effect of plant density on plant growth parameters recorded at different growth stages during experiment 3.

Growth stages	Leaf 5 appearance			Leaf 7 appearance			Awn emergence			HSD*
Plant density (plants m^{-2})	150	300	600	150	300	600	150	300	600	(P=0.05)
PARAMETER										
Main shoot lamina area (cm^2 $plant^{-1}$)	31.6	31.1	33.1	95.7	86.7	92.1	150.3	139.2	126.4	13.7
Main shoot lamina dry weight (mg $plant^{-1}$)	99.0	97.0	88.1	285.9	245.6	235.5	492.3	435.8	323.3	22.7
Main shoot specific lamina area (mm^2 mg^{-1})	32.01	32.03	37.55	33.45	35.27	39.22	30.55	31.91	39.42	NS
Main shoot total dry weight (mg $plant^{-1}$)	140.1	140.4	135.3	457.9	402.6	412.9	1535.0	1365.8	1043.0	75.2
Tiller dry weight (mg $plant^{-1}$)	25	18	5	567	302	124	3854	1946	324	373
Total plant dry weight (mg $plant^{-1}$)	165	158	140	1025	705	537	5389	3312	1367	407
Tiller contribution to plant dry weight (%)	14.85	11.09	3.25	55.01	42.36	22.77	71.46	57.32	21.09	8.67
Tiller number / plant	1.55	1.28	0.67	4.12	2.52	1.22	4.32	2.83	1.53	0.58
Nitrogen concentration in plant tissue (%)	5.11	4.92	4.92	3.76	3.54	3.45	1.91	2.04	1.82	NS
Nitrogen uptake by plant (mg $plant^{-1}$)	8.41	7.78	6.90	38.82	25.02	18.63	102.54	69.85	25.11	9.92
Relative growth rate (mg g^{-1} d^{-1})	150.4	148.8	145.2	113.9	93.1	83.9	92.5	85.1	51.0	8.2

* = HSD to compare means within same growth stage
NS = Not significant (P>0.05)
(Data are the means of 2 nitrogen amounts)

the harvests. Total nitrogen uptake and relative growth rate were unaffected by plant density at leaf 5 appearance, but decreased significantly with the increase in plant density both at leaf 7 appearance and awn emergence.

5.3.7.5 Nitrogen and harvest interaction

The effects of nitrogen on the various plant growth parameters, recorded at different growth stages, are presented in Table 5.15. There was no effect of nitrogen on growth at leaf 5 appearance and leaf 7 appearance. However, the area and dry weight of main shoot leaves, total plant dry weight, nitrogen concentration in the dry matter and nitrogen uptake were increased with the application of nitrogen at awn emergence. The effect of nitrogen on tiller number and tiller dry weight was not statistically significant. However, the contribution of tillers to total dry weight did incease significantly ($P<0.05$) with the application of nitrogen.

5.3.8 Yield analysis

The interactions between plant density and nitrogen for grain yield and its components, recorded at final harvest, were not significant ($P<0.05$) (Table 5.2). Therefore, the main effects of plant density and nitrogen amount will only be described.

5.3.8.1 Main effects of plant density

Total biomass yield, grain yield, harvest index and total

Table 5.15 The effects of nitrogen amount on plant growth parameters recorded at different growth stages during experiment 3.

Growth stages	Leaf 5 appearance		Leaf 7 appearance		Awn emergence		HSD*
Nitrogen amount (Kg N ha^{-1})	0	100	0	100	0	100	(P=0.05)
PARAMETER							
Main shoot lamina area (cm^2 $plant^{-1}$)	32.2	31.6	90.4	92.6	128.6	148.6	9.2
Main shoot lamina dry weight (mg $plant^{-1}$)	97.0	92.5	249.0	262.3	383.6	450.6	15.3
Main shoot specific lamina area (mm^2 mg^{-1})	33.31	34.42	36.45	35.51	34.48	33.44	NS
Main shoot total dry weight (mg $plant^{-1}$)	138.9	138.3	419.4	429.4	1274.2	1355.0	50.8
Tiller dry weight (mg $plant^{-1}$)	16	15	322	340	1864	2219	NS
Total plant dry weight (mg $plant^{-1}$)	155	154	742	769	3138	3574	275
Tiller contribution to plant dry weight (%)	9.96	9.50	39.36	40.73	46.01	53.90	5.85
Tiller number / plant	1.18	1.16	2.56	2.68	2.74	3.04	NS
Nitrogen concentration in plant tissue (%)	4.98	4.99	3.19	3.97	1.59	2.26	0.28
NItrogen uptake by plant (mg $plant^{-1}$)	7.70	7.69	24.41	30.56	47.93	83.74	6.70
Relative growth rate (mg g^{-1} d^{-1})	148.2	147.9	95.4	98.6	72.0	80.4	NS

* = HSD to compare means within same growth stage
NS = Not significant (P>0.05)
(Data are the means of 3 plant densities)

Table 5.16 Main effects of plant density on grain yield and its components of spring barley.

Plant density (plants m-2)	150	300	600	HSD (P=0.05)
PARAMETERS				
Total number of shoots / plant	5.01	3.06	1.66	0.93
Number of ears / plant	4.77	2.72	1.39	0.72
Ear bearing shoots (%)	95.30	89.40	84.60	10.05
Number of grains / ear	23.88	22.11	19.86	1.62
Number of grains / plant	114	61	28	20
Specific grain weight (mg grain-1)	42.00	40.81	38.89	NS
Grain yield / plant (g)	4.75	2.42	1.07	0.60
Grain yield / ha (t)	6.84	6.99	6.14	NS
Above ground biomass / plant (g)	10.10	5.13	2.37	1.40
Above ground biomass / ha (t)	14.55	14.78	13.63	NS
Harvest index (%)	47.00	47.33	45.00	NS
Nitrogen concentration in grain (%)	1.82	2.01	2.06	NS
Grain nitrogen / plant (mg)	85.7	47.9	22.0	14.16
Grain nitrogen / ha (Kg)	123	138	126	NS

NS = Not significant (P>0.05)
(Data are the means of 2 nitrogen amount)

nitrogen uptake by grains per hectare were not significantly affected by plant density (Table 5.16). Grain yield per plant was significantly reduced at high plant density. This decrease in grain yield was mainly due to fewer number of ears, grains per plant and grains per ear at high plant density. Specific grain weight was also reduced by increasing plant density but this was not statistically significant.

5.3.8.2 Main effects of nitrogen amount

Generally grain yield and its various components were not affected by nitrogen application (Table 5.17), except number of grains per ear where the increase in number over the control was significant ($P<0.05$).

5.4 Yield determination

Grain yield per plant of cereals is basically determined by the number of grains per plant (Biscoe and Gallagher, 1977), which is in turn determined by the number of tilleers per plant, number of ears per plant and number of grains per ear. In this study an attempt was made to describe the relationship between plant yield and its contributing factors. Data for all the densities and nitrogen levels tested was combined and linear regression analyses between yield and its contributing factors were carried out. These analyses revealed a strong correlation ($r=0.997$) between number of tillers per plant at awn emergence and number of ears per plant (Figure 5.2). Number of grains per plant was strongly correlated ($r=0.997$)

Table 5.17 Main effect of nitrogen application on grain yield and its components of spring barley.

Nitrogen amount (Kg N ha-1)	0	100	HSD (P=0.05)
PARAMETER			
Total number of shoots / plant	3.24	3.25	NS
Number of ears / plant	3.07	2.85	NS
Ear bearing shoots (%)	93.8	85.6	6.7
Number of grains / ear	21.28	22.62	1.05
Number of grains / plant	67.7	66.8	NS
Specific grain weight (mg grain-1)	40.38	40.75	NS
Grain yield / plant (g)	2.76	2.74	NS
Grain yield / ha (t)	6.68	6.64	NS
Above ground biomass / plant (g)	5.96	5.78	NS
Above ground biomass / ha (t)	14.39	14.26	NS
Harvest index (%)	46.56	46.33	NS
Nitrogen concentration in grain (%)	1.93	1.99	NS
Grain nitrogen / plant (mg)	50.4	53.3	NS
Grain nitrogen / ha (Kg)	128.1	130.5	NS

NS = Not significant (P>0.05)
(Data are the means of 3 plant densities)

with the number of ears per plant (Figure 5.3). A significant correlation (r=0.999) between plant grain yield and number of grains per plant was also observed (Figure 5.4). Regression analyses also showed that plant grain yield is also highly correlated with number of ears per plant (r=0.997), number of grains per plant (r=0.900) and specific grain weight (r=0.869). It could therefore be concluded that all of the above mentioned yield components are important for determining the yield of a barley plant. To determine the contibution of these factors towards determining the grain yield a stepwise regression analysis between the plant yield and its componets was carried out. A highly significant linear correlation (r=0.999) was observed. The calculated regression equation observed was as follows;

$$Y_g = -0.58 + 0.992\ Ne + 0.128\ Ng - 0.059\ SGWT$$

where Y_g is grain yield per plant (mg), Ne is number of ears per plant, Ng is number of grains per ear and SGWT is specific grain weight (mg).

Grain yield per unit area was not significantly affected by plant density but the yield per plant decreased with the increase in plant density and the effect of nitrogen was very small (Figure 5.5). A reciprocal model as suggested by Willey and Heath (1969); Baker and Briggs (1982) was fitted to the data and a significant linear relationship between the reciprocal of grain yield per plant and plant density was observed. 97.1% of the variability in grain yield was

Figure 5.2 Relationship between number of tillers per plant and number of ears per plant. (Data are for 2 nitrogen amounts and 3 plant densities). Equation for the fitted line is;

$$Y=-0.341(\pm 0.167)+1.014(\pm 0.047)X, \quad r=0.997$$

Figure 5.3 Relationship between number of ears per plant and number of grains per plant. (Data are for 2 nitrogen amounts and 3 plant densities). Equation for the fitted line is;

$$Y=-0.6966(\pm 3.414)+25.23(\pm 1.047)X, \quad r=0.997$$

Figure 5.2

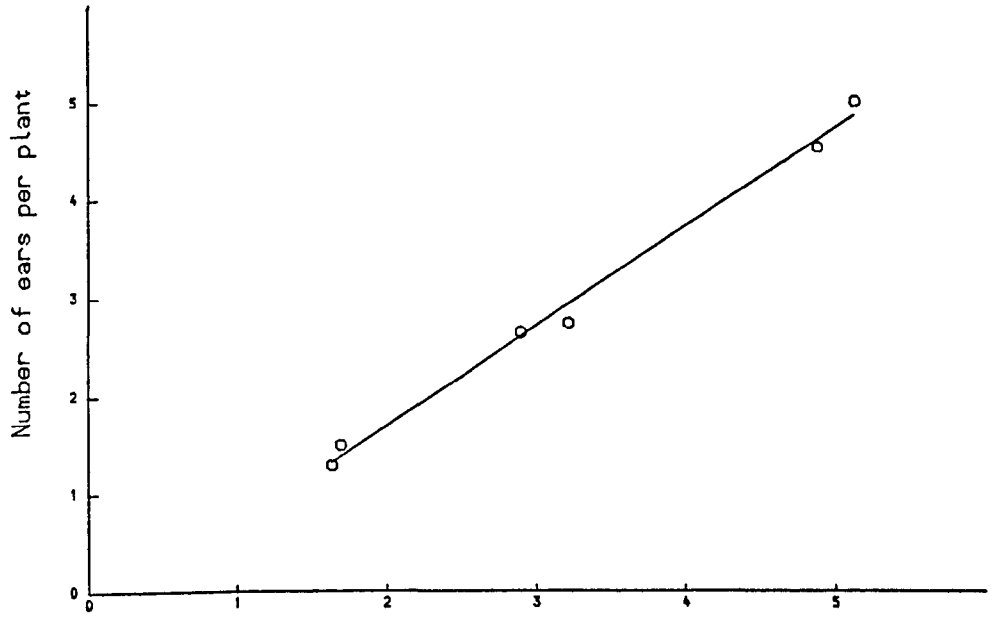
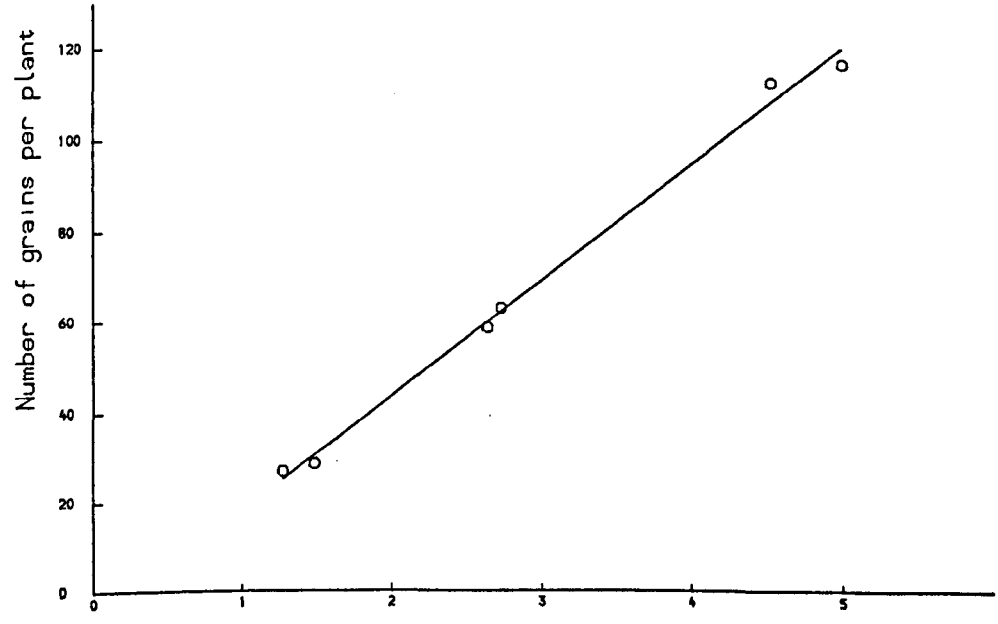


Figure 5.3



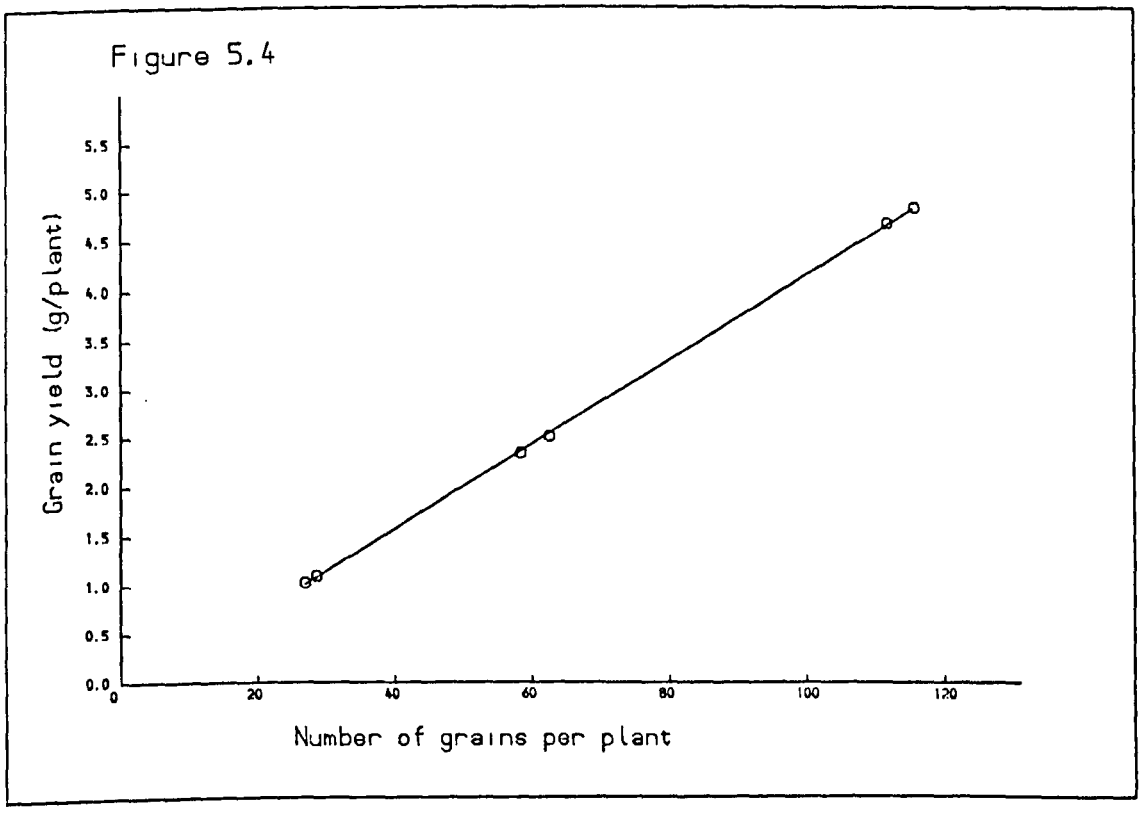


Figure 5.4 Relationship between number of grains per plant and grain yield per plant. (Data are for 2 nitrogen amounts and 3 plant densities). Equation for the fitted line is;

$$Y=-0.149(\pm 0.025)+0.0429(\pm 0.0003)X, \quad r=0.999$$

Figure 5.5 The effects of plant density and nitrogen supply on grain yield per plant.

Figure 5.6 Relationship between plant density and reciprocal of grain yield per plant. (Data are for 2 nitrogen amounts and 3 plant densities). Equation for the fitted line is;

$$Y=-0.053(\pm 0.032)+0.00164(\pm 0.00008)X, \quad r=0.998$$

Figure 5.5

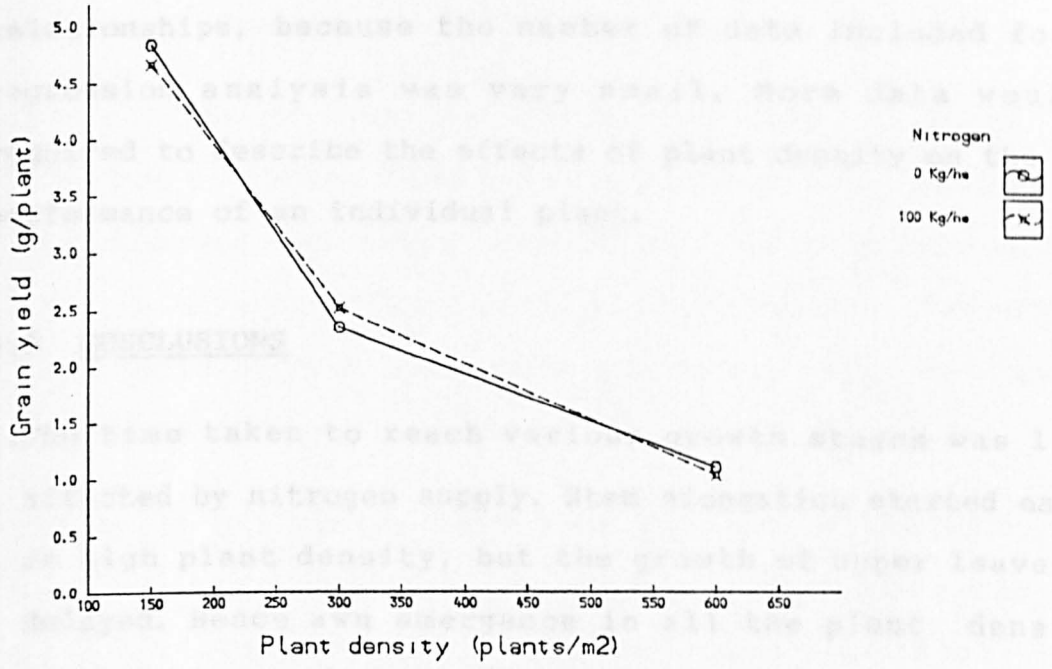
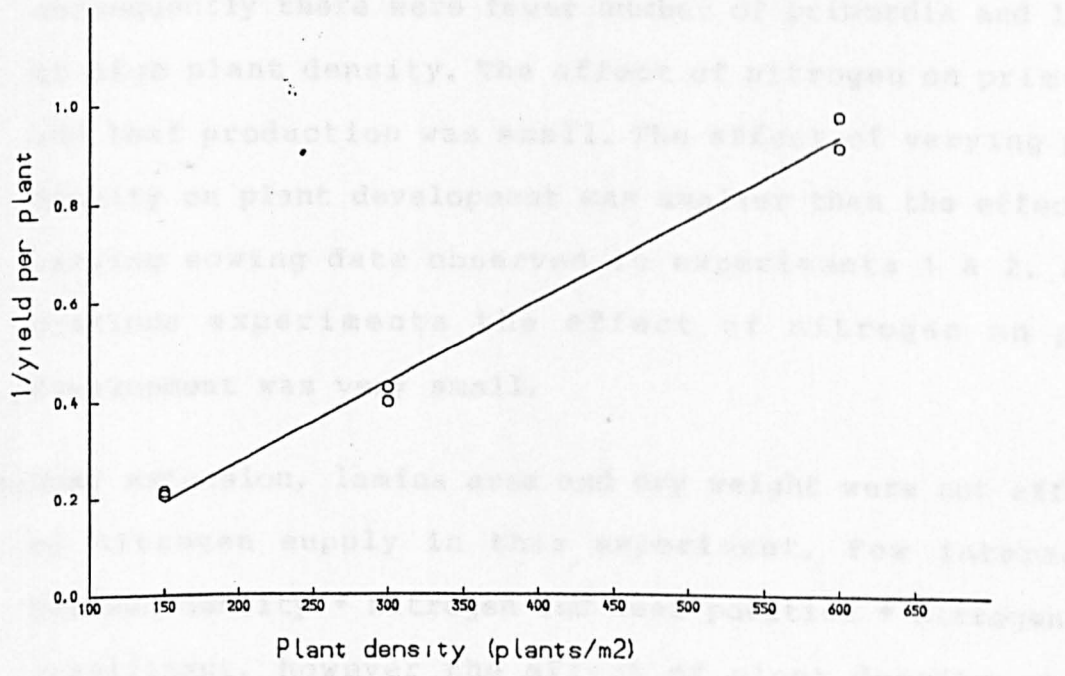


Figure 5.6



accounted for by the variability in the plant density (Figure 5.6). However care should be taken in considering these relationships, because the number of data included for the regression analysis was very small. More data would be required to describe the effects of plant density on the yield performance of an individual plant.

5.5 CONCLUSIONS

1. The time taken to reach various growth stages was little affected by nitrogen supply. Stem elongation started earlier at high plant density, but the growth of upper leaves was delayed. Hence awn emergence in all the plant densities occured more or less at the same time.

2. The rates and durations of primordia initiation and leaf appearance were reduced by increasing plant density and consequently there were fewer number of primordia and leaves at high plant density. The effect of nitrogen on primordia and leaf production was small. The effect of varying plant density on plant development was smaller than the effects of varying sowing date observed in experiments 1 & 2. As in previous experiments the effect of nitrogen on plant development was very small.

3. Leaf extension, lamina area and dry weight were not affected by nitrogen supply in this experiment. Few interaction between density * nitrogen and leaf position * nitrogen were significant, however the effect of plant density on leaf growth depended on leaf position. Lamina area of leaves 1-4

was increased with plant density, leaf 5 was not affected but area of leaves 6-8 decreased with plant density. This was mainly due to the trends found in LED.

4. The effects of plant density and nitrogen increased with time but no interaction between plant density and nitrogen was observed i.e. extra nitrogen was not able to compensate for the adverse effects of high plant density. Therefore it is speculated that some other factor eg. light was limiting leaf growth.

5. Generally the plants were much smaller, there were fewer tillers, lower relative growth rates and lower grain yield at high plant density, due to reduction in all yield components. The effects of plant density on the main shoot were smaller than effects on tillers because main shoot was buffered. The effects of nitrogen were small due to extra nitrogen availability from soil.

CHAPTER 6

GENERAL DISCUSSION

6.1 PREFACE

This study is concerned with the influence of sowing date (and hence the natural variation in env ironmental variables i.e. temperature, photoperiod and radiation) and nitrogen supply on leaf growth and plant development in barley. A series of experiments on sequentially sown spring barley (cv. Claret) were conducted in glasshouses with no control over temperature, photoperiod and radiation. Therefore the variations in these env ironmental variables in the glasshouse were caused by the natural changes in the external environment.

During all the experiments plants were kept well watered so availability of water could not be a variable factor. Pests and diseases were not a serious problem during this study and if and when there was any occurance of pests and diseases, plants were immediatly sprayed with appropriate chemicals. Therefore the differences in various plant growth and development parameters recorded, could only be due to the different nitrogen supply, sowing dates, plant densities, growing media and size of the growing containers used.

Instead of discussing each set of experiments in isolation it was thought logical to pool the results of all the experiments together and examine the effects of the variables, tested in this study, on the developmental and growth processes. Since different measurements were taken in the three series of experiments, complete comparisons for all the parameters and sowing dates cannot be made.

The discussion first considers the advantages of the approach adopted in these experiments. Effects of different growing media are then considered. Finally the factors influencing leaf appearance and leaf growth are considered.

6.2 Advantages and disadvantages of using this particular experimental approach

The advantages and disadvantages of conducting experiments in growth rooms and in the external environment have already been discussed in the literature review (section 2.5). When carrying out and analysing these experiments several additional problems were detected.

1. A major factor which became apparent is the complex nature of responses to nitrogen, sowing date and leaf position. The present experiments were factorial experiments and many interactions were significant. For example the effects of nitrogen and sowing date depended upon the position of the leaf on the main shoot. Many of the past studies (eg. Gallagher, 1979) used one sowing date and one nitrogen level. Very few studies have looked at interactions as in this study. Because interactions were significant the effects of a single factor cannot be considered in isolation.

2. It was not possible to isolate effects of a single environmental factor due to the correlations associated with seasonal changes in temperature, radiation and photoperiod. However, when the results were analysed it was found that

changes in certain parameters eg. LAR, LER and LED were better correlated with certain environmental variables than others. This suggests that certain variables may have a controlling influence on certain plant growth and development processes, but we may need to go back to controlled environments to prove these hypotheses.

3. Because past experiments have tested single factors whereas a multifactorial approach was used in these experiments, there is little comparable data available with which the results of this study could be compared. Therefore the discussion is limited in this extent.

6.3 Effects of growth media

In experiment 1 the plants were grown in a nutrient free medium (i.e. perlite) and nutrients were added in solution form. In experiment 2 plants were grown in soil and sand in small pots. In experiment 3 plants were grown in soil and sand in large tanks with greater depth for root growth.

Although the plant growth parameters which were recorded were slightly different in each set of experiments, extension growth of leaf 5 was recorded in all the experiments. Data on extension growth of leaf 5 in each set of experiments, for either March or April sowings, are shown in Table 6.1 to permit comparisons between growing media. The results show that leaf 5 was larger with greater lamina area and dry weight when plants were grown in soil. Lamina area was greatest when

plants were grown in large tanks mainly due to faster extension rate. The effect of growing media on extension duration was much smaller. These differences in leaf extension between the growing media are most probably due to the availabilty of residual nitrogen in the soil which was released during plant growth and also due to less physical constraints on the spread of root volume in the large tanks.

Use of different growing media has also affected the response of plant growth to nitrogen supply. The effect of nitrogen application was much greater in plants grown in perlite than in plants grown in soil due to residual nitrogen supply in soil.

6.4 Growth of the foliage canopy

Growth of the foliage involves three processes :

1. Initiation of leaf primordia at the shoot apex,
2. leaf appearance,
3. leaf (lamina + sheath) expansion.

In winter wheat and winter barley because of cold temperatures leaf primordia are initiated over a long time period and rates and durations of leaf initiation can be determined (Kirby, 1981; Gallagher, 1979; Gallagher and Baker 1981). In spring wheat and spring barley most of the leaf primordia are initiated before crop emergence. In these cereals leaf initiation cannot be studied unless seeds are excavated and microdissected between the time of sowing and time of crop

emergence. In this study only leaf appearance and final number of leaves on the main shoot were recorded.

Table 6.1 Effect of growing media on extension growth of leaf 5 of main shoot

	Experiment 1*	Experiment 2+	EXperiment 3x
Sowing date	28 April	14 April	17 March
Growth media	Perlite	Soil+Sand	Soil+Sand
Growing container	Small pots	Small pots	Large tanks
LER (mm $^{o}Cd^{-1}$)	1.25	1.74	2.55
LED (^{o}Cd)	162	215	213
FLL (mm)	203	373	512
LA (cm2 $leaf^{-1}$)	9.47	19.12	31.53
LWT (mg $leaf^{-1}$)	36.11	80.81	89.87

* For experiment 1 data are the means of 4 levels of nitrogen
+ For experiment 2 data are the means of 4 levels of nitrogen
x For experiment 3 data are for a plant density of 300 plants m^2 and 2 levels of nitrogen

6.4.1 Leaf appearance

For different species rate of leaf appearance in thermal time units has been shown to be a function of rate of change of daylength at crop emergence (Baker, Gallagher and Monteith, 1980; for winter wheat; Ellis and Russell, 1983; for spring and winter barley; Hay and Abbas-Alani, 1983; for forage rye grass; for spring barley; Kirby and Ellis, 1980;for spring barley). A good correlation (r=0.877) between rate of change of daylength at crop emergence and rate of leaf appearance per day degree was also observed in this study. Results from the current experiments (expressed as the means of all nitrogen levels tested) together with the lines of best fit calculated by other workers are shown in Figure 6.1. The spread of points around the regression lines is quite uniform and the correlation coefficients for all the regression lines are significant. However, such correlation could be highly influenced by the points at the extremes. Variation in daylength is such that rate of change of daylength varies little for a large part of the year. The rate changes more rapidly in mid summer and mid winter at the time of the solstice. Most crops are sown in the field around the time of the equinox, when rate of change of daylength is changing little. To more thoroughly test this relationship there is a need to make alot of sowings during the short time period when rate of change of daylength is changing rapidly. Since leaf appearance is related to crop growth stage (Zadoks, Chang and Konzak, 1974) this relationship could be used to predict crop

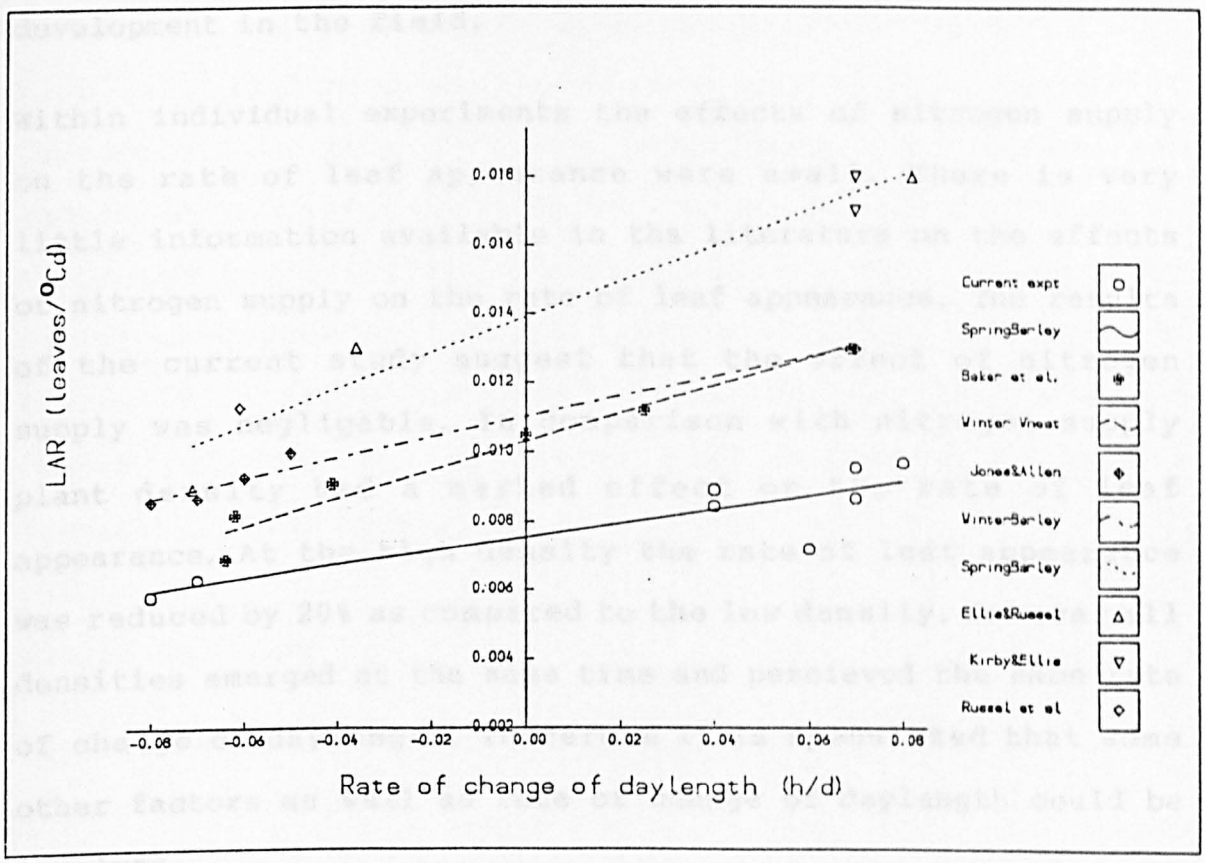


Figure 6.1 Main shoot leaf appearance rate (LAR in thermal time unit) as a function of rate of change of daylength at crop emergence. (Data for current experiment are the means of nitrogen levels tested). Regression equation for the current experiment is :

$$Y=0.0075(\pm 0.0002)+0.0207(\pm 0.0038)X, \quad r=0.8773$$

development in the field.

Within individual experiments the effects of nitrogen supply on the rate of leaf appearance were small. There is very little information available in the literature on the effects of nitrogen supply on the rate of leaf appearance. The results of the current study suggest that the effect of nitrogen supply was negligable. In comparison with nitrogen supply plant density had a marked effect on the rate of leaf appearance. At the high density the rate of leaf appearance was reduced by 20% as compared to the low density. However all densities emerged at the same time and percieved the same rate of change of daylength. Therefore it is speculated that some other factors as well as rate of change of daylength could be involved.

6.4.2 Final number of leaves

In the first experiment plants were destructively harvested when leaf 5 had attained its maximum length and hence data on final number of leaves for this experiment is not available. However number of leaves was recorded in other experiments. In experiment 2 nitrogen supply and sowing date had only small and nonsignificant effects on final number of leaves. All sowings and nitrogen amounts had 7 leaves. In published experiments final number of leaves has been shown to vary systematically with sowing date (Jones and Allen,1986) but the physiological mechanisms underlying this response are not clearly understood. The process of leaf initiation in spring

cereals has received little attention by physiologists and we know very little about the factors controlling number of leaves in this crop. In these experiments leaf number was reduced by incresing plant density in experiment 3 as found by Kirby and Faris (1972). Number of leaves was increased by sowing in September in experiment 2 as found by Jones and Allen (1986) and Kirby (1986). This increase in number of leaves is probably associated with shorter photoperiod (Aspinall, 1966; Fairery et al., 1975).

6.4.3 Leaf area

In discussing the effects of nitrogen and sowing date on leaf area we must consider :

1. the effects of nitrogen and sowing date on LER, LED and FLL of various main shoot leaves,
2. the relationship between FLL and lamina area.

LER, LED and FLL were significantly affected by time of sowing, nitrogen supply, leaf position and plant density in these experiments. Most of the first and second order interactions involving these variables were also significant, which makes interpretation and discussion of results more complex.

For all the treatments and replicates in all the experiments the correlation coefficients between leaf length and thermal time (which was used to derive LER and LED) were always significant. Therefore temperature is an important factor

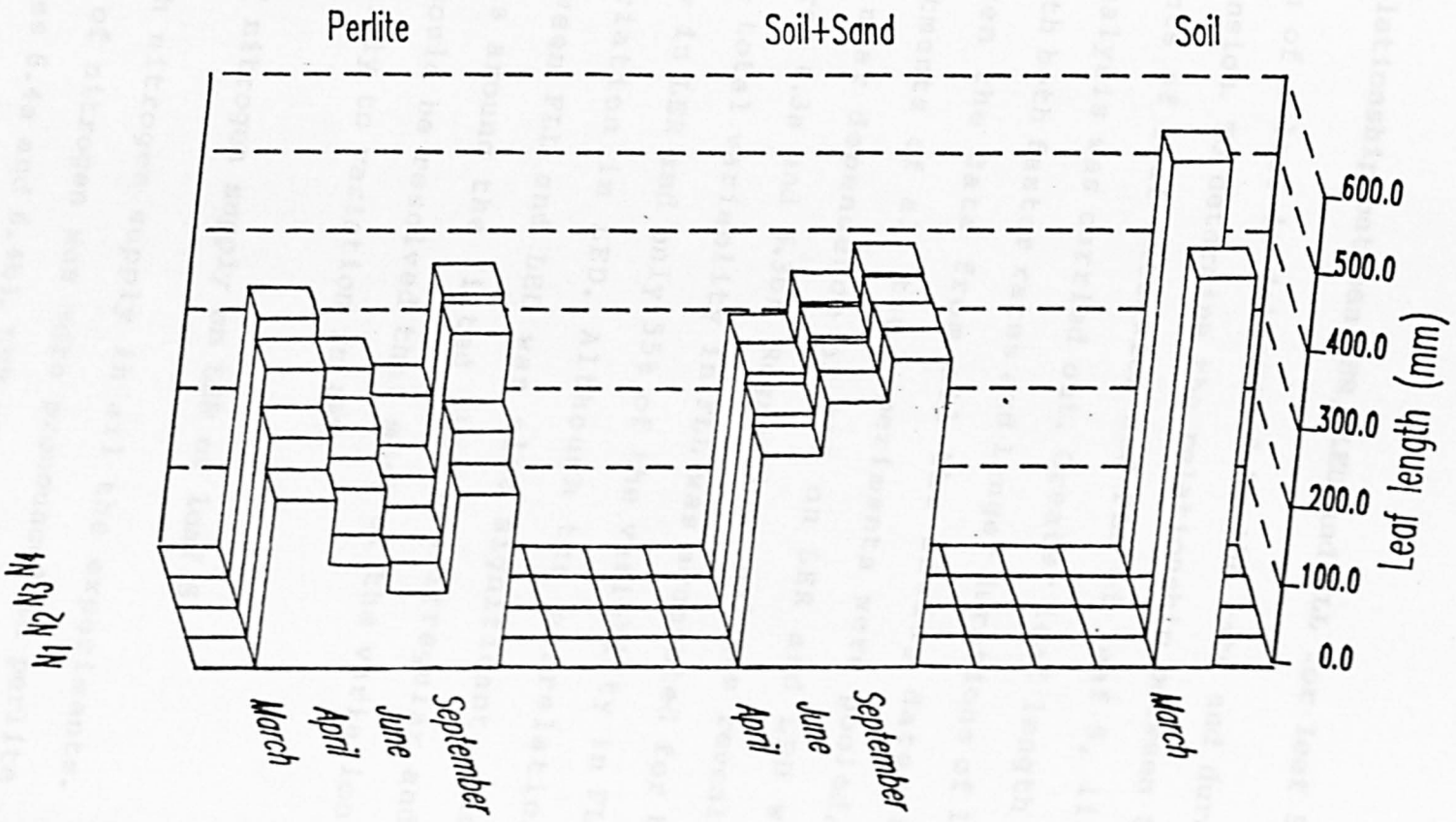
influencing LER as reported by Gallagher (1979) and others. Because of the importance of the effect of temperature on leaf extension, in this study LER and LED were calculated in thermal time units. This was done so that comparisons between sowing dates could be made. If LER had been measured in Julian time units (mm day $^{-1}$) the differences between sowings and leaf positions could be due to differences in temperature experienced.

In experiment 1 measurements of leaf extension were restricted to leaf 5 on the main shoot, whereas for experiment 2 and 3 these measurements were made on all of the first 6 main shoot leaves. Hence extension growth of leaf 5 in all the experiments will firstly be considered and an attempt will be made to use this leaf as a standard to make comparisons between experiments. However, because leaf extension varied with the leaf position and not all the sowings had the same number of leaves, accepting leaf 5 as a standard may not be strictly valid.

6.4.4 Extension of leaf 5 of main shoot

Variations in the FLL of leaf 5 of the main shoot in response to sowing date and nitrogen supply were observed in all the experiments (Figure 6.2). Leaf length increased with nitrogen supply and was greater in plants sown in March and September than in plants sown in April and June. Plants grown in soil had longer leaves than plants grown in perlite and the nitrogen effect was much greater in plants grown in perlite.

Fig.6.2 The effects of sowing date, nitrogen supply and growing media on length of 5th main shoot leaf (sheath+lamnia).



Leaves were longest in the third experiment, where plants were grown in soil in large tanks.

6.4.4.1 Relationship between LER, LED and FLL for leaf 5

Final length of a leaf is determined by the rate and duration of leaf extension. To determine the relationship between these two components of leaf extension and FLL of leaf 5, linear regression analysis was carried out. Greater leaf length was associated with both faster rates and longer durations of leaf extension. When the data from all the sowing dates and nitrogen treatments of all the experiments were pooled, a significant linear dependence of FLL on LER and LED was observed (Figures 6.3a and 6.3b). Regression analyses revealed that 88% of the total variablity in FLL was accounted for by the variability in LER and only 55% of the variabilty in FLL was due to variation in LED. Although the correlation coefficient between FLL and LED was also significant, the scatter of points around the fitted line was irregular and large. Hence it could be resolved that most of the variation in FLL was due mainly to variation in LER.

6.4.4.2 Effect of nitrogen supply on LER of leaf 5

LER increased with nitrogen supply in all the experiments. However the effect of nitrogen was more pronounced in perlite than in soil (Figures 6.4a and 6.4b). LER was different in the different sowing dates. Much of this variation in LER between sowing dates was removed when LER, for each set of

Figure 6.3 Relationship between leaf extension rate (LER) and final leaf length of leaf 5 on the main shoot. (Data are for all the sowing dates and nitrogen levels tested). Equation of the fitted line is :

$$Y=-54.34(\pm 29.90)+245.83(\pm 17.71)X, \quad r=0.938$$

Figure 6.4 Relationship between leaf extension duration (LED) and final leaf length of leaf 5 on the main shoot. (Data are for all the sowing dates and nitrogen levels tested). Equation of the fitted line is;

$$Y=-304.63(\pm 112.20)+3.121(\pm 0.535)X, \quad r=0.742$$

Figure 6.3

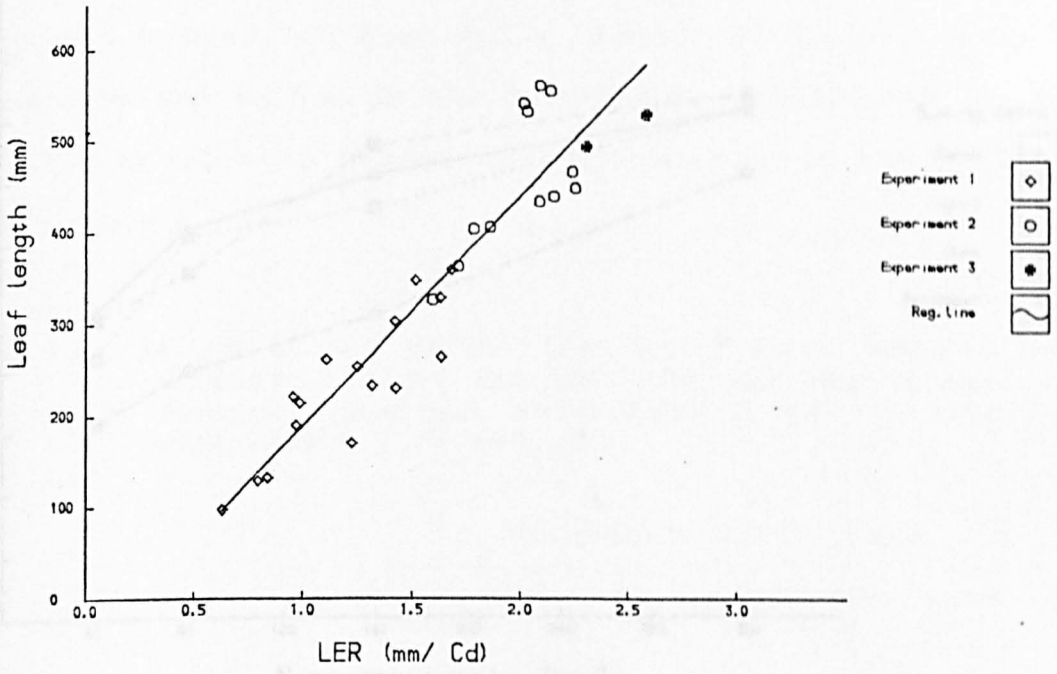


Figure 6.4

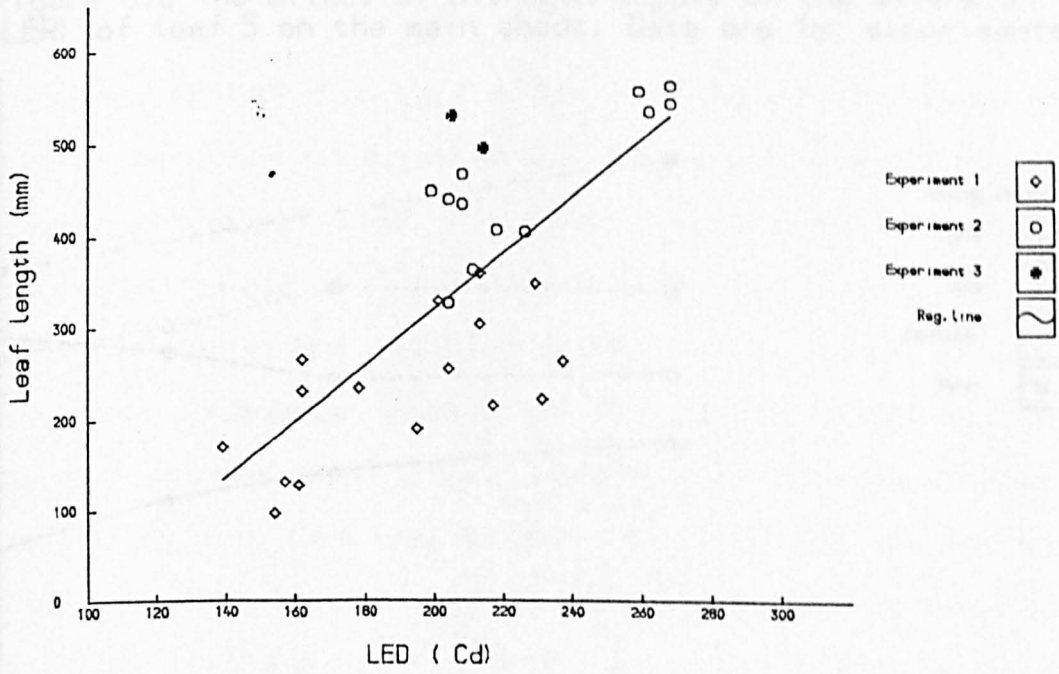


Figure 6.5 The effect of nitrogen supply on the extension rate (LER) of leaf 5 on the main shoot. Data are for experiment 1.

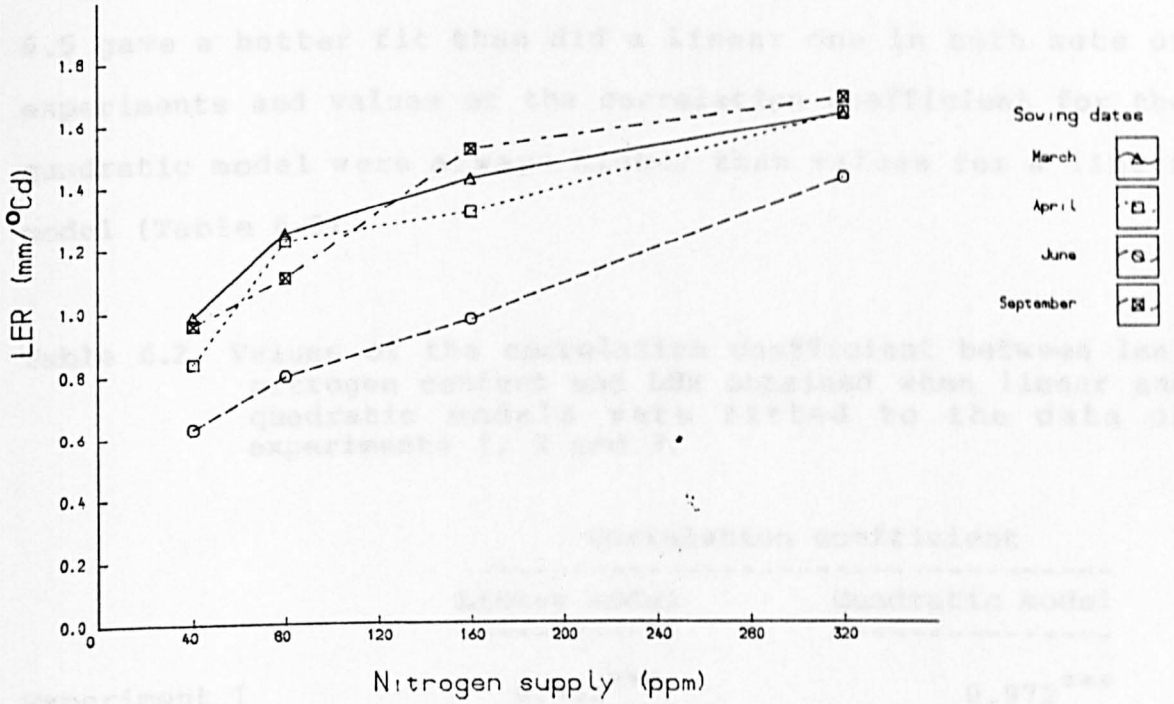
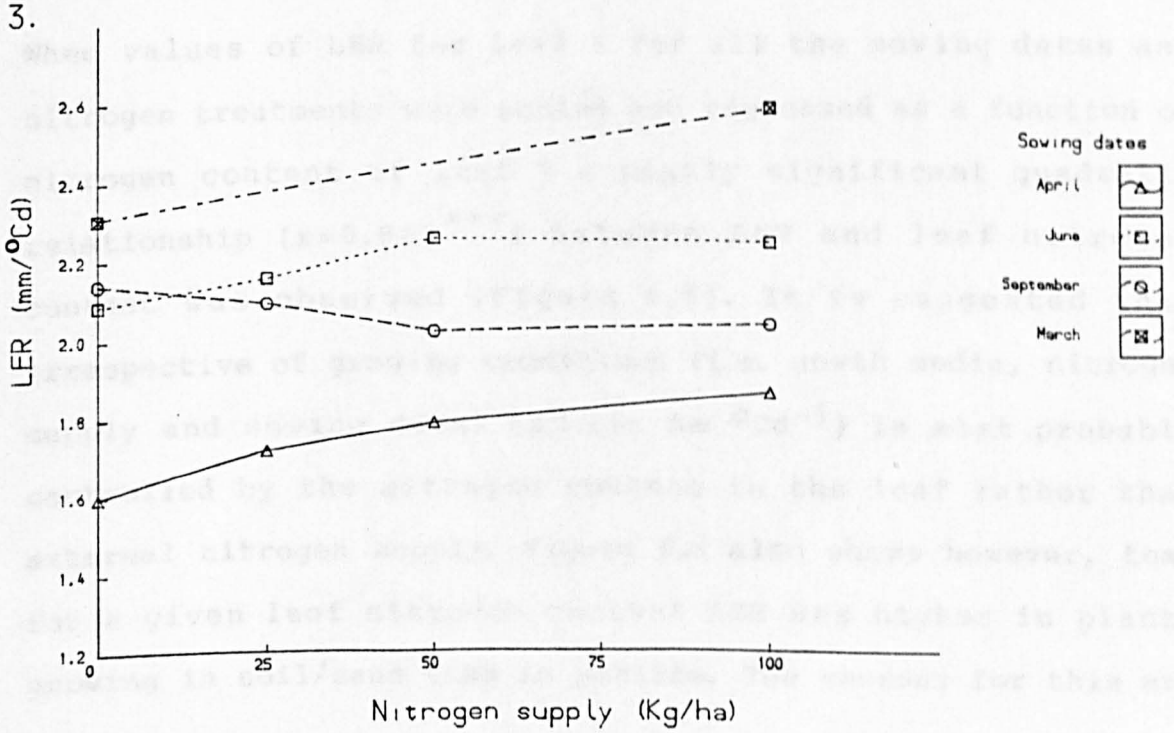


Figure 6.6 The effect of nitrogen supply on the extension rate (LER) of leaf 5 on the main shoot. Data are for experiments 2 & 3.



experiments, was plotted against nitrogen content of the leaf (Figure 6.5). The quadratic relationship shown in the Figure 6.5 gave a better fit than did a linear one in both sets of experiments and values of the correlation coefficient for the quadratic model were always higher than values for a linear model (Table 6.2)

Table 6.2 Values of the correlation coefficient between leaf nitrogen content and LER obtained when linear and quadratic models were fitted to the data of experiments 1, 2 and 3.

	Correlation coefficient	
	Linear model	Quadratic model
Experiment 1	0.952^{***}	0.972^{***}
Experiment 2 & 3	0.798^{***}	0.801^{***}

*** = P < 0.001

When values of LER for leaf 5 for all the sowing dates and nitrogen treatments were pooled and regressed as a function of nitrogen content of leaf 5 a highly significant quadratic relationship ($r=0.880^{***}$) between LER and leaf nitrogen content was observed (Figure 6.5). It is suggested that irrespective of growing conditions (i.e. gowth media, nitrogen supply and sowing date) LER (in mm $^{o}Cd^{-1}$) is most probably controlled by the nitrogen content in the leaf rather than external nitrogen supply. Figure 6.5 also shows however, that for a given leaf nitrogen content LER was higher in plants growing in soil/sand than in perlite. The reasons for this are

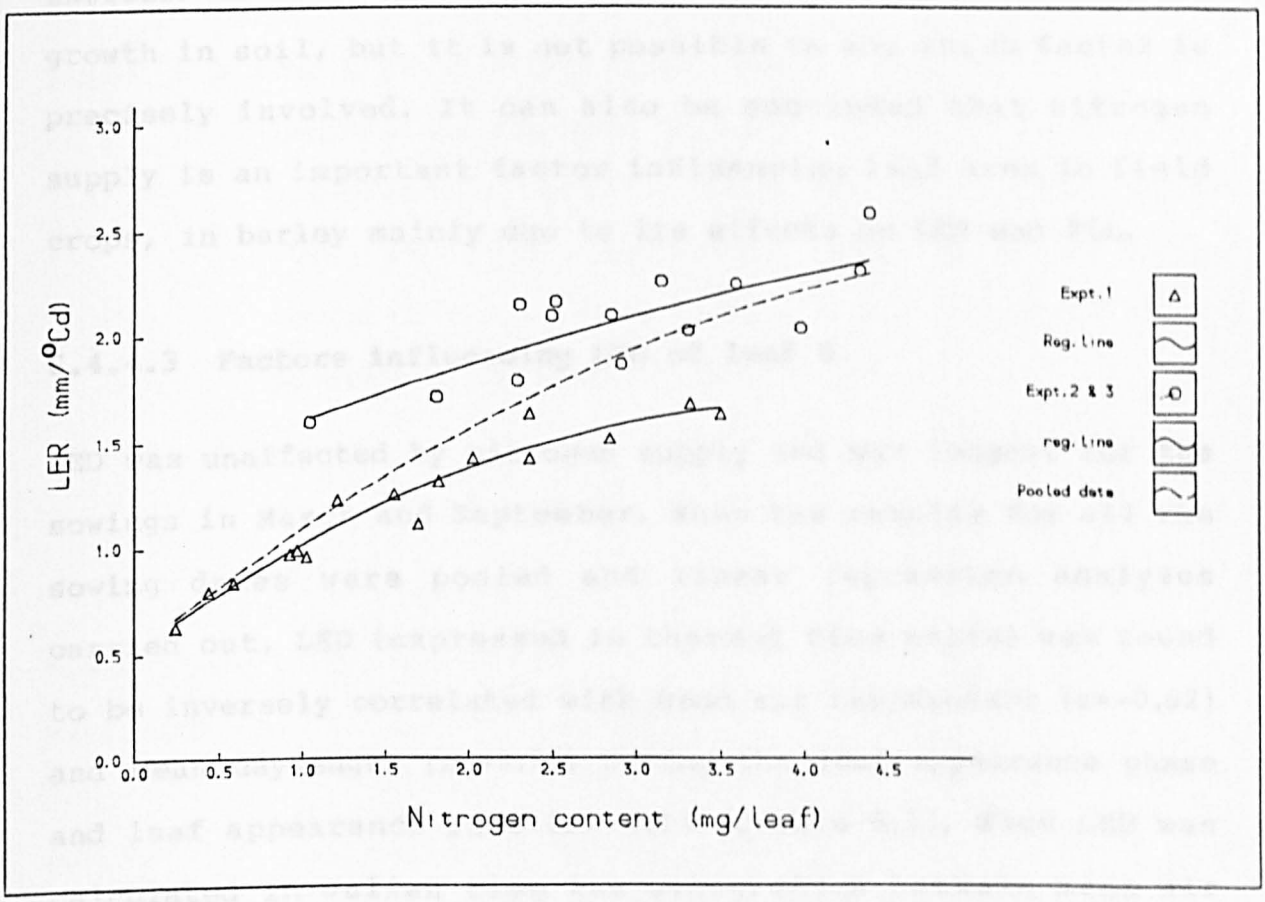


Figure 6.7 Relationship between leaf nitrogen content and leaf extension rate (LER) of leaf 5 on the main shoot. (Data are for all the sowing dates and nitrogen levels tested). Equation for the pooled data is :

$$Y=0.516(\pm 0.189)+0.618(\pm 0.178)X-0.048(\pm 0.037)X^2$$

$$r=0.880$$

unclear. It could be because of better conditions for plant growth in soil, but it is not possible to say which factor is precisely involved. It can also be concluded that nitrogen supply is an important factor influencing leaf area in field crops, in barley mainly due to its effects on LER and FLL.

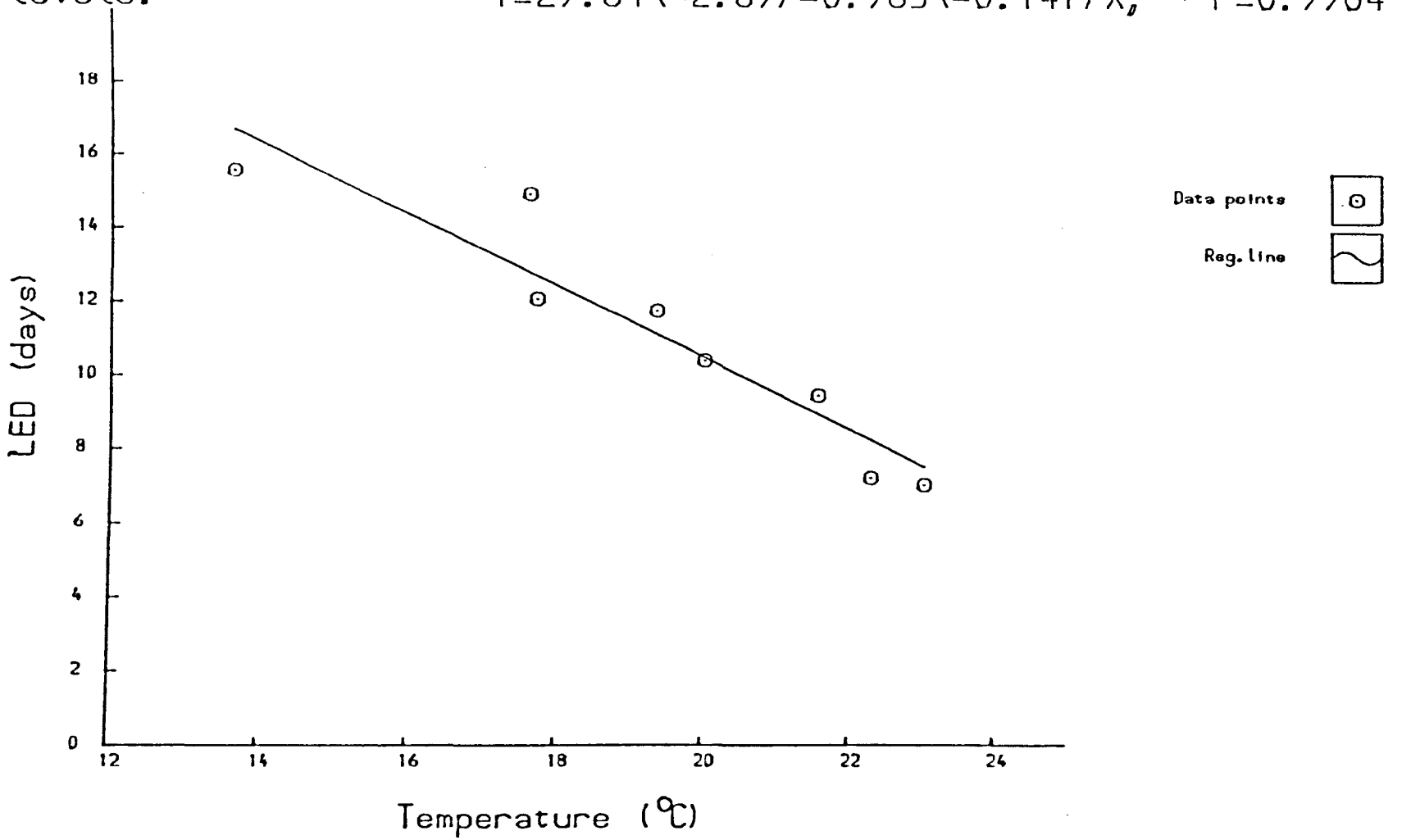
6.4.4.3 Factors influencing LED of leaf 5

LED was unaffected by nitrogen supply and was longest for the sowings in March and September. When the results for all the sowing dates were pooled and linear regression analyses carried out, LED (expressed in thermal time units) was found to be inversely correlated with mean air temperature ($r=-0.62$) and mean daylength ($r=-0.75$) during the leaf appearance phase and leaf appearance rate ($r=-0.54$) (Table 6.3). When LED was calculated in Julian time the correlation between mean air temperature and LED was improved ($r=-0.94^{***}$) and the spread of the points around the regression line was very uniform (Figure 6.6). When the reciprocal of LED (expressed in Julian time) was plotted against mean air temperature a quadratic component in the relationship was observed. This suggests that LED is most probably controlled mainly by temperature. Similar relationships between LED and temperature for spring barley and winter wheat, have been reported by Baker (1979) and Gallagher (1979).

Table 6.3 The linear correlation matrix between mean air temperature and mean daylength during the phase of appearance of leaf 5, mean leaf appearance rate (LAR) and leaf 5 extension duration (LED). Each correlation coefficient has 5 d.f. The corresponding (p=0.05) value of r is :-

	Temperature (°C)	Daylength (h)	LAR (°Cd^{-1})	LAR (d^{-1})	LED (°Cd)	LED (d)
Temperature (°C)	1.0000					
Daylength (h)	0.3335	1.0000				
LAR (°Cd^{-1})	-0.0420	0.9171	1.0000			
LAR (d^{-1})	-0.6982	0.8984	0.6845	1.000		
LED (°Cd)	-0.6213	-0.7530	-0.5395	-0.8211	1.0000	
LED (d)	-0.9407	-0.5447	-0.2072	-0.8246	0.8402	1.0000

Fig.6.8 Relationship between mean air temperature and apparent extension duration (LED) of 5th main shoot leaf. Data are means of N levels. $Y=29.84\ (\pm 2.89)-0.965\ (\pm 0.147)\ X$, $r=0.9904$



6.4.5 Leaf growth of other main shoot leaves

The data on leaf extension growth for the first 6 leaves on the main shoot (experiments 2 and 3) showed that FLL varied with the position of the leaf on the main shoot. The effects of nitrogen supply, leaf position and plant density on LER of these leaves were much greater than the effects on LED. Therefore most of the variation in FLL of different leaves could be mainly due to variation in LER. It has already been shown for leaf 5 (section 6.3.1) that leaf length is mainly determined by LER and the same principle could possibly be applied to other leaves. Figures 6.6 and 6.7 show the relationships bwteen FLL and LER and LED for leaves 1-4 and leaf 6 of main stem. Both correlations are significant although variation in LER accounts for slightly more of the variation in FLL than LED. Clearly both factors (i.e. LER and LED) are important in determining the final leaf length.

6.4.5.1 Relationship between LER and leaf nitrogen content for other main shoot leaves

Figure 6.8 shows the relationship beteen LER and leaf nitrogen content for leaves 1-4 and leaf 6 in experiment 2. Even though the data are for a wide range of sowing dates and nitrogen levels used, LER is strongly related to leaf nitrogen content, although there is little increase in LER above 200 mg N $leaf^{-1}$. The biochemical reasons for this reponse are uncertain but it could be because high nitrogen promotes protein synthesis for cell wall material etc. It would be interesting to see if

Figure 6.9 Relationship between leaf extension rate (LER) and final leaf length of leaves 1-4 & 6 on the main shoot. (Data are for experiment 2). Equation for the fitted line is;

$$Y=-143.89(\pm 23.37)+251.00(\pm 12.41)X, \quad r=0.935$$

Figure 6.10 Relationship between leaf extension duration (LED) and final leaf length of leaves 1-4 & 6 on the main shoot. (Data are for experiment 2). Equation for the fitted line is;

$$Y=-233.00(\pm 30.87)+3.31(\pm 0.18)X, \quad r=0.912$$

Figure 6.9

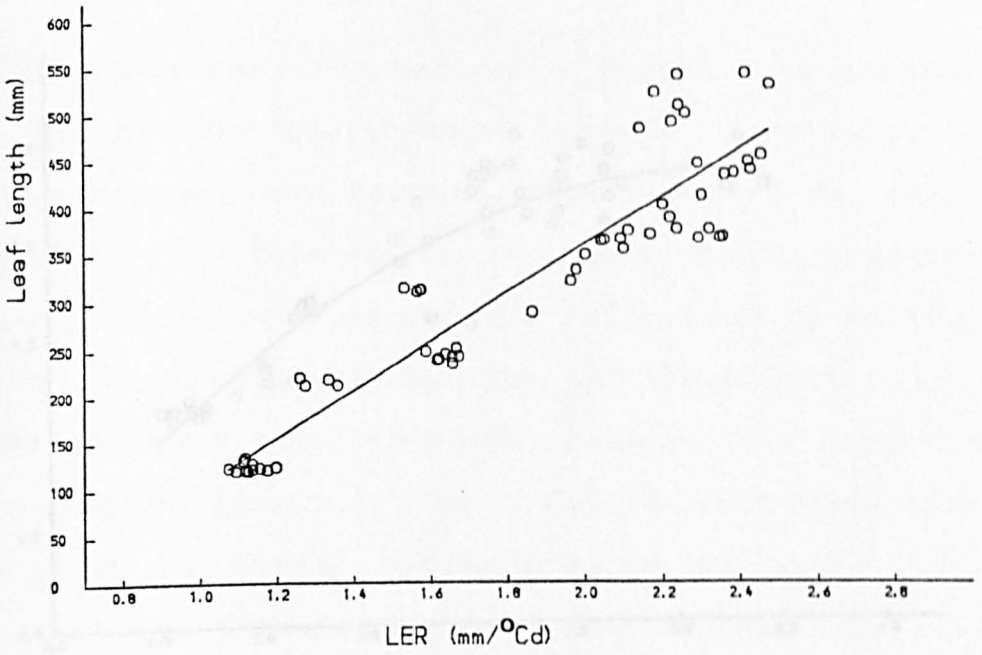
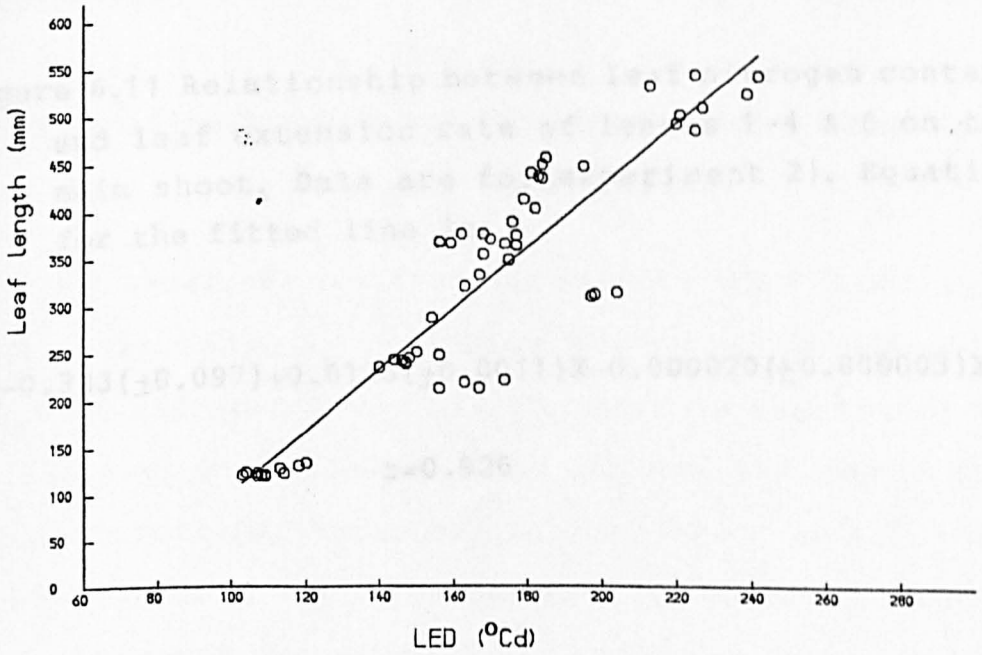


Figure 6.10



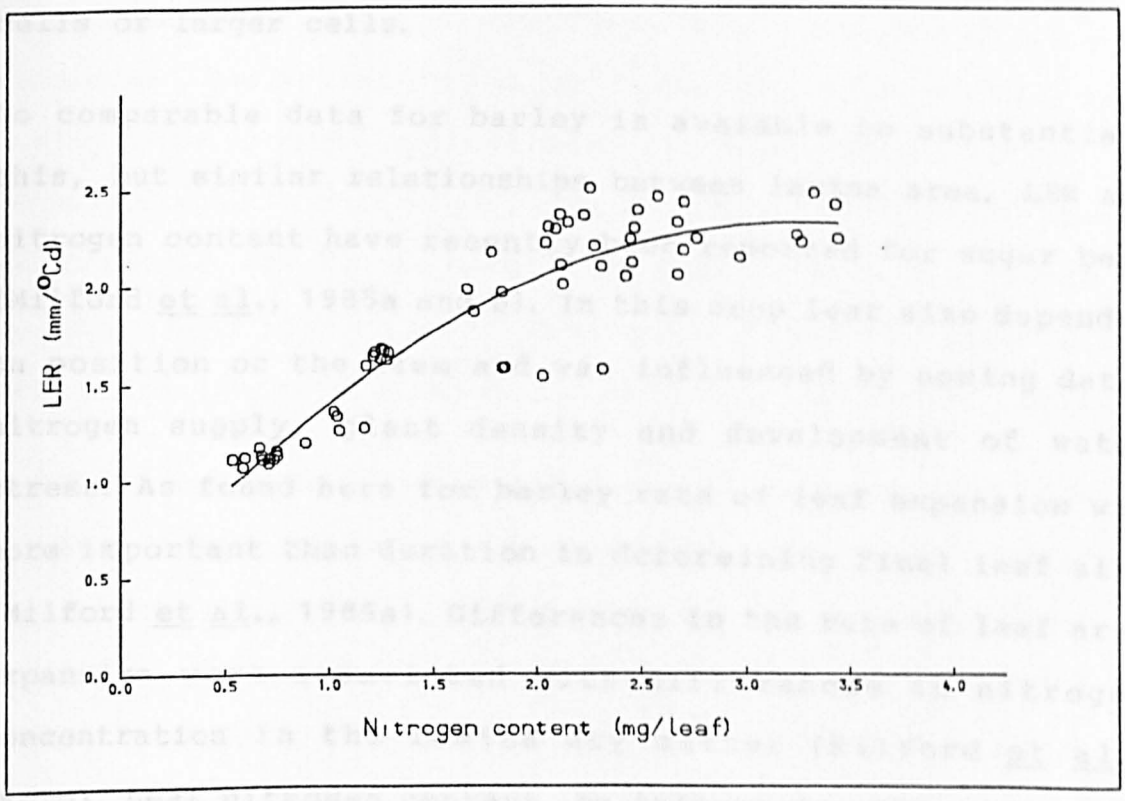


Figure 6.11 Relationship between leaf nitrogen content and leaf extension rate of leaves 1-4 & 6 on the main shoot. Data are for experiment 2). Equation for the fitted line is;

$$Y=-0.333(\pm 0.097)+0.0126(\pm 0.0011)X-0.000020(\pm 0.000003)X^2$$

$$r=0.926$$

the longer leaves, as a result of high nitrogen, had more cells or larger cells.

No comparable data for barley is avaiable to substantiate this, but similar relationships between lamina area, LER and nitrogen content have recently been reported for sugar beet (Milford et al., 1985a and b). In this crop leaf size depended on position on the stem and was influenced by sowing date, nitrogen supply, plant density and development of water stress. As found here for barley rate of leaf expansion was more important than duration in determining final leaf size (Milford et al., 1985a). Differences in the rate of leaf area expansion were associated with differences in nitrogen concentration in the lamina dry matter (Milford et al., 1985b). Leaf nitrogen content, by influencing LER, therefore appears to be an important factor influencing leaf extension and leaf area.

6.4.5.2 Relationship between LED and mean air temperature for other main shoot leaves

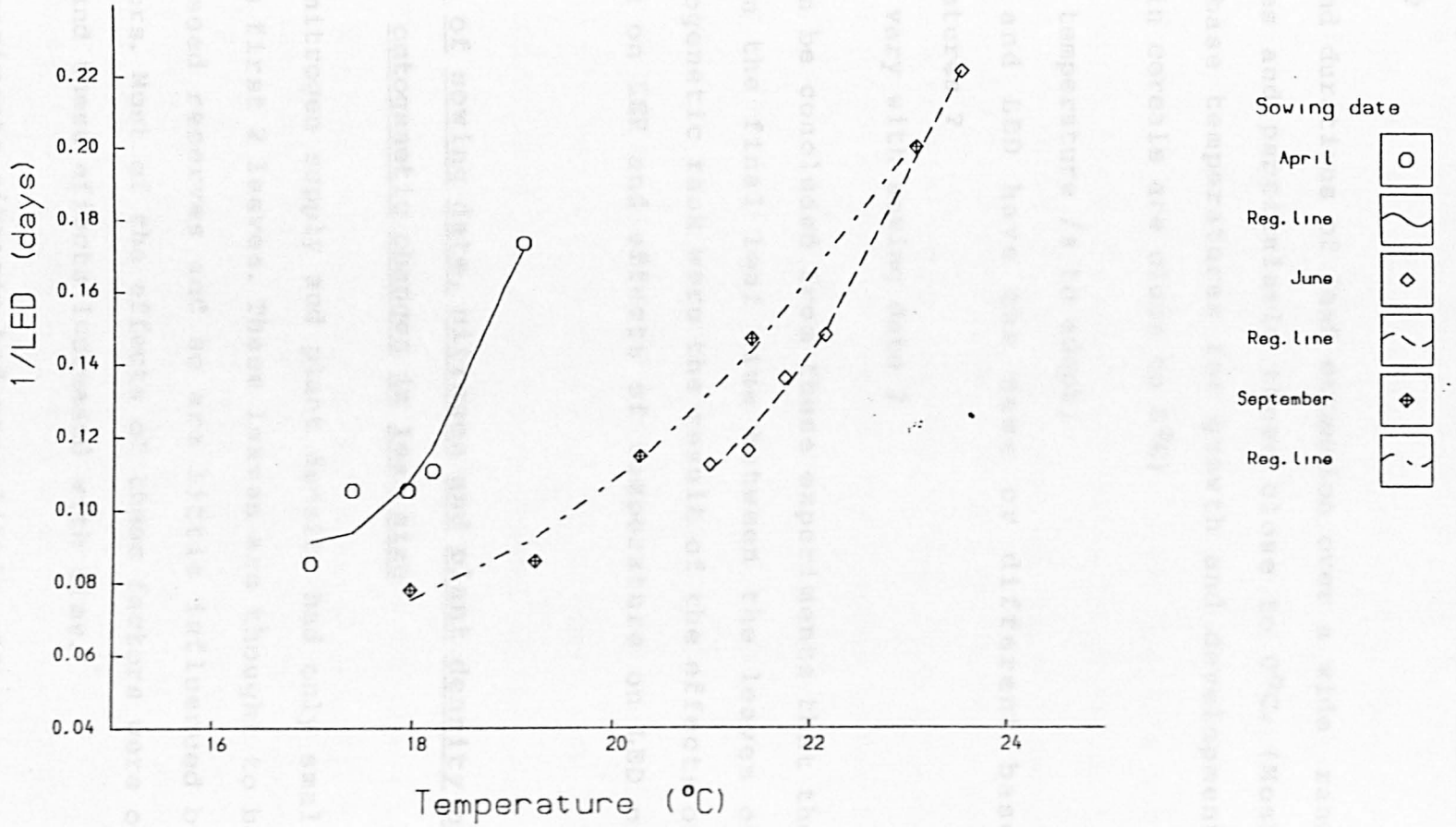
Figure 6.9 shows the relationship between LED (in Julian time) and mean air temperature during the period of extension of leaves 1-4 and leaf 6 of the main shoot in experiment 2. The data are for three sowing dates and are the means of four nitrogen levels. Nitrogen had little effect on LED. Within each sowing there was a strong negative correlation between LED of different leaves and mean air temperature. Gallagher (1979) also found that the reciprocal of the duration of the

linear phase of growth was linearly related to mean air temperature. In this study when the reciprocal of LED (expressed in Julian time) of various leaves within each sowing were plotted against mean air temperature during the extension growth period of these leaves a significant linear relationship was found. However it appears from the spread of the data that probably two regression lines (a linear and a quadratic) can be fitted to the data from different sowings.

The data in Figure 6.9 were extrapolated to 1/LED = zero in an attempt to derive a base temperature for leaf extension. However this yielded values of base temperature of between 14 and 17 ^{o}C which are widely different to the value of 1.2 ^{o}C quoted by Gallagher (1979). Because the data in Figure 6.9 show evidence of curvature as temperature decreases. An attempt was also made to fit a second degree polynomial model to the data. This also yielded no useful values of base temperature. This is because both methods involved extrapolating too far beyond the range of the existing data. The slope of the lines in Figure 6.8 are significantly different, and hence there is no simple relationship between LED and temperature that could be used for predictive purposes. Other factors are important in influencing the differences in response between sowing dates. At any given temperature LED was shortest in the June sowing. However it is not possible to speculate further on this. More information is required on the following topics;

1.Which method should be used to describe leaf growthi.e

Figure 6.12 Relationship between mean air temperature and LED of leaves 1-4 and leaf 6 of main shoot leaf in different sowing dates. Data are means of 4 nitrogen levels.



should leaf growth be described in Julian time or thermal time units?

2. The rates and durations of leaf extension over a wide range of temperatures and particularly those close to 0°C. (Most predicted base temperatures for growth and development processes in cereals are close to 0°C)

3. Which base temperature /s to adopt,
   (a) do LER and LED have the same or different base temeparatures ?
   (b) do they vary with sowing date ?

However it can be concluded from these experiments that the differences in the final leaf size between the leaves of different ontogenetic rank were the result of the effects of leaf nitrogen on LER and effects of temperature on LED of these leaves.

6.4.6 Effects of sowing date, nitrogen and plant density on ontogenetic changes in leaf size

Sowing date, nitrogen supply and plant density had only small effects on the first 2 leaves. These leaves are thought to be dependent on seed reserves and so are little influenced by external factors. Most of the effects of these factors were on later leaves and these effects increased with time.

In all the experiments nitrogen had very little effect on the size of the first 3 leaves. The effect of nitrogen on leaf size was only apparent in leaf 4. The primordia of the first 3

leaves are already present on the embryonic apex in the seed and these are the first to grow after imbibition. Therefore leaf 4 is the first new leaf developed on the apex and up until that time the shoot can obtain nitrogen from the growing medium and seed reserves. The appearance of leaves 4 and 5 is also associated with double ridge formation and appearance of the first tiller on the main shoot. It was also observed in this study that the internodes of at least the first 2 leaves are very short and it was the internode of leaf 4 which was the first to show considerable elongation. Hence the effects of nitrogen supply on leaf 4 and upper leaves could be due to increased demand and internal competition for substrates and metabolites and reduced nitrogen supply within the plant. In wheat greatest demand for nitrogen occurs during the phase of stem extension (Gregory, Crawford and McGowan, 1979). Hence competition for nitrogen due to build up of internal nitrogen deficits will depend upon the phasic development of the plant. Earlier onset of reproductive development and stem extension might be expected to be associated with earlier response to nitrogen. This was the pattern observed in experiment 2. In the April and the June sowings, which respectively reached double ridge 14 and 13 days after sowing there was response to nitrogen in leaf 4 and upper leaves. The September sowing reached the double ridge stage much later, 17 days after sowing and response to nitrogen was delayed up until leaf 6.

The effects of sowing date on leaf extension rate were not consistent in experiments 1 and 2. In experiment 1 the June

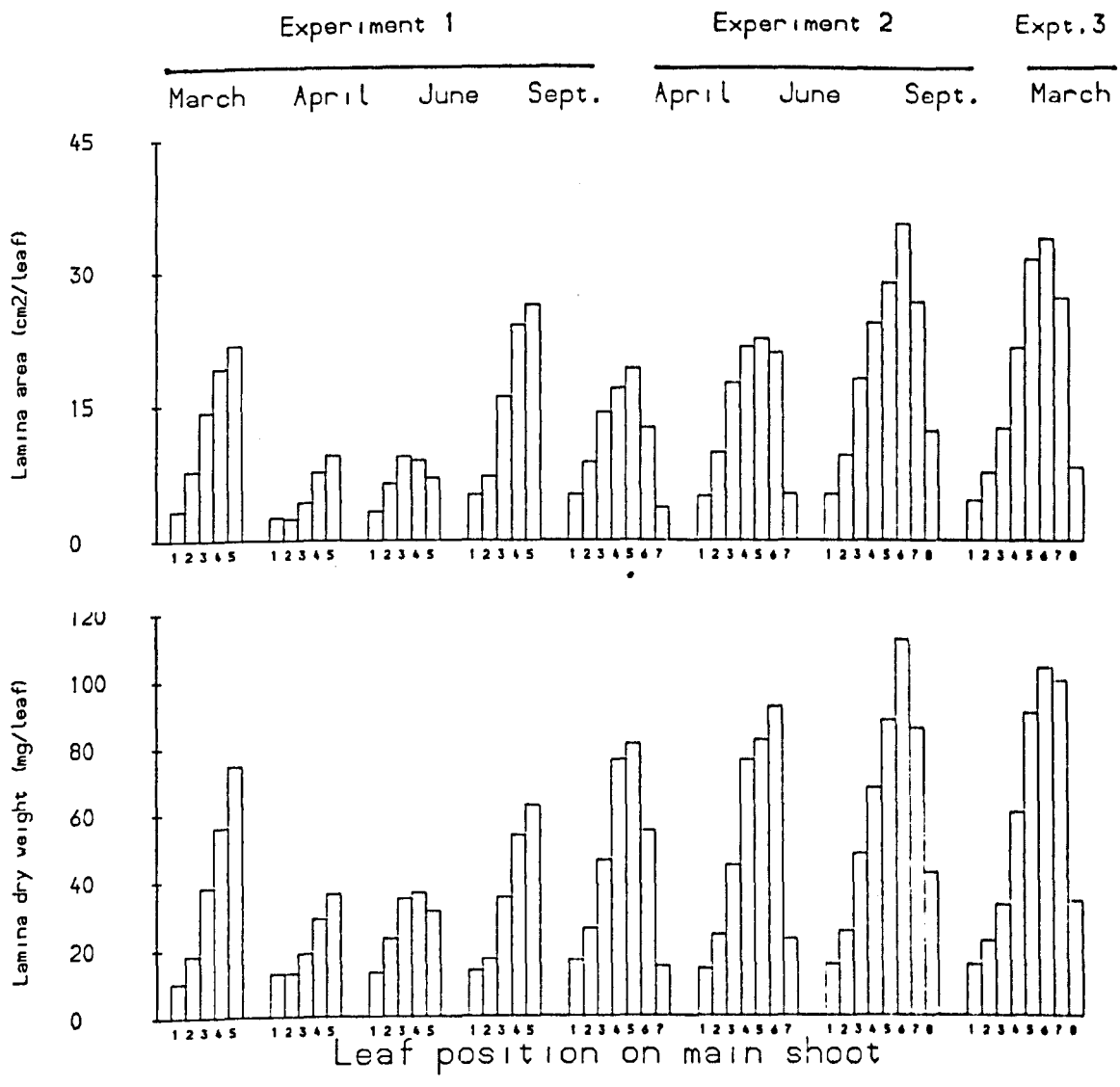


Figure 6.13 Ontogenetic and sowing date effects on the leaf size of main shoot leaves. (Data are means of nitrogen levels tested for experiment 1 & 2 and means of nitrogen levels and for the density of 300 plants m^2 for experiment 3).

sowing had the slowest LER but in experiment 2 it had the fastest. Plants in both the experiments were kept well watered and mean air temperatures during these experiments were very similar (i.e. 23°C and 21°C repectively). However LER in experiment 2 for the June sowing was almost twice that of the corresponding sowing in experiment 1. In general the leaves were shorter and LER were much lower in experiment 1 (in perlite) than in experiment 2 (in soil), possibly due to lower nitrogen supply. Figure 6.5 shows that at the same leaf nitrogen content LER were lower in perlite than in soil. It is suggested that the lower LER in the June sowing of experiment 1 could be due to internal water stress. Perlite has a very low water absorbing capacity and it is likely that the plants growing in soil, due to greater water holding capacity, had much better water supply. It has been shown that bright sunshine causes leaf water potential to decrease and at any given temperature LER slows down in direct proportion to decrease in water potential (Gallagher and Biscoe, 1979). It is therefore possible that lower avaiabilty of water and bright sunshine (9-14 MJ m^2d^{-1}) during the June sowing in experiment 1 could have caused internal plant water deficits and slowed the LER.

The effects of plant density on FLL in these experiments are similar to those observed by Kirby (1974) and Kirby and Faris (1972). At high plant density the size of the lower leaves was increased but the size of the upper leaves was markedly decreased. Kirby (1974) and Kirby and Faris (1972) attributed these effects of plant density to changes in gibberellic acid

concentrations.

It was also observed that high nitrogen was unable to compensate for the adverse effects of high density on plant growth. Therefore it is suggested that some other factor is limiting growth at high plant density, presumably light availability.

6.5 Relationship between lamina area, lamina length and lamina dry weight

Estimation of lamina area is an essential component of plant growth analysis and is widedly used in agronomic and plant physiology research. Lamina area measurements are often needed as an index of canopy development and to measure the capacity of light interception and dry matter production of field crops. It is also used in evapotranspiration modelling. A great variety of methods exist for its estimation (Marshall, 1968), from the simplest such as the product of lamina length and breadth, which has a high probability of error, to the very accurate electronic area meters. In field studies involving many plant samples, using any direct method for estimating lamina area is time taking and costly. In the current study an attempt was made to develop a relatively accurate and rapid indirect method for determinig lamina area of barley plants. The data on lamina length, lamina area and lamina dry weight of fully expanded main shoot leaves for all the nitrogen levels and the sowing dates for experiment 2 and the nitrogen levels and the plant densities for experiment 3

Figure 6.14 Linear relationship between lamina length and lamina area of main shoot leaves. (Data are for experiment 2 & 3). Equation for the fitted line is;

$$Y=-4.92(\pm 0.58)+0.91(\pm 0.02)X, \quad r=0.957$$

Figure 6.15 Linear relationship between lamina dry weight and lamina area of main shoot leaves. (Data are for experiments 2 & 3). Equation for the fitted line is;

$$Y=0.746(\pm 0.500)+0.293(\pm 0.008)X, \quad r=0.943$$

Figure 6.14

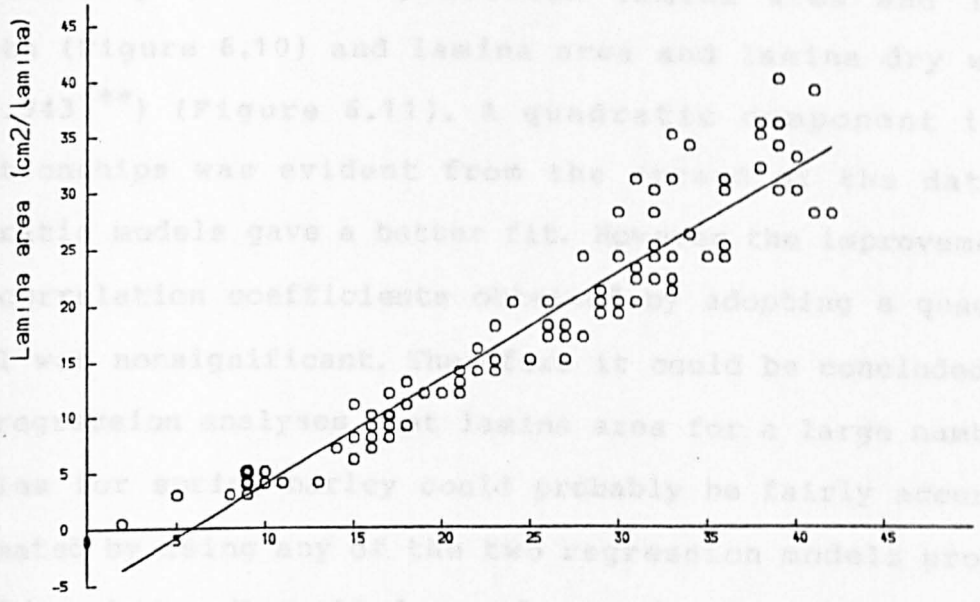
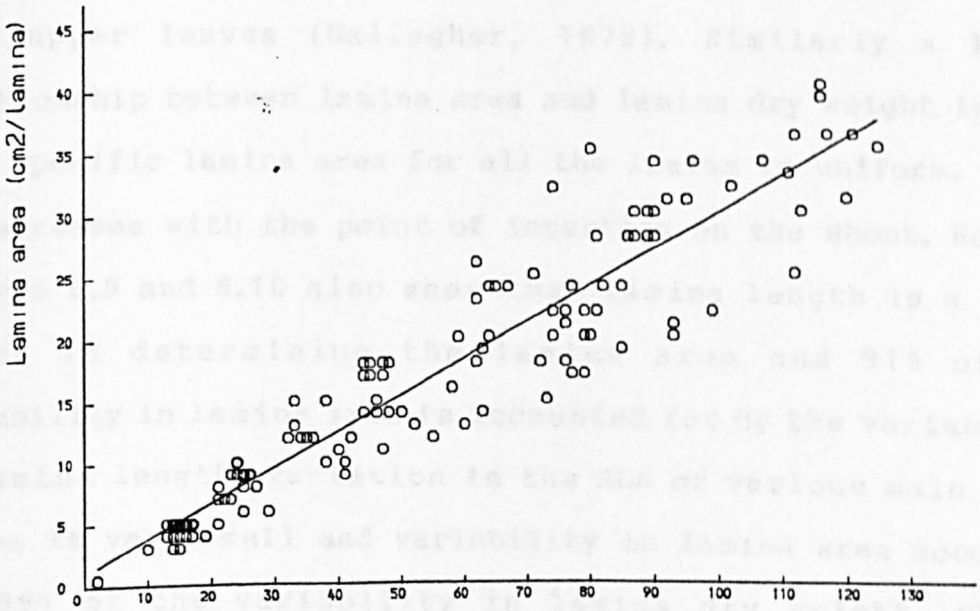


Figure 6.15



were combined. The regression analyses showed a strong linear relationship ($r=0.957^{***}$) between lamina area and lamina length (Figure 6.10) and lamina area and lamina dry weight ($r=0.943^{***}$) (Figure 6.11). A quadratic component in the relationships was evident from the spread of the data and quadratic models gave a better fit. However the improvement in the correlation coefficients obtained by adopting a quadratic model was nonsignificant. Therefore it could be concluded from the regression analyses that lamina area for a large number of samples for spring barley could probably be fairly accurately estimated by using any of the two regression models proposed in this study. Nevertheless the quadratic model could be biologically more accurate and meaningfull. The linear model for lamina length and lamina area assumes that lamina breadth does not vary with the position of the leaf, but clearly this not true. Lower leaves in barley and wheat are much narrower than upper leaves (Gallagher, 1979). Similarly a linear relationship between lamina area and lamina dry weight implies that specific lamina area for all the leaves is uniform, while it decreases with the point of insertion on the shoot. However figures 6.9 and 6.10 also show that lamina length is a major factor in determining the lamina area and 91% of the variability in lamina area is accounted for by the variability in lamina length. Variation in the SLA of various main shoot leaves is very small and variability in lamina area accounted for 89% of the variability in lamina dry weight. SLA is modified by the environmental factors, mainly by light and temperature. A similar study for winter wheat was carried out

Figure 6.16 Quadratic relationship between lamina length and lamina area of main shoot leaves. (Data are for experiments 2 & 3). Equation for the fitted line is;

$$Y=0.541(\pm 0.964)+0.302(\pm 0.091)X+0.014(\pm 0.002)X^2$$

$$r=0.963$$

Figure 5.17 Quadratic relationship between lamina dry weight and lamina area of main shoot leaves. (Data are for experiments 2 & 3). Equation for the fitted line is;

$$Y=0.032(\pm 0.828)-0.0003(\pm 0.0003)X+0.328(\pm 0.033)X^2$$

$$r=0.944$$

Figure 6.16

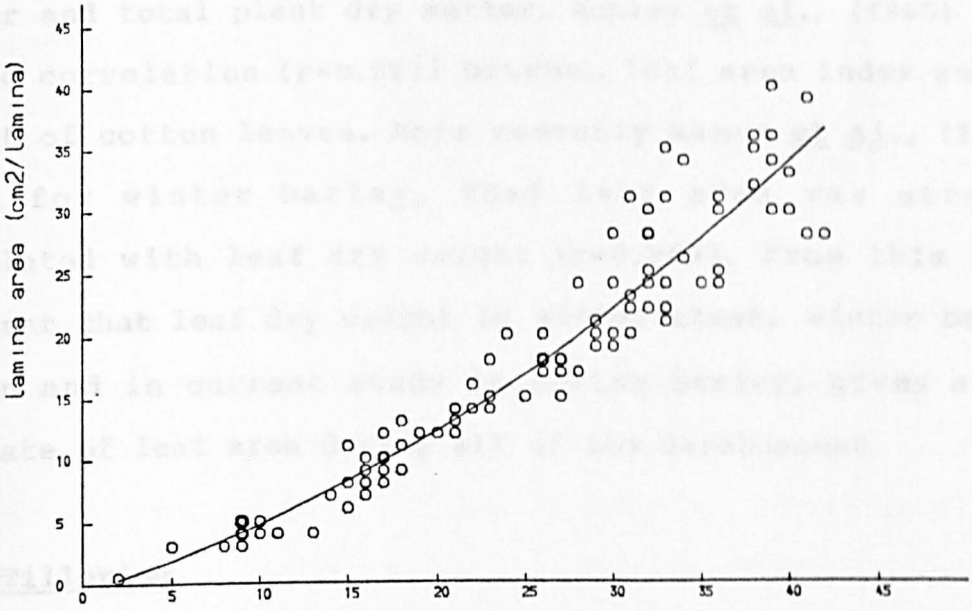
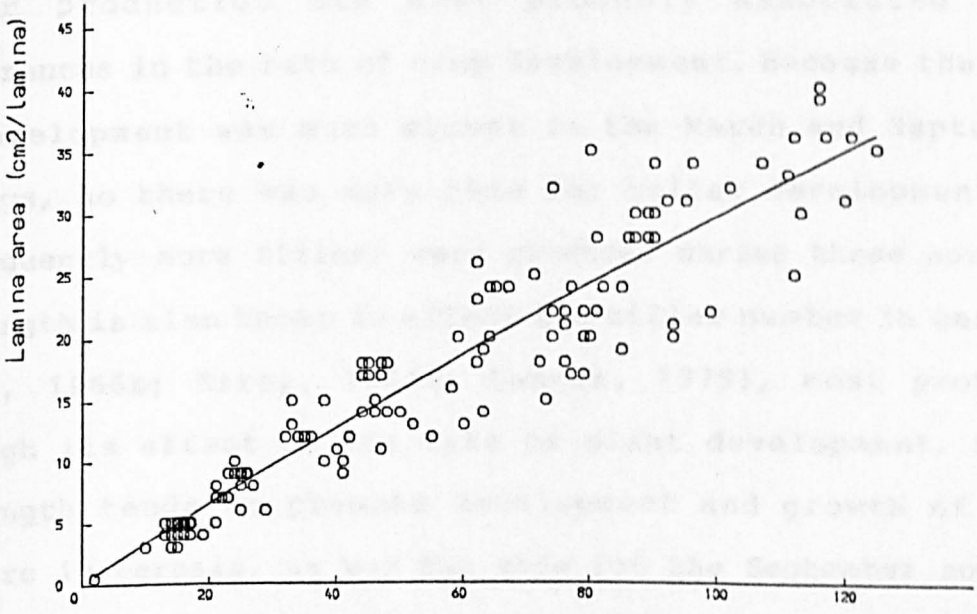


Figure 6.17



by Aasi (1978), who found a good correlation between leaf dry matter and total plant dry matter. Ashley et al., (1965) found a good correlation (r=o.961) between leaf area index and dry weight of cotton leaves. More recently Ramos et al., (1983), found for winter barley, that leaf area was strongly correlated with leaf dry weight (r=0.969). From this it is apparent that leaf dry weight in winter wheat, winter barley, cotton and in current study in spring barley, gives a good estimate of leaf area during all of its development.

6.6 Tillering

Tillering was affected by sowing date, nitrogen supply and plant density. There were fewer tillers in the June sowing and more in the March and September sowings of experiment 1 and in the September sowing of experiment 2. These differences in tiller production are most probably associated with differences in the rate of crop development. Because the rate of development was much slower in the March and September sowings, so there was more time for tiller development and consequently more tillers were produced during these sowings. Daylength is also known to effect the tiller number in cereals (Ryle, 1966b; Kirby, 1969b; Langer, 1979), most probably through its effect on the rate of plant development. Short daylength tends to promote development and growth of more tillers in cereals, as was the case for the September sowings in this study. Leaf appearance rate also modifies the rate of tiller appearance on the shoot. The appearance of the first

primary tiller on the main shoot of barley coincides with the appearance of leaf 4 on the main shoot. If the leaves on the main shoot are appearing at a fast rate so there will be less time for tllers to develop. In addition there may also be some effect of apical dominance on tiller development created by the apex.

The number of tillers per plant is chiefly determined by the availability of nutrients. Tiller number and dry weight were significantly increased with the application of nitrogen. Similar effects of nitrogen application on tiller production in cereals have been reported by many workers and more recently by Bauer, Frank and Black (1984) and Frank and Bauer (1984).

At high plant density the number of tillers per plant was sigificantly reduced. This reduction in number of tillers is probably the effects of; (a) interplant competition basically for light, nutrients and water (Darwinkel, 1978) and (b) competition within the plant for resources such as carbon assimilates or nitrogen compounds (Kirby, Appleyard and Fellowes, 1985) at high plant density. Similar effects of plant density on tiller production have been noted by many other workers.

6.7 Primordia production

Total number of primordia was affected by sowing date and plant density. In experiment 2 the rate of primordia initiation was much faster in the June sowing than in the

April sowing, but the duration of primordia initiation was shorter so that the maximum numbers of primordia for the June and April sowings were very similar. Due to shorter days and lower temperatures during the September sowing the rate of primordia initiation was slower and the duration of primordia initiation was much longer, hence there were more primordia in the September sowing. Similar results have been reported by many workers. For example Holmes (1973), for spring wheat, found that increasing photoperiod increased the rate, but decreased the duration of primordia initiation and hence there were fewer number of spiklets. For spring barley Russell et al., (1982) reported that in the autumn sowing the rate of initiation of spikelet primordia was slower, due to the lower temperatures encountered, but the initiation phase lasted longer. The duration of the period of primordia initiation produced variation in the maximum number of primordia (Appleyard et al., 1982).

The effect of nitrogen supply on the initiation rate, duration and maximum number of primordia was not significant, possibly because the soil was well supplied with nitrogen.

At high plant density both rate and duration of primordia initiation were reduced and fewer number of primordia were initiated. Similar effects of plant density on the initiation of primordia on the main shoot were reported by Kirby and Faris (1970). However within the range of plant densities used in the field this density effect is not going to be too important.

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APPENDIX 1

NUTRIENT SOLUTION

The Long Ashton Nutrient Solution described by Hewitt (1966) is one of the most widely used culture solution and been successfully used for sand and water culture of a wide range of crop plants. The recipe for 100 l of working strength solution, used in this study, is as follows:

Salt	Stock solution ($g\ l^{-1}$)	Volume of stock solution ml/100l nutrient sol
Na NO3	340	300
k_2SO_4	87	400
Ca $Cl_2.H_2O$	438	200
$MgSO_4.7H_2O$	184	200
$NaH_2PO_4.2H_2O$	208	100
Fe EDTA (monosodium complex)	37.3	50
$MnSO_4.4H_2O$	22.3	10
$CuSO_4.5H_2O$	2.5	10
$ZnSO_4.7H_2O$	2.9	10
H_3BO_3	31	10
$Na_2MoO_4.2H_2O$	1.2	10

This gives a diluted culture solution of the following composition:

	ppm		ppm
K	156	Mg	36.0
N	170	Fe	2.8
P	41	Mn	0.55
Na	308	Cu	0.064
S	112	Zn	0.065
Ca	160	B	0.54
Cl	284	Mo	0.048

APPENDIX 2

Length of daylight plus 2 X civil twilight for College Farm - Assuming 54° N (metric clock)

Values for 1,5,9,13,17,21,25 of each month from Smithsonian Tables. Remainder by linear extrapolation.

Month	January	Fabruary	March	April	May	June	July	August	September	October	November	December
Days												
1	8.92	10.18	12.00	14.23	16.52	18.47	18.85	17.23	14.96	12.76	10.69	9.18
2	8.95	10.24	12.06	14.31	16.59	18.51	18.82	17.16	14.89	12.69	10.63	9.15
3	8.97	10.31	12.13	14.39	16.66	18.55	18.79	17.09	14.82	12.61	10.58	9.13
4	9.00	10.37	12.19	14.46	16.73	18.58	18.76	17.01	14.74	12.54	10.52	9.10
5	9.02	10.43	12.25	14.54	16.80	18.62	18.73	16.94	14.67	12.46	10.46	9.07
6	9.06	10.49	12.32	14.62	16.87	18.66	18.70	16.87	14.60	12.39	10.40	9.05
7	9.09	10.55	12.39	14.69	16.95	18.70	18.66	16.81	14.52	12.33	10.34	9.02
8	9.13	10.60	12.46	14.77	17.02	18.74	18.63	16.74	14.45	12.26	10.28	9.00
9	9.16	10.66	12.53	14.84	17.09	18.78	18.59	16.67	14.37	12.19	10.22	8.97
10	9.19	10.72	12.61	14.91	17.16	18.81	18.54	16.60	14.30	12.12	10.16	8.95
11	9.22	10.79	12.68	14.98	17.23	18.83	18.50	16.53	14.23	12.05	10.11	8.92
12	9.24	10.85	12.76	15.05	17.30	18.86	18.45	16.45	14.15	11.98	10.05	8.90
13	9.27	10.91	12.83	15.12	17.37	18.88	18.40	16.38	14.08	11.91	9.99	8.87
14	9.31	10.98	12.90	15.20	17.43	18.90	18.35	16.31	14.01	11.85	9.94	8.87
15	9.34	11.05	12.96	15.28	17.50	18.93	18.30	16.24	13.94	11.79	9.89	8.87
16	9.38	11.12	13.03	15.35	17.56	18.95	18.24	16.16	13.87	11.73	9.84	8.86
17	9.41	11.19	13.09	15.43	17.62	18.97	18.19	16.09	13.80	11.67	9.79	8.86
18	9.46	11.26	13.17	15.51	17.69	18.97	18.14	16.01	13.73	11.60	9.74	8.85
19	9.50	11.32	13.25	15.59	17.75	18.97	18.08	15.94	13.65	11.54	9.69	8.85
20	9.55	11.39	13.33	15.67	17.82	18.97	18.03	15.86	13.58	11.47	9.64	8.84
21	9.59	11.45	13.41	15.75	17.88	18.97	17.97	15.78	13.50	11.40	9.59	8.83
22	9.65	11.51	13.49	15.83	17.94	18.96	17.91	15.71	13.42	11.34	9.54	8.83
23	9.70	11.58	13.57	15.91	18.00	18.95	17.85	15.63	13.35	11.28	9.49	8.84
24	9.76	11.64	13.64	15.98	18.06	18.94	17.79	15.56	13.27	11.22	9.44	8.84
25	9.81	11.70	13.72	16.06	18.12	18.93	17.73	15.48	13.19	11.16	9.39	8.84
26	9.86	11.76	13.79	16.14	18.17	18.92	17.66	15.41	13.12	11.09	9.36	8.85
27	9.92	11.82	13.87	16.21	18.22	18.90	17.59	15.33	13.05	11.03	9.32	8.86
28	9.97	11.88	13.94	16.29	18.27	18.89	17.52	15.26	12.97	10.96	9.29	8.87
29	10.02	11.94	14.01	16.37	18.32	18.88	17.44	15.18	12.90	10.89	9.25	8.89
30	10.07		14.08	16.44	18.37	18.86	17.37	15.11	12.83	10.82	9.22	8.90
31	10.13		14.16		18.42		17.30	15.30		10.76		8.91