HGCA

PROJECT REPORT No. 234

PREDICTION OF OPTIMUM PLANT POPULATION IN WINTER WHEAT

AUGUST 2000

Price £5.00

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by

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This is the final report of a three year project which started in October 1996. The work was funded by a grant of £236,231 from HGCA (project no. 1814).

CONTENTS

ABSTRACT

Field experiments were set up at ADAS Rosemaund (Herefordshire) and Sutton Bonington (Leicestershire) to examine the effects of reducing seed rate on the yield and yield components of 4 varieties of winter wheat, in harvest years 1996-9. Each variety was sown at six seed rates from 20 to 640 seeds m^{-2} and at 3 sowing dates at ADAS Rosemaund. Sampling, at harvest and at major growth stages, facilitated comparisons of yield, crop growth and yield components. A second series of experiments at ADAS Rosemaund only, investigated interactions between seed rate and variety (using two seed rates and up to 22 varieties).

Economic optimum plant populations were significantly lower than current commercial practice. Increased tiller number per plant was the main compensatory mechanism, although increased grain number per ear and to a lesser extent grain size also contributed. Increased shoot number per plant was not due to increased tiller production rate, but due to an increase in the duration of the tillering phase. A reduction in plant density from 218 to 30 plants m^{-2} increased duration of tillering by 37 days in 1996/7 and by 97 days in 1997/8. There was also an increase in tiller survival with reductions in plant density. When sown at 218 plants m^{-2} there was a mean tiller survival of only 43% but at 19 plants m^{-2} 87% of initiated shoots survived. It was apparent that tiller production and death were not closely linked to the development of the crop, as is currently the perceived wisdom in much of agronomy. The time at which tiller production ceases and tiller death commences appeared to be almost completely controlled by competition for resources between shoots. Increased tillering was insufficient to maintain ear number m^{-2}, but there was an increase in green area per shoot with decreases in plant density. It was calculated that green area index (GAI) of approximately 5.6 would be required to intercept 90% of available photosynthetically-acitive radiation (PAR). To produce this canopy size, 68 plants m^{-2} were required in 1996/7 and 35 plants m^{-2} in 1997/8. Reduced GAI, with a reduction in plant density, was also compensated for by an increase in the efficiency of radiation use at low populations, with nearly 50% more dry matter being produced for each unit of light intercepted. Thus, by the critical phases of yield formation differences in radiation capture between high and low population crops were negligible.

The optimum seed rate was calculated using a grain price of £80 t^{-1} and seed cost of £300 t^{-1}, however, the optima were found to be relatively insensitive to changes in the seed cost to grain price ratio. The economic optimum plant population was significantly affected by the sowing date, due to the reduced ability of the crop to compensate through increased tillering. Other aspects of compensation were unaffected by drilling date. The optimum plant population averaged 62 plants m^{-2} at the end of September and increased by 1.6 plants per day delay in drilling. This gave optimum populations of about 90 plants m^{-2} in mid-October and 140 plants m^{-2} in mid-November. These optima are, however, likely to be higher in the north of the country, this is the subject of an ongoing HGCA-funded project (No 2249). Varietal differences in tillering ability did not have a significant effect on compensation for reduced plant population. In the absence of lodging, no interaction was found between variety and plant population.

Potentially significant savings in input costs, particularly in earlier sown crops, are therefore available to the grower. Careful account must, however, be taken of likely establishment percentage and of the optimum population applicable to each specific situation, as yield falls rapidly when crops are grown at populations below the optimum. Currently this is best estimated on a site-by-site basis, based on soil type, seed bed crumb structure, moisture content and risk of pest damage. There is the potential for future research to address this issue for cereals using an approach similar to that used in HGCA-funded work on oilseed rape (HGCA Project Report OS31).

SUMMARY

Introduction

The aim of any crop production system is to provide inputs to a level where the additional output more than pays for the input, or to apply the economic optimum. Seed costs for UK grown wheat represent on average 19% (£47.50/ha) of the variable costs of growing the crop (Nix, 1999). As one of the largest single inputs to the crop it represents a priority target for the reduction of production costs.

Cereals have the ability to compensate for a reduction in plant density by producing and maintaining more tillers per plant, more grains per ear and larger grain size (e.g. Donald, 1963; Darwinkel, 1978). Therefore it may be possible to reduce the seed rate of winter wheat without losing grain yield. As pressure on wheat margins continues to increase, information to exploit this ability whilst avoiding yield reductions offers potentially large savings in input costs.

Yield may be considered to be made up of three components:

ears m^{-2}
grains ear^{-1}
grain size

The number of ears m^{-2} is determined by the number of plants m^{-2}, the number of tillers produced and the proportion of these which survive to produce ears. The number of grains per ear and final grain weight are then determined by the radiation absorbed by the canopy while the ear is developing.

Wheat varieties may maintain near maximal yields at reduced plant densities by these distinct mechanisms: adjusting the yield components to different extents to maintain grain yield. The proportion of maximal yield lost by decreasing seed rate may also differ between varieties.

It was also expected that mechanisms by which the crop compensates for reduced plant populations would be affected by sowing date. As drilling is delayed the duration of the period over which the crop has to tiller will be reduced (Kirby *et al.*, 1999), thus the ability to compensate for low plant populations through increased ear number per plant will be restricted. The optimum plant population is therefore expected to increase as drilling is delayed.

Aims and objectives

1. To establish the principles governing the relationship between seed rate and yield response for a range of variety types with differing tillering characteristics.

2. To investigate the interactions between sowing date and seed rate and variety with respect to final yield.

Materials and methods

Experimental design and treatments

Field experiments were undertaken at two sites: experiments 1 and 2 at ADAS Rosemaund, Herefordshire, and experiment 1 at Sutton Bonington, Leicestershire.

Experiment 1

Four varieties (Cadenza, Haven, Soissons and Spark) chosen for their differences in tillering ability (Foulkes *et al*., 1998), were sown at six seed rates: 20, 40 80, 160, 320 and 640 seeds m^{-2}. These were sown at three sowing dates at Rosemaund and at one sowing date at Sutton Bonington (Table 1)

Table 1. Sowing dates (SD) of winter wheat in 1996/97, 1997/98 and 1998/99 season at Rosemaund and Sutton Bonington.

		1996/97	1997/98	1998/99
Rosemaund	SD1	27/9/96	23/9/97	02/10/98
	SD2	25/10/96	18/10/97	20/10/98
	SD3	14/11/96	16/12/97	11/11/98
Sutton Bonington		03/10/96	3/10/97	12/10/98

At Rosemaund the experimental design was a split plot plus 2-way factorial with three replicates. The effect of time of sowing treatment was expected to be large and therefore require a less precise test than other variates so it was placed on main plots. Seed rate and variety were factorially combined and fully randomised on sub plots, providing the most accurate test for a variety by seed rate interaction. Each plot size was 2m * 24m. Sutton Bonington used a similar experimental set up but without sowing date treatments, i.e. a randomised 2-way factorial design. The soil was a stoneless silty clay loam (Bromyard series) at Rosemaund and a medium stony loam to 80 cm over clay (Dunnington Heath Series) at Sutton Bonington.

Experiment 2

Between 16 and 22 varieties per year were sown at either a high (320 seeds m^{-2}) or low (80 seeds m^{-2}) seed rate. The plots were sown on 27 September 1996, 26 September 1997 and 3 October 1998. A total of 26 varieties were evaluated, of these 12 were included in all three years, and 18 in two out of three years. The varieties were chosen to represent a range of physiological types, older varieties which have previously been the subject of much experimental work and new and 'up and coming' commercial varieties. Varieties evaluated in each year are listed below:

1997	1998	1999
Abbot	Abbot	Abbot
Avalon	Avalon	Avalon
Brigadier	Brigadier	-
Buster	Buster	Buster
Cadenza	Cadenza	Cadenza
Caxton	Caxton	Caxton
Charger	Charger	Charger
-	-	Claire
Consort	Consort	Consort
Crofter	-	-
Drake	Drake	Drake
-	Equinox	Equinox
-	Harrier	Harrier
Haven	Haven	Haven
-	-	Madrigal
-	-	Malacca
-	-	Maverick
Mercia	Mercia	Mercia
Raleigh	-	-
-	Reaper	Reaper
-	Rialto	Rialto
Riband	Riband	-
-	-	Savannah
-	-	Shamrock
Soissons	Soissons	Soissons
Spark	Spark	Spark

Measurements

Detailed growth and development measurements were taken on experiment 1 at ADAS Rosemaund to provide an understanding of how the different varieties maintained yield at reduced seed rates. Growth analysis was done across varieties and seed rates concentrating on the first sowing date in 1996/7 and 1997/8, and the second sowing in 1998/9. Developmental characteristics such as leaf production, tiller production and the dates of critical growth stages were measured across varieties and sowing dates on a restricted set of seed rates. Grain yield was measured using a plot combine from a 10m by 2m area of each plot. Grain was analysed for moisture content and specific weight using GAC 2000 grain analysis computer (Dickey-John Corporation).

Results and Discussion

Plant population

Achieved plant population varied from site to site, year to year, and decreased with delay in date of sowing. Establishment was consistently better (20-40% higher establishment) on the slightly lighter soils at Sutton Bonington than at Rosemaund. At Sutton Bonington establishment averaged 89% (1997), 95% (1998) and 100% (1999), compared with 68%, 76% and 61% for similar sowing dates (SD) in each year at Rosemaund. At Rosemaund in 1996/97, the mean percentage establishment was 68.3, 69.8 and 65% for SD1, SD2 and SD3 respectively. In 1997/98, mean percentage establishment was 75.8, 60.1 and 10.4%; and in 1998/99, it was 61.4, 52.4 and 41.9% respectively. Every effort was made to sow seeds at optimal soil conditions; however, in 1997/98 season it was not possible to sow in November due to wet seedbed conditions, and thus sowing was delayed until December, but seedbed conditions were still very poor, which resulted in extremely low plant counts. For this reason, this sowing is not included in any further results. As well as the effect of sowing date on percentage establishment a larger proportion of plants emerged at the low seed rates than at the high seed rates, as found by Fischer *et al.* (1976). The range of seed rates used (20 to 640 seeds m^{-2}) resulted in plant densities in SD1 of 16-326, 18-377 and 13-318 plants m^{-2} in the 1996/7, 1997/8 and 1998/9 respectively.

This is a good demonstration of the variability in the field establishment factor, which must be taken into account when deciding on the seed rate necessary to achieve the target plant population. Currently this is best estimated on a site-by-site basis, based on soil type, seed bed crumb structure, moisture content and risk of pest damage. There is however, the potential for future research to address this issue for cereals using an approach similar to that used in HGCA-funded work on oilseed rape (HGCA Project Report OS31)

Yield response to reduced plant population

As plant population increased from less than 20 plants m^{-2} yield initially increased rapidly, however, once a population of 80 to 150 plants m^{-2} had been achieved there was no further significant increase in yield (e.g. Fig 1). In a lodging situation the same response was seen from low to moderate seed rates but above this yield declined due to increased lodging reducing yield potential (e.g. Fig 2).

In order to estimate the optimum target plant population, the cost of seed needed to increase the population and the value of any grain returned needs to be taken into account. In order to do this linear plus exponential curves were fitted to the data and a nominal seed price of £300/t and grain price of £80/t (ratio 3.75:1) have been used. For the September-sown crops at Rosemaund in 1997 and 1998 this gives economic optimum plant populations of 65 and 59 plants m^{-2} respectively.

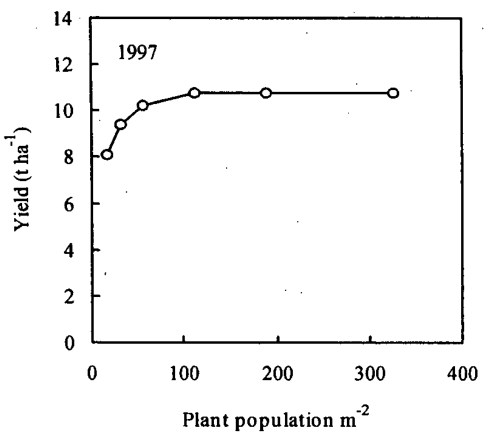

Fig. 1. Grain yield of September-sown wheat (mean of 4 varieties) in non-lodging year (1997) at various plant population densities.

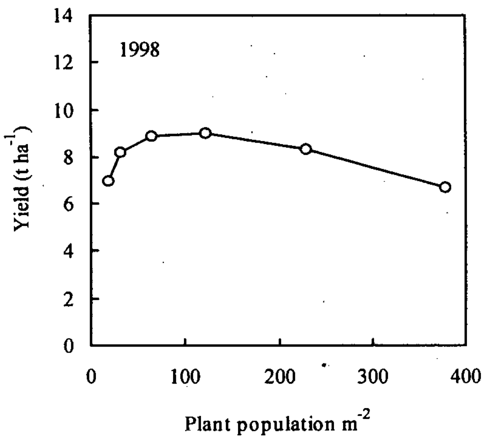

Fig. 2. Grain yield of September-sown wheat (mean of 4 varieties) in a lodging year (1998) at various plant population densities.

In order to establish the reliability of these optima the sensitivity to changes in the ratio of seed cost to harvested grain value was tested. Assuming home-saved seed once cleaned and treated will cost about twice its value as harvested grain, and that high value hybrid seed may cost £800/t when the grain price is £60/t this gives ratios of seed to grain from 2:1 to 13:1. The optima in this test ranged from 105 plants m^{-2} at a ratio of 2:1 to 76 plants m^{-2} at 13:1 (Fig 3), within the normal range of 2:1 to 5:1 the optimum changed by only 12 plants m^{-2}.

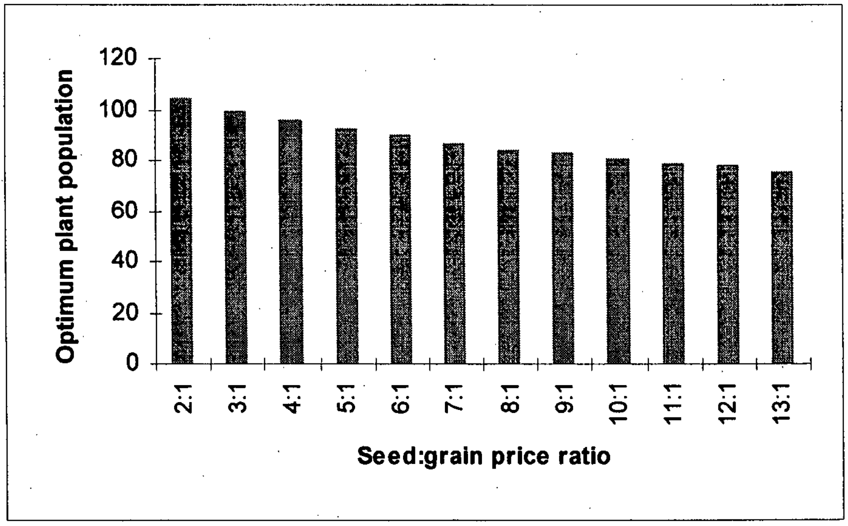

Fig. 3. Effect of the seed cost to harvested grain price ratio on the optimum plant population m^{-2}.

Compensation for reduced plant population

As plant population was reduced the main mechanism by which yield was maintained was increased tiller production and retention. The initial rate of tiller production was unaffected by plant population but as plant population was reduced, tiller death was delayed and reduced. As plant population was reduced further the duration of tillering was also increased, the lowest populations still producing tillers in May, and producing in the order of 20 shoots per plant (Fig 4). It is apparent from this result that tiller production and death are not closely linked to the development of the crop. The time at which tiller production ceases and tiller death commences appears to be almost completely controlled by competition for resources between shoots. This is an area worthy of further work as there are significant implications for other aspects of crop production, such as nutrition and growth regulation.

Analysis of crop growth and resource capture shows that compensation in terms of canopy production is significant even by the start of stem extension. By the critical phases of yield formation differences in radiation capture between high and low population crops are negligible. Calculation of the plant population needed to intercept most of the light showed that only 68 plants m^{-2} and 25 plants m^{-2} were required in 1997 and 1998, respectively (Appendix 2).

Increasing shoot number per plant as population was reduced, was insufficient to maintain the same ear number m^{-2} as at higher populations, but had a great impact in delivering the ear population to an optimal level of around 400 ear m^{-2} (see Table 2 and section below). Yield was maintained, however, by a compensatory increase in grain number per ear, and sometimes by an increase in grain size (e.g. Table 2).

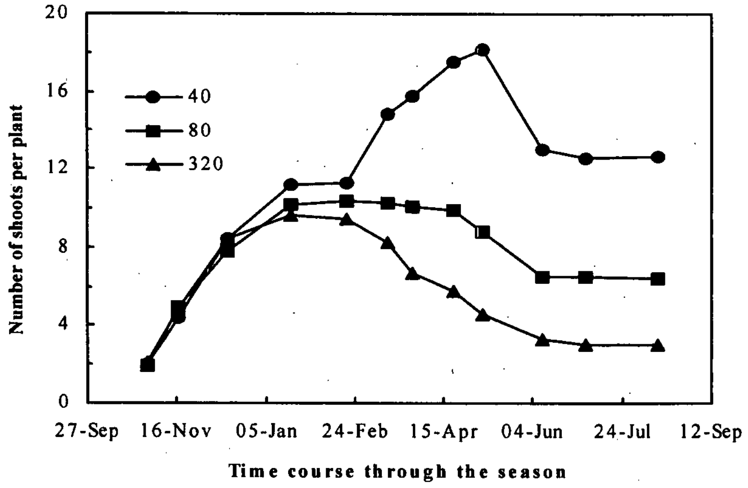

Fig. 4. Number of shoots per plant of September-sown wheat (Haven) as the season progressed in 1998 at 40, 80 and 320 seeds m^{-2} at Rosemaund.

Table 2. Yield and yield components (ear number per plant, number of grains per ear, grain weight, and number fertile shoots per plant) of September-sown wheat (mean of 4 varieties) in 1997 at Rosemaund.

Plant density m^{-2}	Yield, t/ha	Ear no. m^{-2}	Grains per ear	1000 grains wt, g	Fertile shoot no. per plant
16	8.1	311	49.6	53.3	19
31	9.5	350	52.8	53.5	11
57	10.2	415	47.8	52.5	7
113	10.8	470	44.2	52.7	4
190	10.9	563	39.0	51.5	3
326	10.8	700	31.8	49.8	2

Sowing date

The yield response to increasing plant population was similar at each sowing date, except for a consistently higher economic optimum population, and greater yield penalty for sub-optimal population at later sowing dates (e.g. Fig. 5). The response to decreasing plant population in terms of grain number per ear and grain size was similar at all sowing dates. As sowing was delayed, however, there was a small but consistent reduction in ear number per plant. Across years and sowing dates at Rosemaund about 400 ears m^{-2} were required to maintain yield potential; below this level yield started to drop off rapidly. Increasing plant population to compensate for reduced tiller production leads to a further reduction in shoot number per plant. Optimum plant populations for later drilling dates are therefore disproportionately higher than would be expected from the reduction in shoot number per plant due to delayed sowing alone. The economic optimum seed rate for a given sowing date was surprisingly consistent between years at Rosemaund (Fig. 6). This indicates that, with a starting target of 60 plants m^{-2} at the end of September, the target should be increased by 1.6 plants per day or 11 plants per week as sowing is delayed after that date.

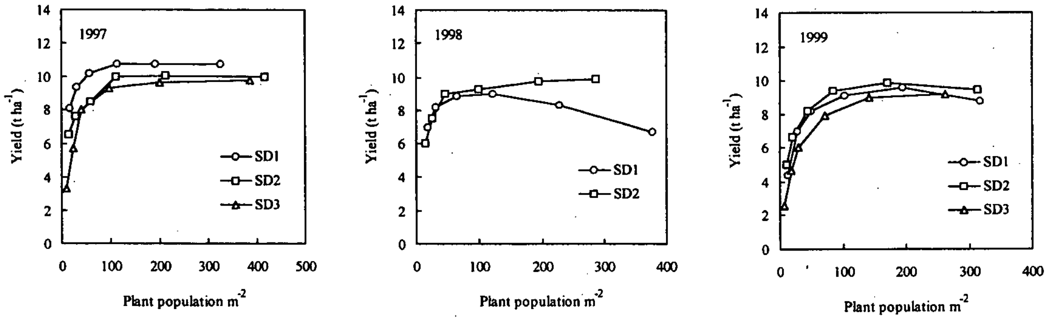

Fig. 5. Grain yield response to plant population density m^{-2} at each sowing dates (SD) in harvest years 1997, 1998 and 1999 at Rosemaund.

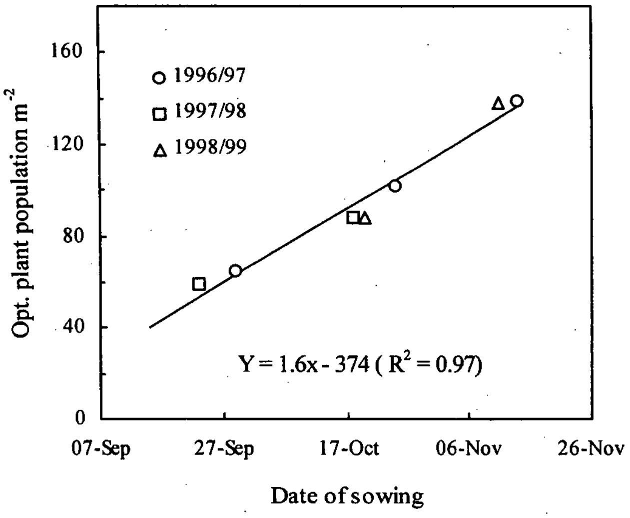

Fig. 6. The relationship between sowing date and economic optimum plant population density for winter wheat from results of three years study (1996/97, 1997/98 and 1998/99). The value 374 in the equation $Y = 1.6x - 374$) refers to the number of days since 1st January.

The results from Sutton Bonington agree closely with the relationship found at Rosemaund, although there may be an indication that the optima at Sutton Bonington may be slightly higher at 93, 98 and 92 plants m^{-2} in the three years respectively. However, it must be remembered that relative differences in optima for a given date may well be larger at other sites.

The accumulated temperature between emergence and when the plant becomes vernalised relates closely to the number of leaves it will have on the main stem (Kirby, 1992). In turn the number of leaves on the main stem determines the plant's ability to tiller (Kirby, 1994), and hence the population required to maintain yield potential. A knowledge of meteorological conditions for a site should therefore prove useful in determining the plant population required, and the rate at which the target population should be increased as sowing is delayed. Whilst the above relationship has worked well at Rosemaund even over three seasons, it indicates qualitatively, rather than quantitatively, the need to increase target plant population as sowing is delayed, until it can be tested and validated more widely.

Variety

Despite the initial hypothesis that varieties would differ in their response to reduced plant population, there was no statistically significant interaction or consistent trend between variety and seed rate in experiment 2 (Table 3). This is in agreement with results from experiment 1 where in the absence of lodging, there was also no statistically significant interaction between variety and seed rate. Where lodging was a problem there was a variety by seed rate interaction: this was, however, only manifested at higher seed rates and reflected the differences in variety standing power.

It is also worth noting that in experiment 2 there was no significant reduction in yield, when seed rate was reduced from 320 to 80 seeds m^{-2}, in either 1997 or 1998 and in 1999 although there was a significant reduction it was only 0.2 t/ha overall.

Table 3. Yield (t/ha @ 85% dm) of varieties sown at high (320 seeds m^{-2}) and low (80 seeds m^{-2}), in late September or Early October.

	1997		1998		1999	
Varieties	320 seeds m^{-2}	80 seeds m^{-2}	320 seeds m^{-2}	80 seeds m^{-2}	320 seeds m^{-2}	80 seeds m^{-2}
Abbot	10.8	9.8	7.7	7.8	10.6	9.9
Avalon	9.8	9.4	6.9	7.1	9.2	8.6
Brigadier	11.6	10.9	9.2	9.4	-	-
Buster	10.6	10.4	8.1	8.3	10.4	10.0
Cadenza	11.3	11.1	8.2	8.5	10.0	9.8
Caxton	10.4	10.2	7.8	7.8	9.6	10.0
Charger	10.8	10.5	8.5	8.8	9.3	8.8
Claire	-	-	-	-	10.8	10.7
Consort	11.4	11.5	9.5	9.5	10.4	10.7
Crofter	11.2	10.6	-	-	-	-
Drake	11.5	11.1	9.1	8.9	10.9	10.6
Equinox	-	-	8.5	8.8	10.3	10.3
Harrier	-	-	9.2	9.5	10.0	10.4
Haven	11.8	11.1	9.3	9.5	10.6	10.4
Madrigal	-	-	-	-	11.2	10.6
Malacca	-	-	-	-	10.1	10.0
Maverick	-	-	-	-	11.2	11.0
Mercia	9.4	9.2	7.1	7.3	9.6	8.7
Raleigh	11.5	11.7	-	-	-	-
Reaper	-	-	8.4	9.1	10.9	10.6
Rialto	11.0	10.9	9.1	8.8	10.2	9.9
Riband	11.5	11.2	9.0	9.2	-	-
Savannah	-	-	-	-	11.4	10.8
Shamrock	-	-	-	-	10.0	10.3
Soissons	9.4	9.4	6.8	7.8	9.6	9.4
Spark	10.9	10.4	7.7	8.2	10.1	9.1
	P	SED	P	SED	P	SED
Variety	<0.001	0.19	<0.001	0.27	<0.001	0.38
Seed rate	0.116	NS	0.238	NS	0.028	0.11
Interaction	0.210	NS	0.806	NS	0.945	NS

APPENDIX 1

The physiological response of winter wheat to reductions in plant density

The objective of this section of the work was two-fold. Firstly, to quantify the response of canopy production, radiation capture, above ground dry matter production and assimilate partitioning to reductions in plant density. Secondly, to define the economic optimum plant density for September-sown winter wheat. In order to avoid complications due to small scale changes in environmental conditions and the phasing of crop growth, the growth and development of one variety of winter wheat (cv. Haven) was analysed to achieve these aims.

Methods

Agronomy

Experiments established at ADAS Rosemaund, Herefordshire, in 1996/7 and 1997/8, were studied. The soil was a stoneless silty clay loam of the Bromyard series. The experiment was planted after oilseed rape in both years. The experimental design was a split plot with three replicates. Sowing date was on the main plot; seed rate and variety were factorially combined and fully randomised on sub plots. Six seed rates were used, ranging from above commercial practice to sub-optimal densities (Table 1.1). Target sowing dates were September, October and November. As this paper is to focus on the ability of wheat to compensate fully for large reductions in plant density results shown are from September sowings only that is the 29 September 1996 and 23 September 1997. Four varieties were used: Haven, Cadenza, Soissons and Spark. To understand how early sown wheat may compensate for reductions in plant density only one variety, Haven, has been used in this section. This variety has good standing power (NIAB, 1996) and high tillering capacity, although it suffers considerable tiller death at "normal" crop densities (Foulkes *et al.*, 1998).

A prophylactic programme of nutrition, disease, weed and pest control and plant growth regulators was applied to maintain undisturbed and healthy crop growth.

Crop Measurements

The timing of measurements was based on the decimal code of growth stages (GS) devised by Zadoks *et al.* (1974) as revised by Tottman and Broad (1987). Plant density was assessed as the third leaf was unfolding (GS13). Plant number was counted in four 0.5 * 0.5m quadrats placed randomly in the plot.

Before the onset of tillering, at seed rates 40, 80 and 320 seeds m^{-2}, 15 plants per plot were labelled with small tags. The number of main stem leaves were recorded on these plants at regular intervals until flag leaf emergence (GS39). The number of fertile shoots per plant through the season were also determined on the tagged plants and counts continued until harvest.

Growth analysis based on the development of the main stem took place at the onset of stem extension (GS31), mid stem extension (GS33; in 1997/8 only), at GS39, and when 50% of all shoots reached mid-anthesis (GS65). In 1997-8 a further growth analysis was performed at mid-senescence calculated at 750 °Cd after GS39 (Foulkes and Scott., 1998). There was little difference between the years in the date of growth analyses.

An area 1 m * 6 rows (0.81 m^2) was sampled leaving 3 rows on each side and at least 0.5 m between samples to avoid edge effects (Austin and Blackwell, 1980). The plants were cut at ground level and taken to the laboratory for analysis, except at GS31 where plants were removed from the field intact and plant number counted before cutting off the roots at ground level. The dry weight and number of potentially fertile and dead and dying shoots were assessed. A shoot was classified as dying when no further leaf was emerging and the most recently emerged leaf was yellowing (Thorne and Wood, 1987). Tiller survival was calculated as the proportion of tillers maintained from maximum tiller count (at GS31 or GS33) until final ear number was determined (counted at GS65, mid-senescence and harvest). The projected area of the green tissue was measured using an image analyser (Decagon Devices) and green area index (GAI) calculated.

The extinction coefficient (k_{PAR}) of the crop was determined using ceptometers (Sunfleck meters) which record photosynthetically active radiation (PAR), that is wavelengths between 0.4 and 0.7 µm. One ceptometer was held horizontally above the canopy and concurrent readings were taken below the canopy. This was performed at GS 39 in 1996/7 and at GS33, 39 and 65 in 1997/8. A modified version of Beer's law was applied to the data to determine k_{PAR} (Equation 1), where I_o is the incident PAR, and I the amount of PAR transmitted below a GAI of value L (Monsi and Saeki, 1953; cited by Saeki, 1960).

$$k = -\ln\left(\frac{I}{Io}\right)\Big/L$$

Equation 1

At GS33 and 39 in 1997/8 in plots of 59 and 218 plants m^{-2} PAR measurements were again taken but at 10 cm intervals from the top of the canopy to determine light attenuation through the canopy.

The water soluble carbohydrate (WSC) content of the stems was determined at mid-anthesis when it has been reported to be near maximum (Foulkes *et al.*, 1998). This was determined on 8 shoots randomly selected from each plot and flash dried at 105 °C for 2 hours. The WSC content was then assessed using the spectrophotometery method described by Thomas (1977).

At harvest, samples of 0.81 m^2 were removed from the field. Final crop dry weight and ear number were recorded. The ears were then threshed, grain dry weight measured and harvest index calculated. The thousand grain weight (TGW) was determined on grain samples taken from the combine. The number of grains per ear were then calculated using the combine grain yield, the TGW and the number of ears m^{-2}.

Analyses of variance, comparison of regressions and orthogonal polynomial contrasts were performed using Genstat 4.1 (Lawes Agricultural Trust).

Meteorological Measurements

Maximum and minimum temperatures, rainfall and incident sun hours were recorded at the ADAS Rosemaund Agro-Meteorological station 1 km from the experimental site. Thermal time was calculated after Kirby and Weightman (1997) using a base temperature of 0 °C. The daily number of sun hours was converted to the quantity of incoming PAR using a model that takes into account latitude and time of year (Berry, 1964).

Results

Plant Density

The range of seed rates used (20 to 640 seeds m^{-2}) resulted in plant densities of 18-358 plants m^{-2} pre-winter (Table 1.1). A larger proportion of plants emerged at the low seed rates than at the high seed rates. There was a tendency for better emergence in 1997/8 than in 1996/7 (P=0.054). Plant counts pre-winter were less variable than those performed at GS31, due to plant size and sampling regime. Over both years there was a negligible change in plant density over winter. However, in 1997/8 there was a trend for greater decreases in plant number over winter at the high plant densities than at the low densities. Due to the greater accuracy of the emergence plant counts and the relatively small amount of over winter plant death emergence counts will be used in the following analyses.

Table 1.1. Number of plants emerged from each seed rate treatment and each season.

	Plant emergence (Plants m^{-2})			Plant number in Spring (Plants m^{-2})		
Seeds m^{-2}	1996/7	1997/8	Mean	1996/8	1997/9	Mean
20	18	19	19	23	22	22
40	25	35	30	42	52	47
80	51	66	59	83	69	76
160	110	128	119	151	140	145
320	195	240	218	239	159	199
640	318	358	338	319	314	316

Canopy Production

Following a reduction in plant density from 338 to 19 plants m^{-2} GAI at GS31 was reduced, on average, from 2.95 to 0.48 (Table 1.2). However, even by this early stage of crop growth, there had been considerable compensation by the crops sown at low densities. This 18 fold reduction in plant density had led to only a 6 fold reduction in GAI. Larger GAIs were obtained by GS31 in 1997/8 than in 1996/7. Crop emergence occurred on 13 October in 1996 and 2 October in 1997. GS31 occurred 31 March in 1997 and 4 April 1998. Thus the larger GAI produced by GS31 in 1997/8 may have been in part caused by the longer duration of growth, accompanied by warmer winter temperatures in this year (Table 1.3). In 1996/7, on average, 7.98 leaves had been produced per main stem at GS31, compared with 10.42 in 1997/8. Thus the average shoot size was larger in 1997/8 than 1996/7 (Table 1.2).

Observations of tagged plants showed that this compensation in GAI with reductions in plant density was not due to increased main stem leaf number initiation or tiller production rate, but due to an increase in the duration of the tillering phase. Following a reduction in plant density from 218 to 30 plants m^{-2} duration of tillering increased by 37 days in 1996/7 and by 97 days in 1997/8. There was also a trend for decreasing phyllochron with reductions in plant density, although not statistically significant in either year. No such trend was visible when the phyllochron was calculated before the onset of stem extension.

The handling of tagged plants may result in an increased duration of tiller production because of suppressed growth of nearby plants. This does not appear to have influenced the differences between the treatments as the growth analysis performed at GS31 showed more shoots had been produced per plant at the low plant densities, due to earlier cessation of tillering occurred before GS31 at the high densities.

Table 1.2. Canopy development and growth processes under different plant densities. Phyllochron was calculated using accumulated thermal time from emergence using a base temperature of 0°C. Tiller production rate was calculated from before the cessation of tillering, in 1996/7 calculated until February and in 1997/8 until December. Percentage tiller survival was calculated from the maximum total shoot number and mean final ear number from growth analyses.

		Data from tagged plants				Data from growth analysis				
								Green area per shoot		
	Plant Density	Main stem phyllochron (°Cd)	Final main stem leaf number	Tiller production rate (tillers plant^{-1}d^{-1})	Duration of tillering from emergence (d)	Total shoot number per plant (GS31)	Green area index (GS31)	GS 31 (cm^2)	GS 65 (cm^2)	Tiller survival (%)
1996/7	18	*	*	*	*	20	0.50	15	141	89
	25	111.2	12.73	0.066	198	24	0.79	14	191	59
	51	115.8	12.62	0.066	176	16	1.16	15	163	57
	110	*	*	*	*	9	1.64	17	139	53
	195	116.2	12.26	0.064	161	6	1.84	16	142	52
	318	*	*	*	*	4	1.72	14	130	65
	F Prob.	0.526	0.562	0.519	0.048	0.003	<0.001	0.83	0.112	0.013
	SED	4.51	0.422	0.002	9.8	2.2	0.114	2.4	18	9.1
	df	4	4	4	4	9	10	10	10	10
1997/8	19	*	*	*	*	13	0.46	19	189	85
	35	125.0	14.24	0.079	226	15	1.67	32	200	60
	66	130.4	13.62	0.076	159	9	2.01	33	195	53
	128	*	*	*	*	7	2.79	35	165	54
	240	134.0	13.87	0.073	129	5	4.00	40	151	44
	358	*	*	*	*	3	4.18	45	140	50
	F Prob.	0.38	0.706	0.897	0.018	0.002	<0.001	<0.001	<0.001	0.011
	SED	5.71	0.714	0.004	19.5	4.0	0.419	3.1	8	8.4
	df	4	4	4	4	10	10	9	10	10

Table 1.3. Mean monthly daily temperatures, sun hours and rainfall in 1996/7, 1997/8 and the long term mean (LTM) calculated over 30 years.

	Mean daily temperature (°C)			Monthly sun hours			Monthly Rainfall (mm)		
	1996/7	1997/8	LTM	1996/7	1997/8	LTM	1996/7	1997/8	LTM
Sep	13.6	13.6	13.2	128	130	125	21.2	29.7	58.9
Oct	11.5	9.6	9.8	93	129	92	71.8	62.9	60.0
Nov	5.7	8.2	6.5	80	43	62	59.0	86.8	58.9
Dec	2.7	5.1	4.6	42	39	42	30.9	40.1	64.6
Jan	2.0	5.2	4.0	26	40	49	9.7	89.2	67.6
Feb	6.7	7.2	3.9	57	78	64	72.1	16.0	46.8
Mar	8.1	8.2	6.1	107	72	119	23.0	59.9	47.9
Apr	8.9	7.2	7.8	171	118	136	34.4	142.7	44.8
May	11.1	13.1	11.0	217	206	179	59.9	15.1	46.5
Jun	13.9	14.2	13.8	102	103	170	98.4	95.7	53.6
Jul	16.2	15.5	16.1	227	132	189	15.4	22.3	43.4
Aug	18.8	15.6	15.8	165	192	156	105.7	21.1	56.3

There was an increase in tiller survival with reductions in plant density (Table 1.2). When grown at 218 plants m^{-2} there was a mean tiller survival of only 43%. When sown at 19 plants m^{-2} 87% of initiated shoots survived to produce ears.

There was a general increase in green area per potentially fertile shoot (averaged over all shoot ages) with decreases in plant density (Table 1.2), more so at GS65 than 31. At GS31 in 1996/7 maximum green area per shoot was achieved by 119 plants m^{-2}, but in 1997/8 by 338 plants m^{-2}. At GS65 a mean maximum shoot size of 196 cm^2 was obtained by crops sown at 30 plants m^{-2} in both years. Thus there was compensation for reduced plant density by increased shoot size at later growth stages.

As the season progressed differences between high and low density crops in GAI were proportionally reduced (Fig. 1.1). This was, therefore, achieved by both increased green area per shoot and duration of tillering at the reduced plant densities.

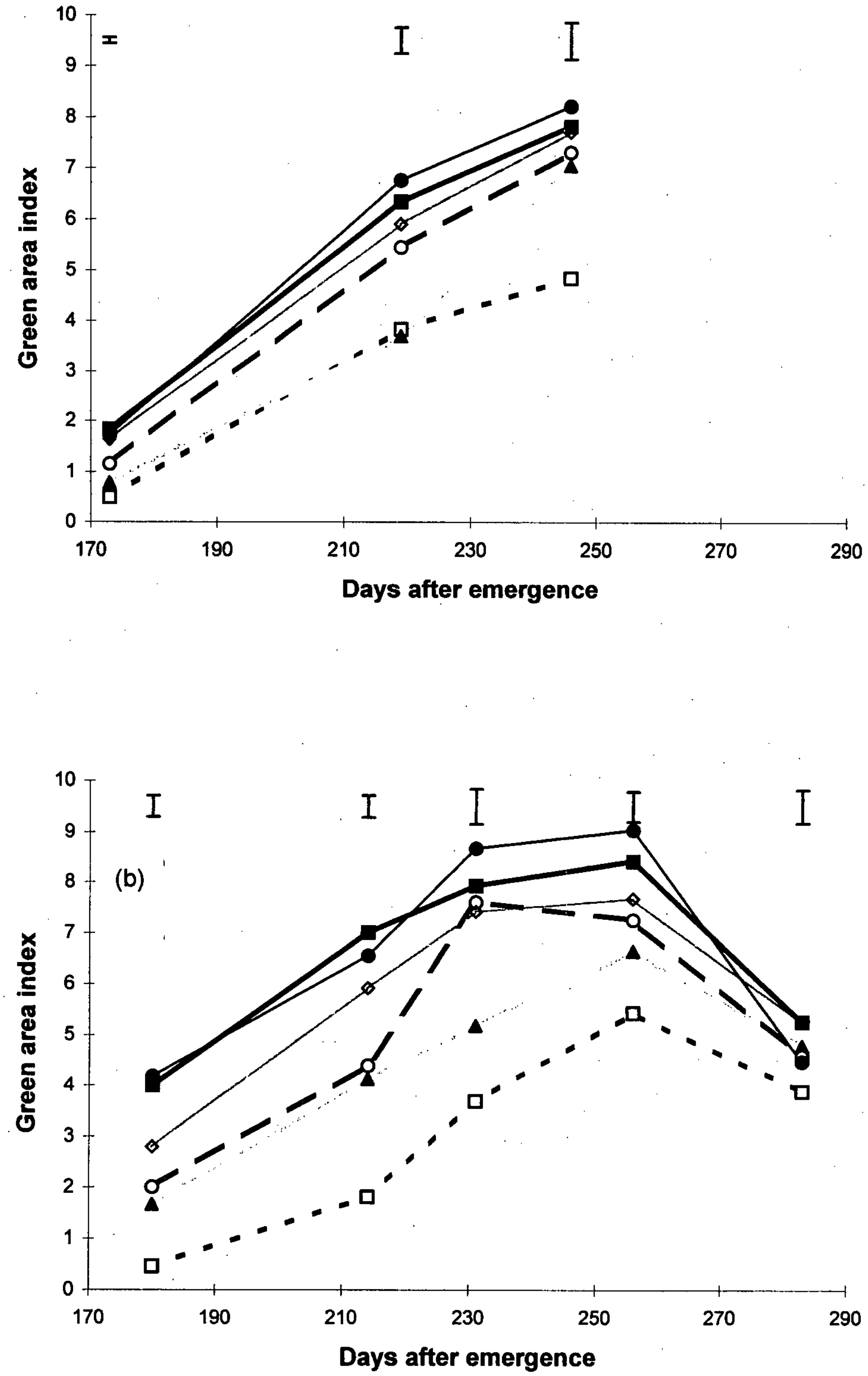

Fig. 1.1. Green area index development during (a) 1996/7 and (b) 1997/8 for different crop densities (mean of plant density of both years shown): 19 (□), 30 (▲), 59 (○), 119 (◊) 218 (■), and 338 plants m^{-2} (●). Bars show SED of effect of plant density.

Radiation Capture

k_{PAR} was recorded as 0.40, on average, from measurements at GS 39 in 1996/7 and at GS33, 39 and 65 in 1997/8 (Table 1.4). Analyses showed that k_{PAR} did not significantly alter with reduction in plant density (P=0.762), growth stage (P=0.261) or season (P=0.065).

Table 1.4. The effect of plant density, growth stage and season on the extinction coefficient (k_{PAR}). SED to compare between plant density treatment in 1997/8: 0.05, 30 df. SED to compare between growth stages in 1996/7 0.04, 6 df. SED to compare individual values in 1997/8 0.09, df 35.63 except where comparing the same growth stage where df is 30. SED to compare k_{PAR} at GS39 in the 2 seasons 0.03, 4 df.

	1997/8				1996/7
	GS33	GS39	GS65	Mean	GS39
19	0.54	0.51	0.32	0.46	0.40
30	0.34	0.37	0.33	0.34	0.47
59	0.44	0.34	0.36	0.38	0.38
119	0.39	0.45	0.44	0.42	0.43
218	0.34	0.42	0.45	0.40	0.39
338	0.42	0.45	0.44	0.44	0.39
mean	0.41	0.42	0.39	0.41	0.41

At GS31, as plant density was reduced from 338 to 19 plants m^{-2} fractional interception (f) decreased, on average, by 73% (Table 1.4). The difference in f was proportionally reduced through the season and by GS65 there was only a 10% reduction in f by the crops sown at the lowest density compared with those sown at the highest density. Between GS31 and 39 the lowest density crop intercepted 80 MJ m^{-2} less than the high density in 1996/7 and 137 MJ m^{-2} less in 1997/8. Between GS39 and 65, there was a loss of 34 MJ m^{-2} in 1996/7 and a loss of 25 MJ m^{-2} in 1997/8 following a reduction in plant density from 338 to 19 plants m^{-2}. With nearly a 6 fold reduction in plant density from 338 to 59 plants m^{-2} a loss of only 7 MJ m^{-2} in 1996/7 and 3 MJ m^{-2} in 1997/8 were incurred during this period of rapid ear growth. Slightly more PAR was intercepted during this period in 1996/7 than 1997/8, due to more incident radiation (Table 1.3).

With a k^{PAR} of 0.40, a GAI of approximately 5.6 would be required to intercept 90% of available PAR at GS39 (Equation 1). During the period between GS39 and GS65 assimilate supply may limit ear growth and therefore restrict grain production. Restricted assimilate supply post-GS65 may limit endosperm cell number and grain filling, thus decreasing TGW. A regression of GAI on plant density was performed for both seasons at GS39 (Fig. 1.2). It showed that in 1996/7 68 plants and in 1997/8 35 plants were required to intercept 90% of incident radiation.

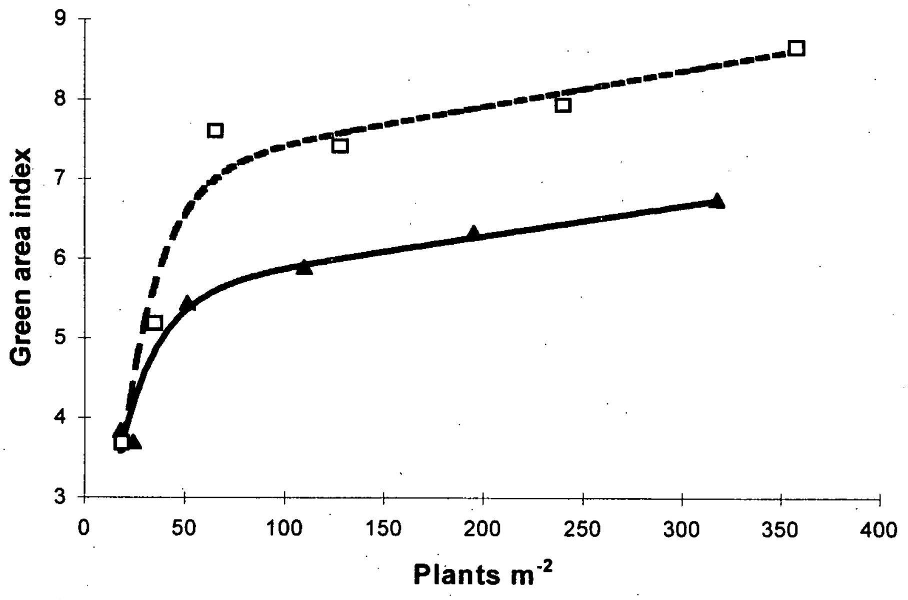

Fig. 1.2. The effect of plant density on green area index at GS39. Curve fitted in 1996/7: 5.509 - 5.144 * 0.9490^x+ 0.003865x, in 1997/8: 7.011 - 9.470 * 0.9490^x+ 0.004492x. S.E. 0.754, variance accounted for 82.0%. Mean data points ▲, 1996/7, ☐,1997/8.

Dry Matter Production

At GS31 there was a large difference in above ground dry matter between crops sown at high and low plant densities (Fig. 1.3). By harvest these differences had largely disappeared. Statistical analysis of these trends by polynomial contrast showed that the low crop densities accumulated dry matter at a faster relative growth rate than the crops sown at high densities ($P<0.001$), this response was similar in both seasons.

Radiation use efficiency (RUE) was calculated by the regression of PAR interception on the concurrent accumulation of dry matter (Table 1.5). As plant density was reduced there was an increase in RUE from 2.4 to 3.4 g MJ^{-1} in 1996/7 and from 2.1 to 3.1 g MJ^{-1} 1997/8.

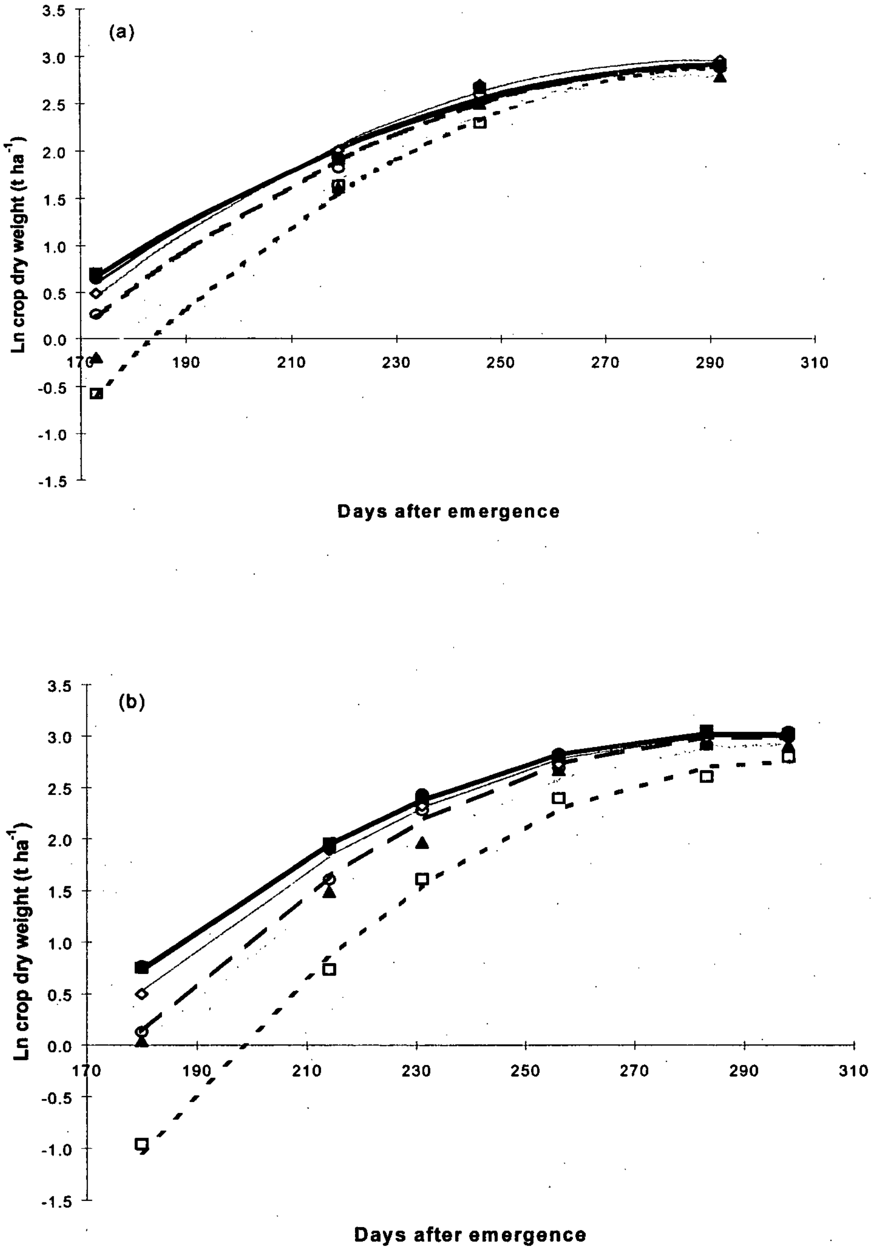

Fig. 1.3. Natural logarithm of above ground dry weight accumulation, measured from GS31 for different crop densities: 19 (□), 30 (▲), 59 (○), 119 (◊), 218 (■) and 338 (●) plants m^{-2}. Line fitted: $A+BX+CX^2$. SE to compare between different levels of plant density at the same DAE in 1996/7 was 0.0734, 36 df, and in 1997/8 was 0.2390, 60 df.

Table 1.5. Radiation capture and conversion under different plant densities. Data calculated from measured GAI, extrapolated linearly between growth analyses. Mean k_{PAR} applied to obtain fractional interception. Radiation use efficiency (RUE) calculated from GS31 to date of 5% flag leaf remaining.

		Fractional interception			PAR intercepted (MJ m^{-2})		RUE
	Density	GS31	GS39	GS65	GS31-39	GS39-65	(g MJ^{-1})
1996/7	18	0.18	0.78	0.85	184	200	3.4
	25	0.28	0.78	0.94	194	215	2.6
	51	0.38	0.89	0.95	236	227	2.6
	110	0.49	0.91	0.96	253	229	2.6
	195	0.53	0.93	0.96	262	231	2.5
	318	0.51	0.94	0.97	264	234	2.4
df=10	F Prob.	<0.001	0.002	0.023	<0.001	0.006	0.005
	SED	0.030	0.035	0.030	12.0	7.1	0.20
1997/8	19	0.17	0.77	0.89	170	152	3.1
	35	0.49	0.87	0.93	255	165	2.8
	66	0.56	0.95	0.95	271	174	2.8
	128	0.68	0.95	0.95	292	174	2.5
	240	0.80	0.96	0.96	308	176	2.3
	358	0.81	0.97	0.97	307	177	2.1
df=10	F Prob.	<0.001	<0.001	<0.001	<0.001	<0.001	0.113
	SED	0.051	0.030	0.012	4.6	2.8	0.36

Dry Matter Partitioning

There was no significant effect of plant density on total above ground dry matter production (Table 1.6), although in 1997/8 there was a trend for decreasing dry matter production with reductions in plant density from 59 plants m^{-2}. HI increased as plant density was reduced and reached a maximum between 59 and 30 plants m^{-2} ($P=0.031$ and 0.022 in 1996/7 and 1997/8).

The increased production of tillers per plant and the increased tiller survival at reduced plant densities did not result in a maintenance of ears m^{-2} which decreased, on average, from 637 to 312 ears m^{-2} with a reduction in plant density from 338 to 19 plants m^{-2} ($P<0.001$). However this represents an average increase in ear number per plant from 2 to 20.

As plant density was reduced from 338 to 19 plants m^{-2} there was a general increase in the number of grains produced per ear from 34 to 45 in 1996/7 and from 31 to 52 in 1997/8 (Table 1.6). Following the same reduction in plant density there was a trend for increased TGW in 1997/8, from 43 to 48g, although this was not quite statistically significant ($P=0.077$). In 1996/7 there was no effect of plant density on TGW. This was despite an increase in canopy duration of 8 days with reductions in plant density from 338 to 19 plants m^{-2} and of 4 days in 1997/8 with a reduction in plant density from 219 to 30 plants m^{-2}. There was also a trend for increased WSC with reductions in plant density, although this was not statistically significant.

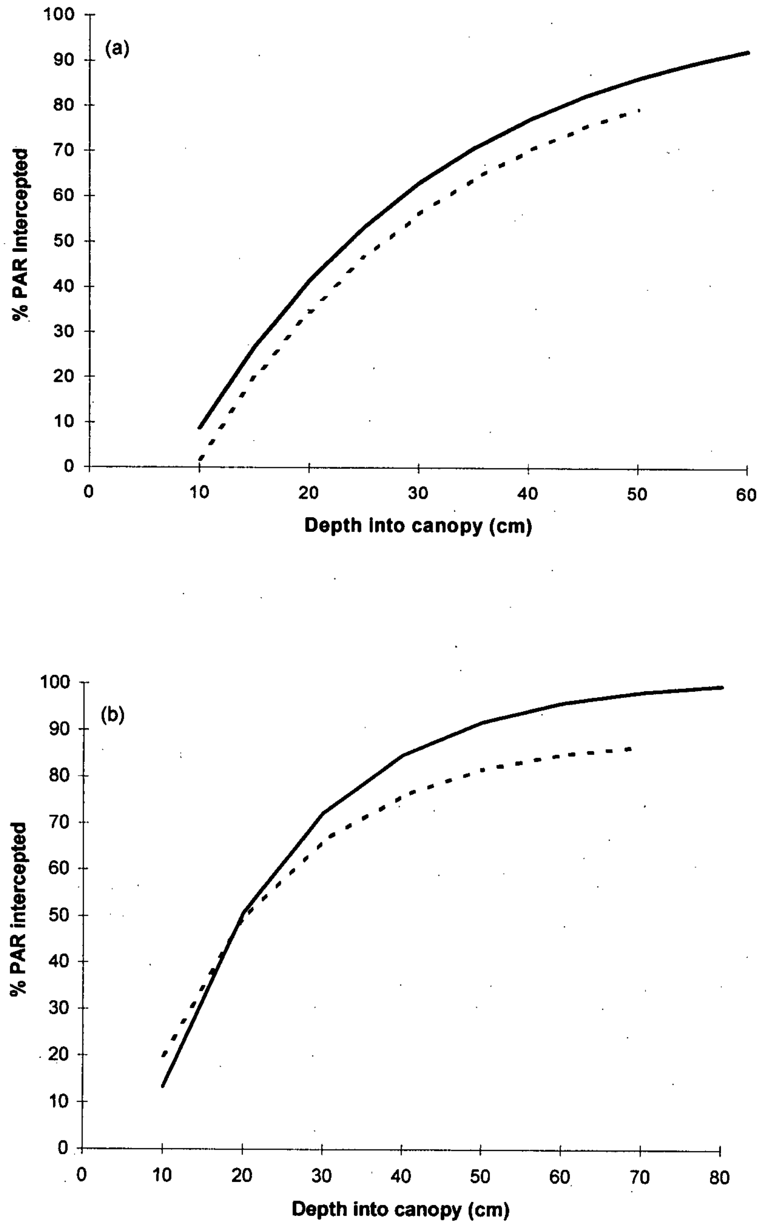

Fig. 1.4. Percentage photosynthetically active radiation (PAR) interception with increasing depth into the canopy at (a) GS33 and (b) GS39 for plant densities of 218 (solid line) and 59 (broken line) plants m^{-2}. Curves fitted at GS33 104-145.3*0.95871^{x} at 218 plants m-^{2} and 97.21-145.3*0.95871^{x} at 59 plants m-^{2} and at GS39 101.4-153.3*0.94617^{x} at 218 plants m-^{2} and 89.16-120.3* 0.94617^{x} at 59 plants m^{-2}.

Table 1.6. Above ground dry matter production and the partitioning of assimilates in the formation of grain yield under different plant density treatments. Ear density calculated as the mean of all post anthesis ear counts, thousand grain weight determined on combine samples and grain number per ear calculated on this basis. Canopy duration calculated from emergence date until date of 5% flag leaf remaining.

	Plant Density	Above ground dry matter at harvest (t ha^{-1})	Harvest index	Fertile ear number (m^{-2})	Grain number per ear	Thousand grain weight (g)	WSC per shoot at GS 65 (g)	Canopy duration (d)
1996/7	18	18.2	0.60	360	44.7	48.6	0.77	296
	25	16.2	0.61	341	55.0	48.1	0.83	295
	51	17.8	0.57	422	45.9	47.4	0.82	292
	110	19.3	0.58	509	41.0	48.5	0.74	291
	195	18.3	0.58	534	40.8	48.3	0.68	290
	318	18.3	0.53	635	33.8	47.1	0.59	288
df=10	F Prob.	0.283	0.031	<0.001	0.041	0.846	0.241	<0.001
	SED	1.20	0.019	48	5.17 (5 df)	1.40	0.163	1.0
1997/8	19	16.4	0.49	264	51.9	48.2	0.81	*
	35	18.2	0.50	325	51.1	46.2	1.06	301
	66	20.9	0.51	378	46.7	46.1	1.03	297
	128	20.4	0.46	466	40.2	47.0	0.88	*
	240	20.6	0.45	559	36.2	44.8	0.76	297
	358	19.9	0.43	638	30.6	43.2	0.69	*
df=10	F Prob.	0.075	0.022	<0.001	<0.001	0.077	0.063	0.021
	SED	1.45	0.021	30.6	2.815	1.45	0.120	1.0 (4 df)

Lodging was minimal in this variety in these experiments. One plot at 358 plants m^{-2} lodged in 1997/8. It lodged by a score of 46.7 after anthesis (that is 45% lodged by over 45° and 5% leant by less than 45° from the perpendicular).

Combine grain yields are more representative of true grain yield than figures obtained from quadrat samples mainly due to reduction in variability associated with larger sample areas (Bloom, 1985). Regression analysis (Fig. 1.5) showed the shape of the response of yield to plant density to be the same in both years ($P<0.001$), although yield was greater in 1996/7 than in 1997/8. Yields were maintained at a maximum for reductions in plant density from 338 to below 150 plants m^{-2}. The yield then diminished with more severe reductions in plant density due to lower radiation capture during the critical period of growth (Table 1.5). The optimum seed rate was calculated using a grain price of £80 t^{-1} and seed cost of £300 t^{-1} with the response curves obtained from these two seasons. The optimum plant density was then calculated using a regression of plant emergence on seed rate. In 1996/7 the optimum plant density was 69 plants m^{-2} and in 1997/8 it was 76 plants m^{-2}. These values were found to be relatively insensitive to changes in the seed cost to grain price ratio.

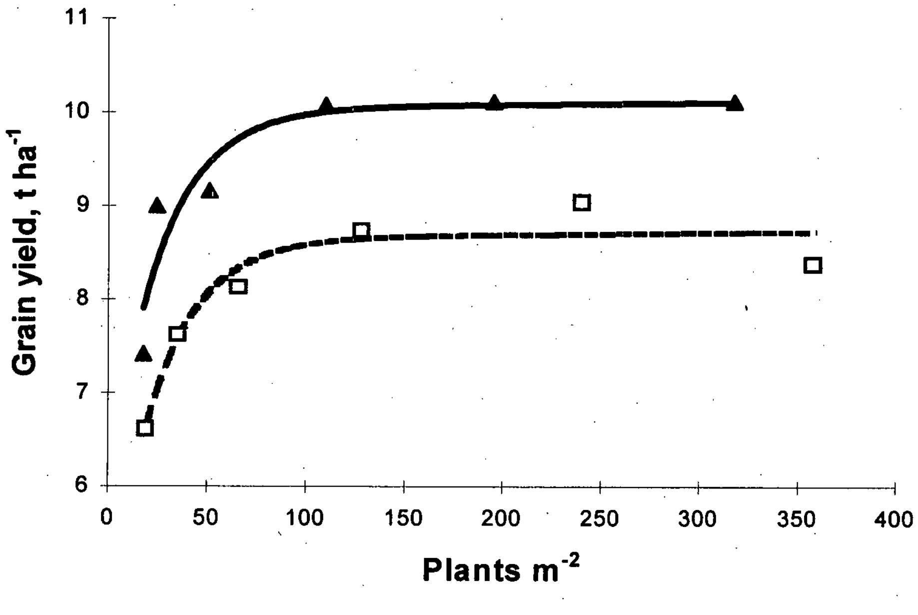

Fig. 1.5. The response of grain yield to crop density in 1996/7, ▲ and 1997/8, □. S.E. 0.644, variance accounted for 71.5%. Curve fitted in 1996/7: $10.04-4.324*0.9617^{x}+0.00022x$ (solid line), in 1997/8: $8.652-4.324*0.9617^{x}+0.00022x$ (broken line).

Discussion

A reduction in plant density from 338 to 19 plants m^{-2} did not result in a significant reduction in total dry matter production. The compensation for reduced plant density was achieved through an increased relative growth rate (RGR) as found in previous work (Kirby, 1967) where barley was sown at seed rates of 100-800 seeds m^{-2}. The low density crop may increase RGR compared with the more dense crops either through more efficient radiation capture or through improved conversion of radiation to assimilates. It is evident that, in the case of early sown Haven, both radiation capture per plant and radiation use are improved with reductions in plant density.

Radiation capture per plant may be increased through a variety of compensatory mechanisms such as increased leaf production, shorter phyllochron, increased tillering, larger shoots, better canopy survival or through a larger extinction coefficient. This study found radiation capture per plant to be greater at low densities mainly due to increased duration of tillering and increased green area per shoot.

The number of main stem leaves produced did not increase with reductions in plant density which agrees with the findings of Puckridge (1968). However, main stem leaf number has been observed to increase with reductions in plant density in other varieties; and Kirby and Faris (1970) found main stem leaf initiation to increase in barley with reductions in plant density, due to increased duration of vegetative primordia initiation. This may therefore be a variety dependent compensation mechanism.

A reduction in phyllochron would allow, firstly, more rapid leaf production and therefore potentially faster canopy growth and, secondly, increased potential rate of tillering. There was a trend for decreases in phyllochron at the reduced plant densities, although only when calculated from measurements including the phase when the stem was extending. Phyllochron, when measured before GS31, displayed no response to plant density. Kirby and Faris (1972) found that when barley was grown densely internodes grew longer, possibly due to an effect of increased giberellic acid. Phyllochron may therefore be decreased at low densities due to decreased distances for leaves to extend during stem extension.

The duration of tillering was significantly increased by reducing plant density. Darwinkel (1978) also found shoot number per plant increased through longer phases of tiller production (rather than through increased tiller production rate). He reported a maximum of 2 shoots per plant were at the beginning of March when grown at 800 plants m^{-2} and 29 shoots per plant at the end of May when grown at 5 plants m^{-2}.

Compensation for reduced plant density was also achieved with increases in green area per shoot (Table 1.5). This was clearly visible at GS65 where maximum green area per shoot was recorded in crop densities of 30 plants m^{-2}. In this experiment the green area per shoot was measured as an average of all shoots. Thus, in crops where there are many relatively young small shoots, for example at low plant densities at GS65, or generally at GS31, the average green area per shoot may be small. There may have been an increase in size of the main stem and primary tillers with the reduction of plant density where the mean green area per shoot was small but this was not recorded. The increase in green area per shoot may have been achieved through the production of larger leaves or through delayed leaf senescence. Our data cannot differentiate between these two compensatory mechanisms. Similar work was performed in 1998/9 at Sutton Bonington in Leicestershire (Shearman, personal communication). The number of culm leaves and the area of each leaf on the main stem of Haven at GS39 sown at 325 and 80 seeds m^{-2} were recorded. The green area per shoot was found to increase with the reduction in plant density but the number of culm leaves present at this time was unaffected. The area of the flag leaf (F) was unchanged by reduction in plant density but the area of the penultimate leaf (F^{-1}), F^{-2} and F^{-3} were significantly larger at the low density than at the high plant density. Puckridge (1968) conversely found when individual plants, grown in tubes, were moved from a high plant density to a low plant density, affecting only the radiation environment, leaves were smaller than those maintained in the dense crop. This was thought to be due to the effect of high light breaking down giberellins in the low density crop limiting cell expansion. The discrepancies between these studies must be caused by the increase in nitrogen availability per plant in this field study with reduction in plant density. The more nitrogen available, the larger leaves may expand and thus a shoot grown at a reduced plant density may produce large leaves.

The extinction coefficient, k_{PAR}, was found not to vary with plant density. This was also found with 2 varieties of barley (Fukai *et al.*, 1990) with a reduction in plant density from 120 to 36 plants m^{-2} there was negligible change in k. In both wheat and barley k has been found to be reasonably constant between sites and seasons, although it may increase post-ear emergence (Thorne *et al.*, 1988). k_{PAR} was not measured post ear emergence. It is possible measurement would have detected a difference in k_{PAR}, firstly, as the ears emerged and, secondly, as the canopy began to senesce when leaves become more prostrate (Ledent, 1976). k_{PAR} is affected by both attitude of the canopy and transmission of radiation through the canopy, which is affected by the nitrogen content of the leaves (Thorne *et al.*, 1988). These results suggest that either these were not significantly affected by the change in plant density or changes in these two factors balanced each other out.

There are two reasons why RUE may increase at reduced plant densities. Firstly, when plant density was reduced GAI decreased and k remained unchanged, resulting in a more even distribution of radiation through the canopy. Therefore fewer leaves in the crop were light saturated and leaves further down the canopy could contribute to crop growth. Secondly, where the nitrogen supply is limited it is probable that sparse sown crops have a higher photosynthetic tissue nitrogen concentration and thus a higher efficiency of conversion of radiation to assimilates (Green, 1987, Whitfield and Smith, 1989).

Tiller survival increased when plant density was reduced, as was observed by Darwinkel (1978). The exception to this was the apparent increase in tiller survival at the highest density where maximum shoot numbers were difficult to assess due to onset of shoot death before GS31 and subsequent difficulty in counting dead tillers. A larger proportion of initiated tillers survive to produce ears when more radiation and nitrogen are available (Masle, 1985). Where tiller survival is increased more tillers may be employed to increase the green area of the plant and thus increase the efficiency of radiation capture of the crops grown at low plant densities. The dying tillers may be considered a waste of resources as although some nitrogen and a little carbohydrate may be retranslocated from the dying shoot to the rest of the plant not all resources may be retranslocated (Lupton and Pinthus, 1969; Thorne and Wood, 1987). Thus at a 'normal' crop density the presence of up to 700 dead shoots m^{-2} may detract from the partitioning of carbohydrate and nitrogen to the grain.

The response of grain yield to reductions in plant density is determined by the response of grain production and grain filling processes to changes in plant density. Darwinkel (1980) reported that as plant density is reduced the potential number of grains is increased through enhanced spikelet production and then further influences the number of grains produced per spikelet. Increases in green area per shoot with reduction in plant density gave rise to increase in radiation interception per shoot. Therefore more assimilates could be produced per shoot allowing increased ear growth and floret survival and therefore grain number per ear. At very low plant densities not all radiation may be absorbed by the crop in this phase, thus the number of grains m^{-2} is reduced.

Grain weight (TGW) did not change significantly in either year, although in 1997/8 there was a trend for increases in TGW with decreasing plant density. This follows mixed reports about the effect of plant density on grain weight. Assimilates for grain fill are derived from both current assimilation and assimilates stored in the stem as WSC (Willey and Dent, 1969). With reductions in plant density there is an increase in PAR interception and WSC per shoot.

However, these sources of assimilates at normal plant densities are often more than that required to fill grain and thus TGW is stable for a wide range of conditions (Gallagher *et al.*, 1975). Reported increases in TGW with decreased plant density may be due to an increase in potential grain size through the increase in endosperm cell number set just post-anthesis. Brocklehurst (1977) found that increased assimilate availability at anthesis, through floret removal, caused an increase in endosperm cell number. One possible explanation for the stability of TGW in this study, particularly in 1996/7, was that a maximum possible grain size had been achieved by plants sown at high seed rates and further increases were limited by space in the ear.

At GS39 in 1996/7 68 and in 1997/8 36 plants m^{-2} were required to produce a canopy of sufficient size to intercept 90% of incident radiation. Thus above these plant densities assimilate supply is limited by incident radiation rather than fractional radiation interception. Thus in 1996/7 higher yields were obtained due to higher incident radiation in July. Any vegetative growth above that required to intercept the majority of incident radiation may be detrimental to grain yield by increasing both the disease risk (e.g. Tompkins *et al.* 1993) and the lodging risk (Berry, 1998) of the crop as well as needlessly increasing seed costs.

APPENDIX 2

Effect of sowing date on the economic optimum plant density of winter wheat

Introduction

This section investigates the underlying mechanisms of yield compensation in winter wheat and how they are affected by sowing date. At present, most seed rate recommendations take account of the sowing date only through altering the expected percentage establishment of seed; this study deals with determining economic optimum plant population at varying sowing dates, i.e. the optimal combinations of plant density and sowing date to obtain maximum yield.

Materials and methods

Three field experiments were conducted at ADAS Rosemaund Research Centre, Herefordshire, UK, in 1996/97, 1997/98 and 1998/99. The soil type was stoneless, silty-clay loam (Bromyard series) with pH between 6.2 and 7.1 and organic matter content between 2.4 and 2.7%. Field sites for 1996/97 and 1997/98 were planted in the preceding season with winter oilseed rape; and 1998/99, with winter beans.

Plots were kept free from weeds, pests and diseases, and plant growth regulators applied following recommended standard agronomic practices. Soil fertility levels were amended to ensure that nutrient availability would not be a limiting factor.

The experiment consisted of three target sowing dates (late-September, SD1; mid-October, SD2; and mid-November, SD3), six target seed rates (20, 40, 80, 160, 320 and 640 seeds m^{-2}) and four varieties (Cadenza, Haven, Soissons and Spark). A split-plot arrangement of treatments in a randomised complete block experimental design with three replicates was used. Main plot treatments were sowing date and sub-plot treatments were seed rate and variety. Plots (2 m x 24 m in size) were drilled using Oyjord tractor mounted seed drill with 13.5 cm row widths. Sowing dates for each year of the study are presented in Table 2.1.

Table 2.1. Sowing dates of winter wheat in 1996/97, 1997/98 and 1998/99 season.

Sowing date	1996/97	1997/98	1998/99
SD1	27/9/96	23/9/97	02/10/98
SD2	25/10/96	18/10/97	20/10/98
SD3	14/11/96	16/12/97	11/11/98

Plant counts were taken at around GS13/14 (three/four leaf stage) from 0.5m x 0.5m quadrats placed randomly in the plots. Crops were harvested on 19, 22 and 29 August in the first, second and third year, respectively. Grain yield was obtained by harvesting 2 m x 10 m using a plot combine, and values were adjusted to 15% moisture. Samples of grain from the combine were counted using a 'Numigral' grain counter for thousands grain weight determination. Six middle rows of 1 m length, from the rest of the plot, were cut at ground level for the determination of ear numbers m^{-2} and grains per ear. Number of tillers per plant were counted, for plots with 40, 80 and 320 target seed rates, at various growth stages through out the season to determine the maximum number of tillers produced per plant.

Data were subjected to analysis of variance and regression analysis using Genstat. The response of the four wheat varieties to increasing plant density up to the optimum was not statistically different. In 1998 there was a significant interaction, but this was due to varietal differences in resistance to lodging affecting crop at the higher seed rates. Therefore to improve the precision of the estimation of the optimum, mean of the four varieties are presented for each year, and emphasis given to the interaction between sowing date and plant density which is the purpose of this paper.

In each year, economic optimum plant populations were determined using linear plus exponential regression equation, $Y = a + br^x + cx$ for each sowing date across varieties. Grain price at the time of study was £80/tonne (£0.36/1000seeds at 45mg/seed), and cost of the seed was £300/tonne (£1.35/1000seeds at 45mg/seed). Linear regression equation, $Y = a + bx$, was fitted for the relationship between optimum plant density and sowing date to enable prediction of plant density. Yield component values at the economic optimum plant densities for each sowing date in each year were calculated from the fitted linear plus exponential regression equation for ears m^{-2}, and from the linear equation for grains per ear and TGW. The number of ears per plant was calculated dividing the number of ears m^{-2} by the corresponding (economic) plant density.

Some analysis like the final leaf number per main stem, maximum tiller number per plant and ear number m^{-2} were also performed in relation to thermal time (TT) to full vernalisation. Weather data on temperature were collected from the experimental weather station with in 1 km distance to the experimental site. Daily TT (using 0 ^{0}C base temperature) and effective vernalisation were calculated using the algorithm shown below (Meteorological Office, Form 3300, cited by Kirby, 1994). The daily TT were then added to give TT accumulated to full vernalisation (TTver), i.e. 50 days for winter wheat varieties.

For daily TT:
- If Tbase < Tmin; daily TT = Tmean - Tbase
- If Tbase < Tmean (for Tmax > Tbase and Tmin < Tbase) ;

daily TT = (Tmax - Tbase)/2 - (Tbase - Tmin)/4
- If Tbase > Tmean (for Tmax > Tbase and Tmin < Tbase);

daily TT = (Tmax - Tbase)/4
- If Tmax and Tmin < Tbase; daily TT = 0

For vernalisation efficiency (V.eff.):
- If Tmean temp > 3 and ^{2} 10, then V.eff. = 1
- If Tmean ^{3} -4 and Tmean ^{2} 3; then V.eff. = (Tmean + 4)/7
- If Tmean > 10 and Tmean ^{2} 17 then V.eff. = (17 - Tmean)/7
- Else V.eff. = 0

Wherever possible, the achieved plant population density have been used in the results section below (e.g. when using graphs). For ease of the presentation of the results, however, the target seed rates are used when using two-way tables. Both plant density and target seed rates have been used in the text when referring to the tables. Moreover, the reader can refer to Table 2.2 if reference to the actual plant density at each target seed rates is needed.

Results

Plant counts

Achieved plant population varied from year to year, and decreased with delay in sowing date (SD) although significant ($P<0.05$) only in 1997/98 (Table 2.2). In 1996/97, the mean percentage establishment was 68, 70 and 65% for SD1, SD2 and SD3 respectively. In 1997/98, mean percentage establishment was 76, 60 and 10%; and in 1998/99, it was 61, 52 and 42% respectively. Percentage establishment also decreased significantly in all years ($P<0.001$) with an increase in seed rates, particularly at 320 and 640 target seed rates m^{-2}. Number of established plants were significantly affected by the interaction between seed rate and sowing date in all years ($P<0.001$); sowing date had a much greater effect on establishment at high seed rates that at low seed rates. Every effort was made to sow seeds in optimal soil conditions; however, in 1997/98 season it was not possible to sow in November due to wet seedbed conditions, and thus sowing was delayed until December (still in less than ideal conditions) which resulted in extremely low plant counts (Table 2.2). For this reason, this sowing is not included in any further results. Plant counts made at GS30/31 for SD1 treatments have shown that there was no significant change in plant counts over-winter (data not shown).

Table 2.2. Plant population density m^{-2} of winter wheat at three sowing dates (SD) and a range of target seed rates (TSR) m^{-2} in 1996/97, 1997/98 and 1998/99 season.

	1996/97			
TSR m^{-2}	SD1	SD2	SD3	Mean
20	16	14	10	13
40	31	29	24	28
80	57	60	41	53
160	113	111	97	107
320	190	213	200	201
640	326	418	387	377
Mean	122	141	127	

SED (P=0.05) for comparing sowing date means = non-significant (NS); for seed rate means = 4.6 (df 137); and for any individual values = 11.3 (df 137) except when comparing with the same levels of SD = 8.0 (df 137).

1997/98	TOS			
TSR m^{-2}	SD1	SD2	SD3	Mean
20	18	14	2	11
40	31	26	3	20
80	65	46	9	40
160	121	99	15	79
320	229	195	35	153
640	377	288	85	250
Mean	140	112	25	

SED (P=0.05) for comparing time of sowing means = 4.8 (df 4); for seed rate means = 4.5 (df 138); and for any individual values = 8.5 (df 138) except when comparing with the same levels of TOS = 7.8 (df 138).

	1998/99			
TSR m^{-2}	SD1	SD2	SD3	Mean
20	13	11	8	11
40	27	20	18	21
80	49	44	29	41
160	102	84	72	85
320	195	170	142	170
640	318	314	262	298
Mean	117	107	87	

SED (P=0.05) for comparing sowing date means = NS; for seed rate means = 4.9 (df 138); and for any individual values = 11.4 (df 138) except when comparing with the same levels of SD =8.4 (df 138).

Grain yield

The main effect of sowing date on grain yield was significant in 1996/97 ($P<0.01$) and 1998/99 ($P<0.05$), but not in 1997/98; whereas, the main effect of plant density was significant in all years ($P<0.001$). Delaying date of sowing from SD1 to SD3 reduced grain yield by 24% in 1996/97 and by 15% in 1998/99 season. An increase in plant density from 11-13 plants m^{-2} to 79-107 plants m^{-2} (i.e. 20 to 160 target seeds m^{-2}) increased grain yield significantly by 67, 65, 120% in 1996/97, 1997/98 and 1998/99 season, respectively. There was also a significant interaction between plant density and sowing date on yield in all years ($P<0.001$): plant density had a much greater effect at late sowings than early sowings (Fig. 2.1). For example, increasing plant density from the lowest to the highest plant density at SD1 increased grain yield by 33% in 1996/97 and by 100% in 1998/99; whereas, at SD3 the increase in grain yield was 197% in 1996/97 and 254% in 1998/99 season.

A yield-density model was developed for the mean of the four varieties from a regression analysis on grain yield against seed rates by fitting linear plus exponential curves to the data. The coefficients of the regression equation are given in Table 2.3. The economic optimum plant population (Opn) corresponding to each sowing date for each year were then plotted against sowing date (Fig. 2.2). The lower optimum seed rate in SD2 compared with SD1 of 1998/99 season was due to yellow cereal fly (*Oopomyza*) infestation which affected early sown plots most severely. For this reason, the value of SD1 for 1998/99 season was not included in the relationship between optimum plant population density and sowing date (Fig. 2.2). The optimum plant population density was predicted reasonably well by the linear model (Opn = 1.6*days + 374; $R^2 = 0.97$) with in the range of the sowing dates used in the study, and ranged from 71 plants m^{-2} on 30th September to 135 plants m^{-2} on 14th November. For every single day delay in date of sowing between late-September and mid-November, 1.6 more plants m^{-2} were required to achieve optimum yield.

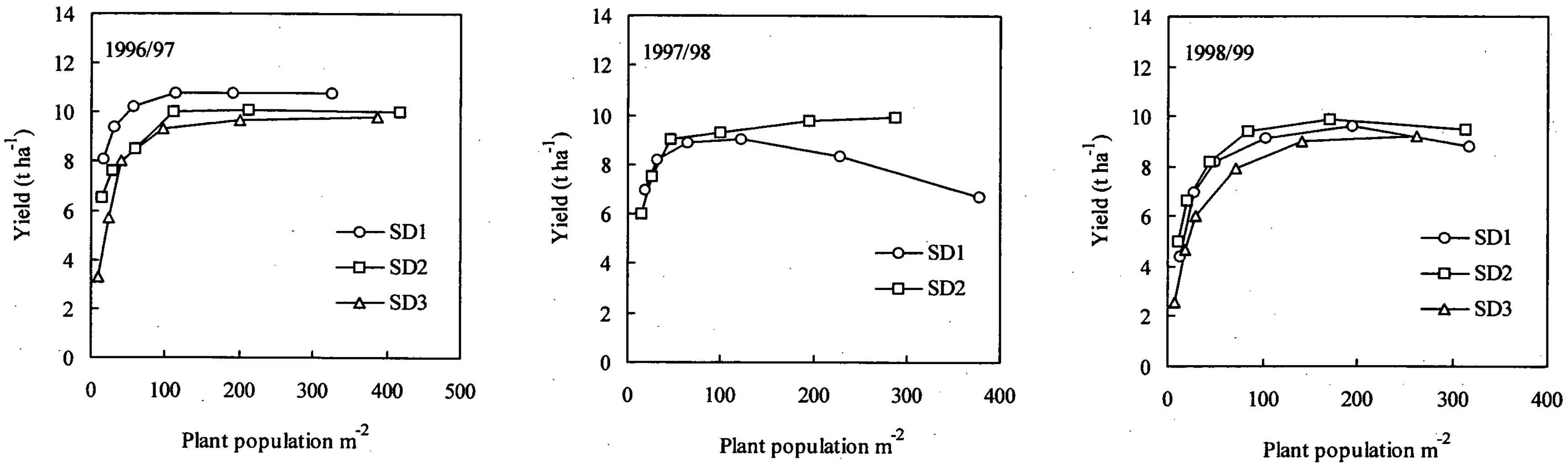

Fig. 2.1. Grain yield (t/ha , 15% moisture) of winter wheat at three sowing dates (-O- SD1, -□- SD2, -△- SD3) and a range of plant population densities m^{-2} in 1996/97, 1997/98 and 1998/99 season. SED (P=0.05) for comparing for any individual values = 0.50 (df 134), 0.36 (df 92) and 0.50 (df 137); except when comparing with the same levels of SD = 0.4 (df 134), 0.35 (df 92) and 0.3 (df 137) in 1996/97, 1997/98 and 1998/99, respectively.

Table 2.3. Relationship between yield and seed rates, and the coefficients a, b, c and r in the linear plus exponential equation $Y = a + br^x + cx$. n refers to the number of entries; % var to % of variance accounted; SE to standard error; % estab to % establishment; opt rate to optimum seed rate; opt popn to optimum plant population density.

Year	Sowing date	n	a =-b	c	r	% var	opt rate	SE opt rate	% estab	opt popn	SE opt popn
1996/97	SD1	70	10.36	0.00082	0.93	43.5	91	9	71.7	65	6
	SD2	70	9.15	0.00166	0.95	35.6	148	106	69.2	102	73
	SD3	72	9.55	0.00041	0.98	85.0	226	20	61.5	139	12
1997/98	SD1	72	9.45	-0.00420	0.94	19.1	72	9	81.5	59	7
	SD2	72	9.10	0.00141	0.95	54.5	141	34	62.1	88	21
1998/99	SD1	71	9.61	-0.00070	0.97	70.6	153	10	63.5	97	6
	SD2	72	9.46	0.00067	0.97	75.7	169	15	52.3	88	8
	SD3	72	8.56	0.00141	0.98	79.1	331	140	41.8	138	59

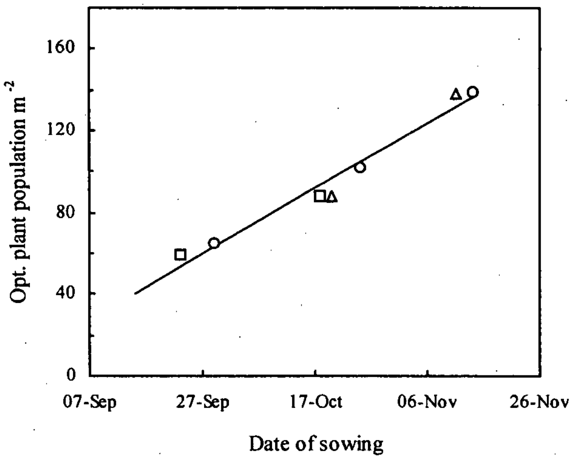

Fig. 2.2. The relationship between sowing date and economic optimum plant population density ($y = 1.6x + 374$; $r^2 = 0.97$; x = Julian days, number of days since 1st January) for winter wheat from results of three years study (1996/97, ○; 1997/98, □; 1998/99, △).

Total biomass

The main effect of plant density on total biomass was significant in all years ($P<0.001$); but the effect of sowing date was significant ($P<0.01$) only in 1996/97. Increasing plant density from 11-13 plants m^{-2} to 79-107 plants m^{-2} (i.e. 20 to 160 target seeds m^{-2}) increased the mean biomass yield significantly by 46, 78 and 56% in 1996/97, 1997/98 and 1998/99 respectively. The reduction in total biomass with delay in sowing date from SD1 to SD2 was 13%, and from SD1 to SD3 was 24% in 1996/97 season.

A sowing date x plant density interaction was significant for total biomass in all years ($P<0.001$). The effect of plant density was much greater at later sowings compared with early sowings; delaying the date of sowing reduced total biomass substantially by 20-60% at plant densities up to 65 plants m^{-2}, but had non-significant effect at higher densities (Fig. 2.3).

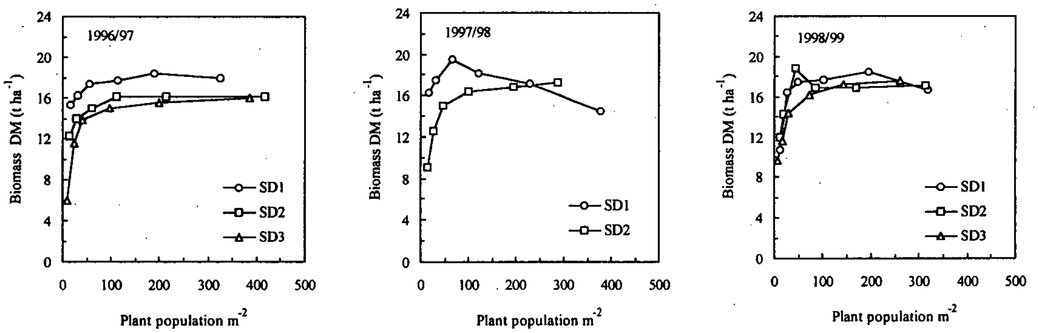

Fig. 2.3. Biomass dry matter yield (t ha^{-1}) of winter wheat sown at three sowing dates (SD) and a range of plant population densities m^{-2} in 1996/97, 1997/98 and 1998/99 season. SED (P=0.05) for comparing for any individual values = 0.94 (df 135), 1.03 (df 90) and 1.17 (df 138); except when comparing with the same levels of SD = 0.79 (df 135), 0.87 (df 127) and 0.91 (df 90) in 1996/97, 1997/98 and 1998/99, respectively.

Ear number m^{-2}

Plant density significantly affected ear number m^{-2} of wheat in all years ($P<0.001$); as did sowing date in 1996/97 ($P<0.01$) and 1997/98 ($P<0.05$). Increasing plant density from 11-13 plants m^{-2} to 298-377 plants m^{-2} (i.e. from the lowest to the highest density) increased ear number m^{-2} from 236 to 658 ears m^{-2} in 1996/97, from 239 to 510 ears m^{-2} in 1997/98, and from 218 to 572 ears m^{-2} in 1998/99 season (Fig. 2.4). Ear number m^{-2} generally declined with delay in date of sowing; comparing the earliest with the latest sowings, the decline was on average from 468 to 380 ears m^{-2} in 1996/97, from 432 to 334 ears m^{-2} in 1997/98, and from 406 to 364 ears m^{-2} in 1998/99 season. There was no significant sowing date x plant density interaction for ear number m^{-2} at $P<0.05$.

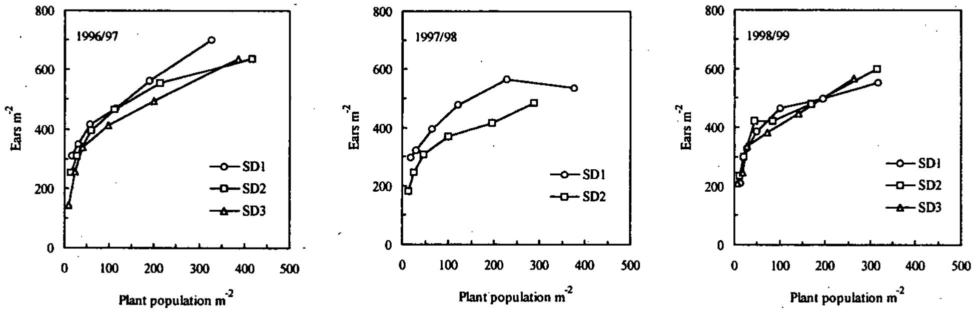

Fig. 2.4. Number of ears m^{-2} of winter wheat at three sowing dates (SD) and a range of plant population densities m^{-2} in 1996/97, 1997/98 and 1998/99 season. SED (P=0.05) for comparing for any individual values = NS in all years.

Maximum number of tillers per plant

The main effect of plant density on maximum tiller number per plant was significant in all years ($P<0.001$); increasing plant density from 20-28 plants m^{-2} to 153-201 plants m^{-2} (from 40 to 320 target seeds m^{-2}) reduced the number of maximum tillers by 60% in 1996/97, 58% in 1997/98, and by 66% in 1998/99 (Table 2.4). The main effect of sowing date was significant ($P<0.01$) only in 1996/97; and delaying sowing date from SD1 to SD2 or SD3 significantly reduced maximum tillers per plant by 31- 35%. There was also a significant ($P<0.05$) sowing date x plant density interaction for maximum tillers in 1997/98; the number of maximum tillers decreased with delay in date of sowing at the lower and higher plant density, whilst it increased at the medium plant density.

Table 2.4. Maximum number of tillers per plant of winter wheat at three sowing dates (SD) and a range of target seed rates (TSR) m^{-2} in 1996/97, 1997/98 and 1998/99 season.

	1996/97			
TSR m^{-2}	SD1	SD2	SD3	Mean
40	14.9	11.1	10.5	12.2
80	12.6	8.1	8.3	9.7
320	6.9	4.3	3.6	4.9
Mean	11.5	7.9	7.5	

SED (*P*=0.05) for comparing sowing date means = 0.42 (df 4); for seed rate means = 0.27 (df 66); and for any individual values = NS.

	1997/98		
TSR m^{-2}	SD1	SD2	Mean
40	17.6	16.4	17.0
80	11.2	12.4	11.8
320	7.7	6.6	7.1
Mean	12.1	11.8	

SED (*P*=0.05) for comparing sowing date means = NS; for seed rate means = 0.44 (df 44); and for any individual values = 0.61 (df 44) except when comparing with the same levels of SD = 0.62 (df 44)..

	1998/99			
TSR m^{-2}	SD1	SD2	SD3	Mean
40	16.2	15.9	17.2	16.4
80	12.3	12.9	13.4	12.9
320	5.4	5.4	6.1	5.6
Mean	12.3	11.4	12.3	

SED (*P*=0.05) for comparing sowing date means = NS; for seed rate means = 0.56 (df 66); and for any individual values = NS.

Number of grains per ear

The number of grains per ear was reduced significantly by increasing plant density in all years ($P<0.001$). The reduction in the number of grains per ear from the lowest density to the highest density was 39, 42 and 37% in 1996/97, 1997/98 and 1998/99 respectively (Table 2.5). Sowing date did not significantly influence grain number per ear. There was a significant ($P<0.001$) interaction between sowing date and plant density for grain number per ear in 1997/98, but not in the other two years. Wheat plants from SD1 produced significantly fewer grains per ear (by more than 12 grains per ear) compared with those from SD2 at plant densities of 121 plants m^{-2} and above (i.e. 160 target seeds m^{-2} and above), but similar numbers of grains per ear at 65 plants m^{-2} and below (i.e. target rates below 80 seeds m^{-2}).

Table 2.5. Number of grains per ear of winter wheat at three sowing dates (SD) and a range of target seed rates (TSR) m^{-2} in 1996/97, 1997/98 and 1998/99 season.

	1996/97			
TSR m^{-2}	SD1	SD2	SD3	Mean
20	49.6	55.0	58.1	54.2
40	52.8	58.1	47.1	52.7
80	47.8	43.4	49.5	46.9
160	44.2	44.6	46.2	45.0
320	39.0	38.0	41.0	39.3
640	31.8	33.5	33.3	32.9
Mean	44.2	45.4	45.9	

SED (P=0.05) for comparing sowing date means = NS; for seed rate means = 3.15 (df 129); and for any individual values = NS.

	1997/98		
TSR m^{-2}	SD1	SD2	Mean
20	52.2	47.9	50.1
40	49.2	49.2	49.2
80	44.9	48.2	46.5
160	31.8	43.7	37.7
320	25.5	40.6	33.1
640	17.3	34.9	26.1
Mean	36.8	44.1	

SED (P=0.05) for comparing sowing date means = NS; for seed rate means = 2.18 (df 92); and for any individual values = 3.43 (df 92) except when comparing with the same levels of SD = 3.09 (df 92).

	1998/99			
TSR m^{-2}	SD1	SD2	SD3	Mean
20	63.4	66.9	61.4	63.9
40	57.2	70.7	67.0	65.0
80	55.0	58.3	62.2	58.5
160	45.4	51.0	57.8	51.4
320	40.4	45.6	49.4	45.1
640	42.0	35.7	42.4	40.0
Mean	50.6	54.7	56.7	

SED (P=0.05) for comparing sowing date means = NS; for seed rate means = 3.21 (df 135); and for any individual values = NS.

Grain weight

Thousand grain weight (TGW) was affected significantly ($P<0.001$) by plant density in 1997/98 season, but not in 1996/97 and 1998/99 season (Table 2.6). With an increase in plant density from the lowest to the highest, there was a decrease in TGW by 5, 11 and 2% in 1996/97, 1997/98 and 1998/99 season respectively. The main effect of sowing date on TGW was significant in all years ($P<0.05$). In 1996/97, TGW was reduced by about 6% with delay in date of sowing from SD1 to SD2 or SD3; and in 1998/99, by 4-6%. By contrast in 1997/98, TGW was increased with delay in date of sowing from SD1 to SD2 by 8% due to lodging.

TGW was significantly ($P<0.001$) affected by the interaction between plant density and sowing date in 1997/98, and not in the other two years. In 1997/98, increasing plant population above 65 plants m^{-2} (80 target seeds m^{-2}) significantly reduced TGW by 18% at SD1; whereas, TGW was not significantly altered by seed rates in SD2 (Table 2.6). Moreover, there was a trend for a decease in TGW with an increase in plant population density regardless of sowing date in all years, except in the SD3 of 1998/99 where TGW was generally increasing with an increase in plant density.

Table 2.6. Weight of thousand grains (g, 15% moisture) of winter wheat at three sowing dates (SD) and a range of target seed rates (TSR) m^{-2} in 1996/97, 1997/98 and 1998/99 season.

	1996/97			
TSR m^{-2}	SD1	SD2	SD3	Mean
20	53.3	50.0	49.5	50.9
40	53.5	49.4	50.5	51.1
80	52.5	50.5	49.3	50.8
160	52.7	49.2	49.6	50.5
320	51.5	48.3	48.6	49.5
640	49.8	48.0	46.9	48.2
Mean	52.2	49.2	49.1	

SED (P=0.05) for comparing sowing date means = 0.04 (df 4); for seed rate means = NS; and for any individual values = NS.

	1997/98		
TSR m^{-2}	SD1	SD2	Mean
20	52.8	54.5	53.7
40	54.0	55.1	54.5
80	52.3	54.5	53.4
160	50.4	54.6	52.5
320	45.3	51.6	48.4
640	43.5	52.0	47.8
Mean	49.7	53.7	

SED (P=0.05) for comparing sowing date means = 1.01 (df 4); for seed rate means = 1.16 (df 92); and for any individual values = 1.85 (df 92) except when comparing with the same levels of SD = 1.65 (df 92).

	1998/99			
TSR m^{-2}	SD1	SD2	SD3	Mean
20	51.3	52.1	45.9	49.8
40	52.8	49.5	47.6	50.0
80	53.9	50.5	46.7	50.4
160	52.4	51.0	49.6	51.0
320	52.8	49.7	51.7	51.4
640	47.6	49.6	49.3	48.8
Mean	51.8	49.6	48.5	

SED (P=0.05) for comparing sowing date means = 0.51 (df 4); for seed rate means = NS; and for any individual values = NS.

Yield components at the economic optimum plant density

On average, around 400 ears m^{-2} were required to produce economic optimum yields whether planting in SD1, SD2 or SD3. Averaging the three years, SD1 produced 414 ears m^{-2} from 74 plants m^{-2}; SD2, 388 ears m^{-2} from 93 plants m^{-2}; and SD3, 383 ear m^{-2} from 139 plants m^{-2} (Table 2.7). This maintenance of ear number per unit area with delay in date of sowing at the optimum plant population densities was accompanied by a decrease in number of fertile ears per plant (on average from 5.9 to 2.8 shoots) and grains weight (from 48.9 to 44.5g per 1000 grains), while the number of grains per ear remained constant at around 48.7 to 48.9 grains per ear (see Table 2.7). The regression coefficients of the linear plus exponential and linear equations used in calculating ears m^{-2}, grains per ear and thousand grains weight at the economic optimum density are presented in Tables 2.8 and 2.9.

Table 2.7. Ear number m^{-2}, number of ears per plant, number of grains per ear and thousand grain weight (TGW, g) of wheat at economic optimum plant population densities (opt popn). Ears m^{-2} and grains m^{-2} from curve fitted using linear plus exponential $Y = a + b(r)^x + cx$, with $b = -a$ (see Table 2.8 below for regression coefficients); and grains per ear and TGW from linear equation $Y = ax + b$. Ears/plant is a calculated value.

Year	Sowing date	opt popn m^{-2}	Ears m^{-2}	Ears/plant	Grains/ear	TGW
1996/97	SD1	65	407	6.2	48.0	49.0
	SD2	102	434	4.2	47.4	47.7
	SD3	139	399	2.9	45.2	46.9
1997/98	SD1	59	409	7.0	46.7	50.0
	SD2	88	330	3.8	41.9	44.0
1998/99	SD1	97	427	4.4	51.9	47.6
	SD2	88	400	4.5	56.7	49.1
	SD3	138	367	2.7	52.2	42.1
3 years average						
	SD1	74	414	5.9	48.9	48.9
	SD2	93	388	4.2	48.7	46.9
	SD3	139	383	2.8	48.7	44.5

Table 2.8. Relationship between ear number m^{-2} and seed rate, and the coefficients a, b, c and r in the linear plus exponential equation $Y = a + br^x + cx$.
n refers to the number of entries; % var to % of variance accounted; opt rate to optimum seed rate.

Year	Sowing date	n	a =-b	c	r	% var	Ear no at opt rate	SE opt rate
1996/97	SD1	70	377	0.52	0.93	72.0	407	14
	SD2	72	404	0.38	0.96	72.4	434	15
	SD3	71	346	0.45	0.97	80.9	399	15
1997/98	SD1	72	453	0.17	0.96	40.8	409	18
	SD2	71	323	0.26	0.97	76.2	330	10
1998/99	SD1	72	429	0.20	0.97	67.4	427	14
	SD2	72	379	0.33	0.96	65.1	400	15
	SD3	72	313	0.40	0.96	71.3	367	15

Table 2.9. Coefficients a and b in the linear relationships ($Y = a + bx$) between plant density and number of grains per ear, and between plant density and thousand grains weight (TGW); r" refers to correlation coefficient.

			Grains/ear			TGW		
Year	Sowing date	n	a	b	r^2	a	b	r^2
1996/97	SD1	6	52.19	-0.064	0.96	53.61	-0.011	0.95
	SD2	6	52.96	-0.054	0.74	49.98	-0.005	0.72
	SD3	6	52.54	-0.053	0.84	50.06	-0.008	0.88
1997/98	SD1	6	49.68	-0.050	0.80	55.10	-0.012	0.80
	SD2	6	50.38	-0.097	0.94	53.94	-0.030	0.94
1998/99	SD1	6	58.37	-0.067	0.72	53.40	-0.014	0.53
	SD2	6	66.05	-0.106	0.87	50.10	-0.005	0.28
	SD3	6	64.63	-0.090	0.93	47.23	-0.014	0.41

Discussion

Increasing plant population density up to 100-150 plants m^{-2} increased grain and total biomass yield rapidly after which little further yield increase was obtained. Studies of the effects of plant population on crop dry matter yield (Holliday, 1960; Donald, 1963) and grain yield (Kirby, 1967; Puckridge & Donald, 1967; Darwinkel, 1978;) have also shown that grain yield increases sharply with an increase in plant density to an optimum level, then reaches a plateau at moderate density, after which it declines at very high population levels. The economic optimum density of winter wheat varied with sowing date: the three years average were 63, 93 and 139 plants m^{-2} for SD1, SD2 and SD3 respectively. About half the plant population density was needed to achieve economic optimum yield when planting in SD1 compared with SD3, indicating that yield compensation was reduced with delayed sowing date. The main reason for the increase in the number of plants needed to achieve optimum yield with delay in date of sowing was the reduced number of fertile ears per plant. The number of ear-bearing shoots per unit area was maintained at around 400 ears m^{-2}; the number of fertile tillers per plant decreased substantially and grain weight decreased slightly, while the number of grains per ear was not altered. Reduction in the final number of ears per plant was clearly evident at higher plant population density as well as with delayed sowing date; but the combined effect was much greater.

Grain yield generally decreased with delay in time of sowing, and the reduction was much greater at low plant density compared with high plant density. Similarly Conry (1998), from a four year of experiments in Ireland, found reduced grain yield of spring malting barley with delay in time of sowing. He also reported no significant difference in yield between seed rates of 120, 160, 200 and 240 kg/ha (180 kg/ha equals 400 seeds m^{-2} at 45 mg grain weight) when plants were sown in February and early March; but the lowest density gave the least yield when sown in April. The strong interaction between plant density and sowing date for grain yield in the current study, however, was not strongly reflected in the response of ears m^{-2}; the number of ears required for economic optimum yield was almost maintained. Kirby (1969) in his studies on dual purpose barley varieties sown in late October, mid-March, and late-April also found identical ear population density for the October and March sowings despite a 20 - 45% reduction in plant population for the autumn sown crops.

Higher seed rates increased fertile tillers m^{-2} but reduced grains size and grains/ear. This is in agreement with the results reported for winter wheat (Darwinkel *et al.* 1977) and for winter barley (Corny & Hegarty, 1992). Yield compensation with delay in time of sowing required an increment of plant density to maintain number of ears per unit area and to reach maximum attainable yields, since individual plant growth was reduced. For every single day delay in time of sowing between late-September and mid-November, 1.6 more plants m^{-2} were required for optimum yield. In contrast, Corny & Hegarty (1992) in their 5 years study in Ireland found that increased seed rates of winter barley did not compensate for the yield reduction due to delayed sowing; yield obtained from mid-October, November and December were smaller than yield obtained with the lowest seed rate of the previous sowing date (early September and late September), mainly due to reduced ears m^{-2}.

Tillering, which affects the number of ears per plant, is affected by differences in the number of leaves per main stem. The number of leaves per main stem is primarily determined by accumulated temperature prior to exposure to low temperature and increasing daylength which initiate the change from production of leaf to spikelet primordia (Kirby, 1994). Increasing thermal time, by sowing early, increased linearly the number of final leaves per main stem; for every increase in one degree days thermal time, there was an increase of 0.0081 leaves per main stem, both at 40 and 320 plants m^{-2} (Fig. 2.5).

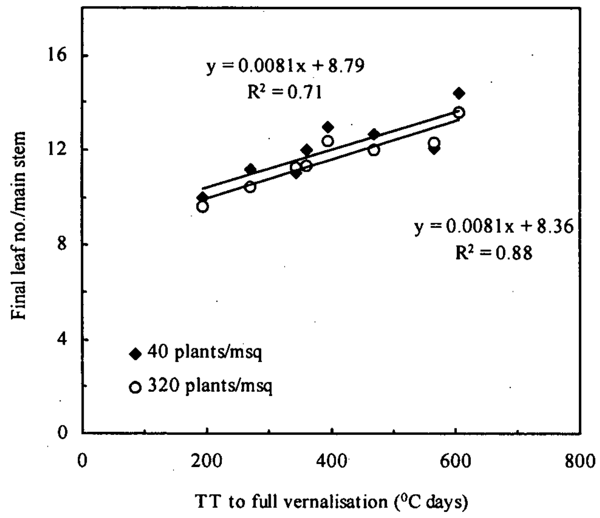

Fig. 2.5. Final leaf number of main stem as a function of thermal time (TT) to full vernalisation at 40 plants m^{-2} and 320 plants m^{-2} .

The fact that the number of tillers are affected by the length of the duration of tiller initiation as well as by plant density suggests that interactions between sowing date and plant population density are bound to influence yield (Dennett, 1999). Maximum tiller number per plant increased linearly with an increase in TT to full vernalisation, i.e. with early sowing (Fig. 2.6). For both maximum number of tillers per plant (Fig. 2.6) and ear number m^{-2} (Fig. 2.7), the rate of increase was greater at lower plant density compared with high plant density. The duration of tillering phase as well as tiller survival were greater at low plant density. Delaying sowing date also increased tiller survival and more so at higher density compared with low density, showing that tiller survival is less important in determining final grain yield. Final number of ears depended more on the maximum number of tillers produced at the end of tillering rather than on the total loss of tillers (Gracia del Moral and Gracia del Moral, 1995).

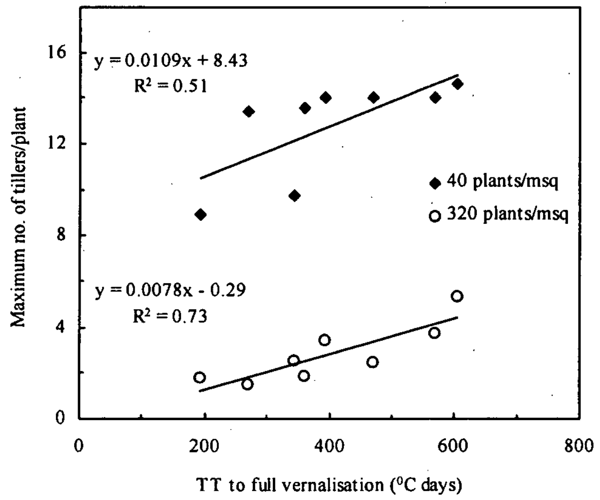

Fig. 2.6. Maximum number of tillers per plant as a function of thermal time (TT) to full vernalisation at 40 and 320 plants m^{-2}.

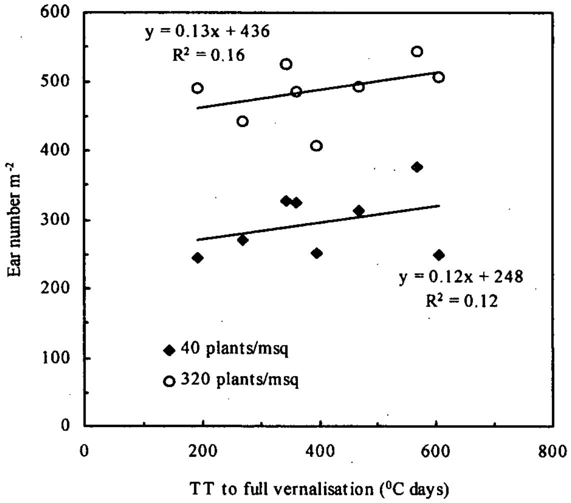

Fig. 2.7. Ear number m^{-2} as a function of thermal time (TT) to full vernalisation at 40 and 320 plants m^{-2}.

The relationship between maximum tiller number per plant and number of leaves per main stem (Fig. 2.8) was also linear; increasing the number of leaves per main stem increased number of maximum tillers per plant, but the effect was much greater at low density compared with high density. Since ear number m^{-2} appears critical in achieving optimum yield and is the product of plant population and tillers per plant, the increase in the number of maximum tillers per plant with an increase in both TT to full vernalisation and final number of leaves per main stem is a clear indication that less plants are needed to achieve maximum yield when sowing early.

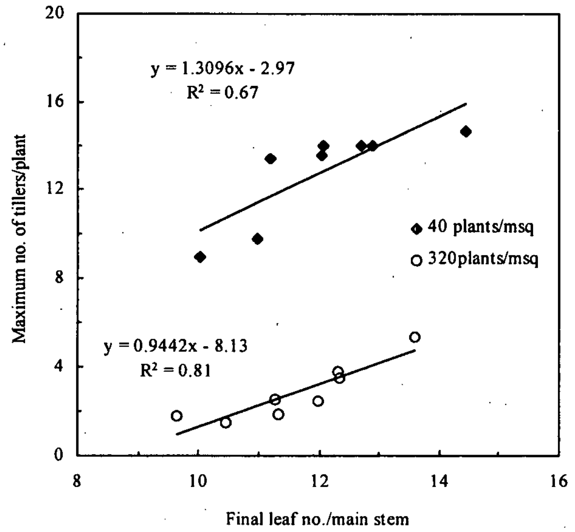

Fig. 2.8. Maximum number of tillers per plant as a function of final leaves/main stem at 40 and 320 plants m^{-2}.

The ability of wheat to compensate for wide population differences in maintaining maximum yield was influenced by sowing date. However, the response of varieties to plant density was very similar in this study, and has also been confirmed in other findings (e.g. Guitard, Newman & Hoyt, 1961; Kirby, 1968; Teich & Smid, 1993). This implies that despite contrasting differences in their tillering characteristics (from shy to profuse tillering), wheat varieties have similar potential for yield compensation at reduced plant population densities. It also shows that tillering is primarily governed by the available soil and light resources per individual plants rather than by the inherent differences in tillering ability.

To obtain highest economic return, September-sown crops require much lower seed rates than the current practice. This was attributed to slower rate of development and greater thermal time accumulated prior to full vernalisation at early sowings compared with late sowings (see above). Therefore, economic optimum plant density in areas with higher altitude or at higher latitudes may be expected to be higher; and further study is recommended to investigates this across a range of sites.

A given seed rate can result in wide ranges of plant population density depending on plant establishment. Plant establishment, in turn, is influenced by seedling mortality and predation before crop emergence, as well as plant losses due to environmental stresses, pests and diseases (Hay & Walker, 1989). Such losses are greater when using greater plant population density due to greater intraspecific competition (Puckridge & Donald, 1967; Masle, 1985). Therefore, plant establishment will be a major consideration when aiming to establish the optimum plant population.

APPENDIX 3

The effect of variety on optimum plant population

Previous work has indicated significant differences between varieties in their production and maintenance of tillers (Foulkes *et al.* 1998). It was hypothesised that this would result in significant differences between varieties in their response to reduced plant population. This was addressed using two approaches. In the first four varieties were chosen to contrast for specific physiological characteristics and sown at a wide range of seed rates and sowing dates to establish the economic optimum plant population (Experiment 1). The second included a range of up to 22 varieties per year sown on one date at either a high or low seed rate to look for significant interactions between variety and seed rate (Experiment 2). The varieties were chosen to represent a range of physiological characteristics, older varieties which have previously been the subject of much experimental work and new and 'up and coming' commercial varieties.

Materials and methods

Experimental design and treatments

Field experiments were undertaken at two sites: experiments 1 and 2 at ADAS Rosemaund, Herefordshire, and experiment 1 at Sutton Bonington, Leicestershire.

Experiment 1

Four varieties (Cadenza, Haven, Soissons and Spark) chosen for their differences in tillering ability, were sown at six seed rates: 20, 40 80, 160, 320 and 640 seeds m^{-2}. These were sown at a three sowing dates at Rosemaund and at one sowing date at Sutton Bonington (Table 3.1)

Table 3.1. Sowing dates (SD) of winter wheat in 1996/97, 1997/98 and 1998/99 season at Rosemaund and Sutton Bonington.

		1996/97	1997/98	1998/99
Rosemaund	SD1	27/9/96	23/9/97	02/10/98
	SD2	25/10/96	18/10/97	20/10/98
	SD3	14/11/96	16/12/97	11/11/98
Sutton Bonington		03/10/96	3/10/97	12/10/98

At Rosemaund the experimental design was a split plot plus 2-way factorial with three replicates. The time of sowing treatment was on the main plot; seed rate and variety were factorially combined and fully randomised on sub plots. Each plot size was 2m * 24m. Sutton Bonington used a similar experimental set up but without sowing date treatments, i.e. a randomised 2-way factorial design. The soil was a stoneless silty clay loam (Bromyard series) at Rosemaund and a medium stony loam to 80 cm over clay (Dunnington Heath Series) at Sutton Bonington.

Experiment 2

Between 16 and 22 varieties per year were sown at either a high (320 seeds m^{-2}) or low (80 seeds m^{-2}) seed rate. The plots were sown on 27 September 1996, 26 September 1997 and 3 October 1998. A total of 26 varieties were evaluated, of these 12 were included in all three years, and 18 in two out of three years the full list of varieties included is given below:

1997	1998	1999
Abbot	Abbot	Abbot
Avalon	Avalon	Avalon
Brigadier	Brigadier	-
Buster	Buster	Buster
Cadenza	Cadenza	Cadenza
Caxton	Caxton	Caxton
Charger	Charger	Charger
-	-	Claire
Consort	Consort	Consort
Crofter	-	-
Drake	Drake	Drake
-	Equinox	Equinox
-	Harrier	Harrier
Haven	Haven	Haven
-	-	Madrigal
-	-	Malacca
-	-	Maverick
Mercia	Mercia	Mercia
Raleigh	-	-
-	Reaper	Reaper
-	Rialto	Rialto
Riband	Riband	-
-	-	Savannah
-	-	Shamrock
Soissons	Soissons	Soissons
Spark	Spark	Spark

Measurements

Detailed growth and development measurements were taken on experiment 1 at ADAS Rosemaund to provide an understanding of how the different varieties maintained yield at reduced seed rates. Growth analysis was done across varieties and seed rates concentrating on the first sowing date in 1996/7 and 1997/8, and the second sowing in 1998/9. Developmental characteristics such as leaf production, tiller production and the dates of critical growth stages were measured across varieties and sowing dates on a restricted set of seed rates.

Grain yield was measured using a plot combine from a 10m by 2m area of each plot. Grain was analysed for moisture content and specific weight using GAC 2000 grain analysis computer (Dickey-John Corporation).

Results and discussion

In experiment 2 higher plant populations were established in 1997 than either of the other 2 years (Table 3.2). Variety did not significantly affect plant population except in 1999, and in this case all varieties established an above optimal population in the high seed rate. There was no significant interaction between variety and seed rate in terms of numbers of plants established.

Table 3.2 Plants numbers m^{-2} of varieties in Experiment 2 sown at high (320 seeds m^{-2}) and low (80 seeds m^{-2}),

	1997		1998		1999	
Varieties	320	80	320	80	320	80
Abbot	210.86	69.14	215.00	52.00	178.33	59.67
Avalon	226.67	65.68	289.33	53.00	213.67	62.00
Brigadier	200.99	70.62	201.33	58.67	-	-
Buster	219.75	66.17	213.67	60.33	195.00	52.67
Cadenza	196.05	67.65	200.00	53.33	188.00	57.00
Caxton	221.23	60.74	216.33	53.67	178.00	62.33
Charger	212.84	66.67	209.00	60.00	184.67	60.67
Claire	-	-	-	-	185.00	53.00
Consort	205.93	67.65	186.00	42.67	179.67	52.33
Crofter	224.20	59.26	-	-	-	-
Drake	209.38	71.11	204.00	45.67	200.33	53.67
Equinox	-	-	178.00	52.00	201.33	60.67
Harrier	-	-	188.67	63.00	177.33	60.33
Haven	211.36	70.62	189.00	55.33	146.00	47.00
Madrigal	-	-	-	-	177.33	74.33
Malacca	-	-	-	-	172.67	47.33
Maverick	-	-	-	-	187.67	59.00
Mercia	200.00	74.57	191.33	58.67	182.33	62.33
Raleigh	217.78	71.60	-	-	-	-
Reaper	-	-	181.33	63.67	193.67	54.67
Rialto	231.11	76.05	214.33	55.00	179.33	53.00
Riband	240.00	75.06	186.00	55.00	-	-
Savannah	-	-	-	-	175.00	58.00
Shamrock	-	-	-	-	177.67	48.00
Soissons	204.94	65.68	184.00	58.33	173.00	47.00
Spark	219.26	62.72	187.67	46.67	173.67	53.00
	P	SED	P	SED	P	SED
Variety	0.525	NS	0.371	NS	0.041	9.01
Seed rate	<0.001	4.17	<0.001	3.13	<0.001	2.72
Interaction	0.528	NS	0.318	NS	0.453	NS

The effect of variety on shoot number m^{-2} both at the beginning and end of stem extension observed in previous work was supported by observations in all years in this work (Tables 3.3 & 3.4) There were significant effects of seed rate on shoot number at GS 32 and 59 in all years. The expected interaction between variety and seed rate on shoot number was significant in 1998, but not in either of the other 2 years.

Table 3.3. GS 32 shoot numbers m^{-2} of varieties in Experiment 2, sown at high (320 seeds m^{-2}) and low (80 seeds m^{-2}),.

	1997		1998		1999	
Varieties	320	80	320	80	320	80
Abbot	800.33	596.36	689.52	420.40	587.38	569.23
Avalon	812.23	601.13	626.61	416.48	545.58	480.94
Brigadier	806.30	593.35	775.25	517.57	-	-
Buster	671.43	550.22	590.79	362.37	716.52	507.07
Cadenza	612.33	415.15	631.51	392.52	748.65	533.18
Caxton	651.97	449.22	491.08	399.44	384.00	341.09
Charger	828.58	524.80	807.04	395.58	672.90	596.91
Claire	-	-	-	-	578.94	549.74
Consort	747.78	546.93	656.86	405.97	599.57	515.51
Crofter	922.52	650.76	-	-	-	-
Drake	1035.45	783.27	887.75	800.41	665.02	614.07
Equinox	-	-	668.24	431.99	569.51	401.14
Harrier	-	-	813.92	695.02	646.60	689.13
Haven	832.56	577.08	837.27	612.90	725.60	645.93
Madrigal	-	-	-	-	754.93	471.71
Malacca	-	-	-	-	626.48	614.81
Maverick	-	-	-	-	667.60	527.68
Mercia	942.16	525.14	684.23	326.39	721.16	666.28
Raleigh	815.77	656.12	-	-	-	-
Reaper	-	-	621.56	437.12	645.35	470.46
Rialto	659.67	399.32	765.59	367.84	774.52	482.48
Riband	805.33	496.80	608.08	373.82	-	-
Savannah	-	-	-	-	490.02	530.54
Shamrock	-	-	-	-	670.69	472.28
Soissons	711.99	355.46	681.82	346.82	694.84	446.72
Spark	943.78	760.27	911.56	453.49	719.48	670.14
	P	SED	P	SED	P	SED
Variety	<0.001	56.32	<0.001	52.38	<0.001	66.9
Seed rate	0.040	51.25	0.002	11.35	<0.001	20.2
Interaction	0.559	NS	0.027	72.88	0.347	NS

Table 3.4. Ear number m^{-2} of varieties in experiment 2, sown at high (320 seeds m^{-2}) and low (80 seeds m^{-2}), in late September or early October.

	1997		1998		1999	
Varieties	320	80	320	80	320	80
Abbot	571.45	398.12	632.13	338.07	491.42	375.31
Avalon	516.50	346.22	436.08	343.10	523.69	422.75
Brigadier	702.96	455.38	572.18	276.70	-	-
Buster	573.16	468.54	564.66	314.10	458.25	427.33
Cadenza	512.00	351.99	564.76	348.75	520.36	413.52
Caxton	529.75	292.92	460.33	303.76	517.01	292.99
Charger	655.25	330.75	600.72	348.95	594.63	430.07
Claire	-	-	-	-	528.68	424.04
Consort	650.20	511.42	460.22	334.28	508.79	426.14
Crofter	515.94	420.01	-	-	-	-
Drake	605.98	503.02	652.47	392.94	539.93	435.36
Equinox	-	-	448.47	314.01	441.47	384.17
Harrier	-	-	582.03	421.45	521.69	433.38
Haven	598.93	438.64	565.19	434.80	490.00	398.72
Madrigal	-	-	-	-	484.12	473.99
Malacca	-	-	-	-	572.31	418.74
Maverick	-	-	-	-	555.26	464.81
Mercia	626.17	436.30	683.24	367.72	512.13	465.71
Raleigh	613.46	475.57	-	-	-	-
Reaper	-	-	518.75	386.46	556.20	408.92
Rialto	504.09	348.94	523.71	320.53	494.10	414.45
Riband	508.26	345.41	445.91	278.63	-	-
Savannah	-	-	-	-	492.59	400.03
Shamrock	-	-	-	-	501.89	359.56
Soissons	571.02	313.59	585.87	387.45	513.34	473.38
Spark	635.70	560.69	624.48	383.42	630.73	504.36
	P	SED	P	SED	P	SED
Variety	<0.001	32.76	<0.001	31.69	0.120	NS
Seed rate	0.029	29.43	0.005	14.26	<0.001	12.81
Interaction	0.028	53.72	0.009	45.82	0.876	NS

Yields were greater in 1997 and 1999 at 10.7 and 10.1 t/ha respectively than in 1998 when the average was 8.5 t/ha. In 1997 & 1998 there was no significant difference between the yields of the low and high seed rates (Table 3.5). However, in 1999 the low seed rate yielded slightly less than the high seed rate: 10.0 compared with 10.3 t/ha. Despite the previously observed differences between varieties in tiller production and survival also being observed in this work, there was no differential response between varieties and seed rate in terms of final yield.

Table 3.5. Yield (t/ha @ 85% dm) of varieties sown at high (320 seeds m^{-2}) and low (80 seeds m^{-2}), in late September or early October.

	1997		1998		1999	
Varieties	320 seeds m^{-2}	80 seeds m^{-2}	320 seeds m^{-2}	80 seeds m^{-2}	320 seeds m^{-2}	80 seeds m^{-2}
Abbot	10.8	9.8	7.7	7.8	10.6	9.9
Avalon	9.8	9.4	6.9	7.1	9.2	8.6
Brigadier	11.6	10.9	9.2	9.4	-	-
Buster	10.7	10.4	8.1	8.3	10.4	10.0
Cadenza	11.3	11.1	8.2	8.5	10.0	9.8
Caxton	10.4	10.2	7.8	7.8	9.6	10.0
Charger	10.8	10.5	8.5	8.8	9.3	8.8
Claire	-	-	-	-	10.8	10.7
Consort	11.4	11.5	9.5	9.5	10.4	10.7
Crofter	11.3	10.6	-	-	-	-
Drake	11.5	11.1	9.1	8.9	10.9	10.6
Equinox	-	-	8.5	8.8	10.3	10.3
Harrier	-	-	9.2	9.5	10.0	10.4
Haven	11.8	11.1	9.3	9.5	10.6	10.4
Madrigal	-	-	-	-	11.2	10.6
Malacca	-	-	-	-	10.1	10.0
Maverick	-	-	-	-	11.2	11.0
Mercia	9.4	9.2	7.1	7.3	9.6	8.7
Raleigh	11.5	11.7	-	-	-	-
Reaper	-	-	8.4	9.1	10.9	10.6
Rialto	11.0	10.9	9.1	8.8	10.2	9.9
Riband	11.5	11.2	9.0	9.2	-	-
Savannah	-	-	-	-	11.4	10.8
Shamrock	-	-	-	-	10.0	10.3
Soissons	9.4	9.4	6.8	7.8	9.6	9.4
Spark	10.9	10.4	7.7	8.2	10.1	9.1
	P	SED	P	SED	P	SED
Variety	<0.001	0.20	<0.001	0.27	<0.001	0.38
Seed rate	0.116	NS	0.238	NS	0.028	0.11
Interaction	0.210	NS	0.806	NS	0.945	NS

In experiment 1 at Rosemaund the main effects of sowing date, seed rate and variety were significant in all years (Table 3.6) except for sowing date in 1998, were only the first 2 sowings were included due to the establishment failure of the final sowing date. There was also a highly significant interaction between sowing date and seed rate in all years. There was no significant interaction between variety and seed rate or sowing date, variety and seed rate except in 1998, which was due to lodging in early sown high seed rate plots. The degree of lodging was dependent on the inherent standing power of the variety and the sowing date (only occurring in SD1) hence the significance of the interaction (Table 3.7). A very similar result was seen at Sutton Bonington where variety and seed rate were significant in all years, but the interaction between variety and seed rate again on significant in the lodging year of 1998 (Table 3.6).

Table 3.6. Significance (F pr) of the sowing date, variety and seed rate and main interactions in experiment 1.

	Rosemaund			Sutton Bonington		
	1997	1998	1999	1997	1998	1999
Sowing date	0.004	0.080	0.041	-	-	-
Seed rate	<.001	<.001	<.001	<.001	<.001	<.001
Variety	<.001	<.001	<.001	<.001	<.001	0.004
Sowing date*seed rate	<.001	<.001	<.001	-	-	-
Variety*seed rate	0.954	<.001	0.197	0.743	0.009	0.991
Sowing date*variety*seed rate	0.999	0.001	0.948	-	-	-

Table 3.7. Pre-harvest lodging index in sowing date 1, Rosemaund 1998

Seed number m^{-2}	Cadenza	Haven	Soissons	Spark	Mean
20	0	0	0	0	0
40	0	0	0	0	0
80	0	0	0	0	0
160	39	0	2	1	10
320	64	0	39	5	27
640	87	16	76	27	51
Mean	32	3	20	5	15

In conclusion, the variety being grown has little or no effect on the economic optimum plant population. However, in a lodging situation the benefits of reduced seed rate are likely to be greater on poorer standing power varieties, and conversely the risks of excessive seed rate are less on varieties which inherently stand well.

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