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EXPLOITATION OF VARIETIES FOR UK CEREAL PRODUCTION (VOLUME II)

VARIETAL RESPONSES TO DROUGHT AND ROTATIONAL POSITION

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(VOLUME II)

PART 1. VARIETAL RESPONSES TO DROUGHT
by

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PART 2. VARIETAL RESPONSES TO ROTATIONAL POSITION
by

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Summary

The main hypothesis under test was that UK winter wheat varietal types exist conferring better performance under drought than others and that these are defined by possession of combinations of desirable physiological traits, namely : deeper maximum rooting depth, earlier flowering date, more restricted maximum canopy green area, larger stem soluble carbohydrate reserves and higher water use efficiency. Over three seasons 1993-4, 1994-5 and 1995-6, the effect of irrigation from mid-April to harvest compared to an unirrigated control was examined for six winter wheat varieties (Haven, Mercia, Maris Huntsman, Rialto, Riband and Soissons) on the loamy sand soil at ADAS Gleadthorpe. Varieties were selected, as far as available data sets allowed, to provide contrasts for the five prioritised physiological traits. In the1993-4 season, with drought post-flowering in unirrigated plots, grain yield was reduced on average by 1.83 t/ha compared to the fully irrigated treatment, whereas in 1994-5 and 1995-6 with pre- and post-flowering droughts in the unirrigated controls, grain yield was reduced by 3.06 and 4.55 t/ha, respectively. Averaged across seasons, there was a significant irrigation/variety interaction. Rialto and Mercia lost only about 2.7 t/ha under drought compared with Haven and Riband which lost about 3.5 t/ha, with intermediate losses for Maris Huntsman and Soissons. The possession of combinations of traits explained, in large part, these differential responses to drought. No meaningful varietal differences in maximum rooting depth or water use efficiency were found, and these traits were discounted from further consideration in relation to yield responses. The varietal range for maximum canopy area was relatively small, of the order of 1.0 green area index (GAI) unit, and did not correlate strongly with patterns of water uptake pre-flowering. Thus leafiness was not a good predictor of yield performance with drought. The varietal range in flowering date (GS 61) was 10 days from Soissons (earliest) to Haven (latest). These differences corresponded with significant varietal variation in water uptake from mid April to flowering (GS 61) under drought, with values in the range 149 to 176 mm ($P< 0.001$). The more rapidly developing varieties generally used less water. As expected, rapidly developing varieties subsequently used more water during grain filling under drought. These varietal difference in the range c. 60 – 75 mm, however, were less than the corresponding differences for water use up to flowering. In summary, early flowering appeared to confer only a marginal advantage in terms of drought resistance. The trait which showed the best relationship with unirrigated yield performance and which provided the best predictor of performance under drought was the amount of stem soluble carbohydrate amassed shortly after flowering. Varieties varied under drought in the range c. 2.0 – 2.9 t/ha. Although, the regression between stem reserves and yield was significant under irrigation, under drought it accounted for a much larger % in yield variation amongst varieties, indicating the importance of this character in influencing yield with drought. The amount of total above-ground harvest dry mass appeared also to bear some correlation with better yield performance under drought. Total harvest dry mass was greater for Rialto compared to all other varieties, in both irrigated and unirrigated conditions ($P< 0.05$). Rialto *was the variety with the most consistent drought resistance across seasons, and its greater propensity for above-ground growth may have been associated with greater investment in below-ground root growth and a more extensive, although not deeper, rooting system. The measurable traits indicative of drought resistance would therefore seem to be (i) date of GS 61, (ii) amount of stem soluble carbohydrate dry matter measured soon after flowering and (iii) harvest index (the ratio of grain weight to total above-ground dry mass at harvest which, with a known combine yield, allows the calculation of total above-ground crop dry mass). As a consequence of the findings in this work, NIAB have added the assessment of stem soluble carbohydrate at the end of flowering to the list of characters routinely assessed in winter wheat RL trials and this information is now published annually in the NIAB Cereals Variety Handbook.*

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PART 1. VARIETAL RESPONSES TO DROUGHT

1. INTRODUCTION

1.1. Distribution of drought-prone soils

For a crop, water availability is a function of rainfall and the available water capacity (AWC) of the soil within the rooting zone. The major variation in AWC is due to soil texture and depth, but there are also effects of soil structural condition and whether the rooting medium is a topsoil or subsoil (Bailey, 1990). Lighter soils with poor soil structure and shallow topsoils have less available water. AWC for wheat (assuming a rooting depth of 1.2 m) ranges from *c.* 110 mm on light sand soils to more than 250 mm on some deep silty clay loam soils. For soils in eight counties, where wheat was judged to be grown most intensively on the basis of parish MAFF June Census data 1992, the percentage of soils in five classes of AWC was estimated using the agricultural databank of the Soil Survey of England and Wales (Hall *et al.*, 1977) by Scott *et al.* (1994) (Table 1.1). A significant proportion of wheat was found to be grown on the lighter soil types, especially in certain counties such as Suffolk and Nottinghamshire. This evidence supported previous findings (Austin, 1978) that on average some 17% of potential wheat yield is lost each year due to drought in the UK.

Table 1.1 Percentage of soils in five classes of AWC and percentage of tilled land including fallow sown to wheat in autumn 1991 for eight counties in England.

County	AWC (mm) to 1.2 m					% sown to Wheat
	< 125	125-150	151-175	176-200	> 200	
Cambridgeshire	26.4	15.0	38.8	0.0	19.8	46.6
Essex	21.1	59.0	19.9	0.0	0.0	46.2
Lincolnshire	27.3	23.4	49.3	0.0	0.0	44.6
Humberside	0.0	80.0	0.0	10.7	9.3	44.0
Suffolk	89.7	10.3	0.0	0.0	0.0	40.2
Nottinghamshire	54.3	42.5	0.0	0.0	3.2	35.5
Norfolk	19.7	72.5	0.0	4.5	3.3	29.5
Herefordshire	85.2	8.5	6.3	0.0	0.0	18.0

The AWC of the soil is an incomplete indicator of water availability which also depends on rainfall. The amount of water passing through a wheat crop grown in eastern England from soil to atmosphere from the time of the end of field capacity to harvest is typically about 300 mm (Goss *et al.*, 1984). The precise amount will vary according to the evaporative demand of the atmosphere (potential evapotranspiration), crop cover and the yield potential of the site. Potential evapotranspiration (Eo) is affected mainly by air humidity, air temperature, solar radiation and wind speed. It varies less than rainfall with location and season (Jones & Thomasson, 1985). It is thus the balance of Eo and rainfall during April, May, June and July which ultimately defines the amount of water required from the soil if yield is not to be limited by supply of water.

From the distribution of wheat with AWC for English counties (Table 1.1), it follows that, in years with rainfall significantly below average, serious yield-limiting water deficits will occur in an appreciable percentage of UK wheat fields. Tinker & Widdowson (1982), on the basis of irrigation trials at Rothamsted and Woburn in 1970-81, concluded that yield losses would be significant in certain seasons on lighter soils, but questioned the size of Austin's (1978) overall estimate of 17% annual yield loss. On the basis of the distribution of wheat with AWC reported here (Table 1.1), it seems likely that Austin's estimate was accurate, and that, in most seasons, varieties suited to drought-prone soils will be of value to a significant number of UK growers.

1.2. Timing of drought

Although the frequency of UK drought has been observed by other authors (Austin, 1978; French & Legg, 1979), possibly enough emphasis has not been attached to the timing of drought in relation to crop development. Bailey (1990) has described a critical soil moisture deficit, defining drought as when the water holding capacity within the rooting zone becomes 50% depleted. Using this definition, Foulkes *et al.* (1993) estimated incidence of drought using the MORECS model (Thompson *et al.*, 1981) across eight NIAB regional trial centres over a five year period, 1987-91 (Table 1.2). The estimated available water capacities (mm) to 1.2 m for trial centres examined were: Cockle Park (> 200), Rosemaund (180), Morley (180), Seale-Hayne (175), Cambridge (170), Harper Adams (155), Bridgets (140) and Wye (140). With the exception of the Cockle Park site, AWC fell within a relatively narrow range of 140 - 180 mm. Similar exercises had rarely been carried out previously because of the difficulty of obtaining sufficient site-seasons managed to a standard protocol.

Table 1.2 *Frequency of pre- and post-anthesis drought at NIAB regional trial centres 1987- 1991*

	No drought	Pre-anthesis drought	Post anthesis drought	Pre-and post-anthesis drought
Cockle Park	5	0	1	0
Rosemaund	3	0	3	0
Morley	5	0	1	0
Seal-Hayne	3	0	2	1
Cambridge	3	0	2	1
Harper Adams	3	0	2	1
Wye	2	0	3	1
Bridgets	4	0	2	0
Total (%)	58	0	34	8

Average rainfall in England is distributed uniformly between months, whilst Eo progressively exceeds rainfall from April to June. Thus, greatest soil moisture deficits (SMDs) tend to occur after flowering towards the end of the summer (Bailey, 1990), and drought is more common at this time. Earlier onset of drought can occur before anthesis, but is reported to be much less frequent (Innes & Thomasson, 1983). In present work, it was estimated that post-anthesis drought occurred in 34% of cases, pre-and post anthesis droughts in 8% of cases and no drought in 58% of cases for the 40 site-seasons examined (Foulkes *et al.*, 1993). While pre-and-post anthesis droughts were rare between 1987 and 1991 at the eight NIAB sites, the effects of such droughts can be serious (Innes *et al.*, 1981). It follows that varietal types combining traits conferring resistance to both early and late onset of drought will be of more long-term benefit to farmers than types with resistance solely to late onset of drought.

1.3. Effects of drought on grain yield

Although national average yield tends to be greatest in dry years, e.g. 1984, 1995 and 1996, growers on lighter, drought-prone soil types in these years will encounter yields below the norm for their particular field circumstances. Even on the high AWC soil types there may be sub-clinical effects on certain days during the season. Critical soil moisture deficits for drought are often expressed as the SMD which limits yield, i.e. the limiting deficit (LD); and LD changes with soil type. For example, LD on the silty clay loam of Rothamsted has been reported as 140 mm (French & Legg, 1979), but on the sandy soil at IACR Woburn, LD it has been shown to be as little as *c.* 40 mm (Penman, 1970). Thus, as a proportion of AWC, LD is smaller on lighter than on heavier soil types.

On the lightest of soils sown to winter wheat in England, e.g. the loamy medium sand at ADAS Gleadthorpe with AWC to 1.2 m of *c.* 120 mm, yield responses to irrigation of over 2 t/ha have been recorded in dry years such as 1984 when large SMDs accumulated (Bailey, 1990). On soils of higher AWC, yield responses to irrigation in dry years are less frequently observed. On the silt loam at the Letcombe laboratory, Oxford, it was shown that a SMD of 150 mm, expected in only about 15 yrs in a 100, had a small non-significant effect on yield compared to a fully irrigated treatment (Gales & Wilson, 1981). Similarly, on the silty clay loam of Rothamsted, winter wheat did not respond to irrigation in 1972 and 1974, when the maximum SMD was 141 and 134 mm, respectively (French & Legg, 1979). In contrast, at the Plant Breeding Institute, Cambridge, on a sandy clay loam of AWC to 1.2 m of *c.* 160 mm, irrigation increased yield by 1.8 t/ha compared to drought induced by using mobile shelters (Innes *et al.*, 1985). The authors did not present SMD data but did provide meteorological data indicating that the maximum SMD was likely to have been in the order of 80 - 100 mm.

In England, winter wheat is grown in fields with AWC to a depth of 1.2 m typically in the range 150 - 250 mm, with most fields tending towards the middle of this range. Based on the above reports, it appears that large SMDs will not cause large yield reductions across all soil types. However, there is evidence that yield is reduced in dry years on sandy loam or sandy soil types. In summary, at the outset of Sub-Project work, current UK literature indicated that the largest sorts of responses to irrigation reported were in the order of 2 t/ha occurring on the medium to light loams and sands in seasons where SMD exceeded about 100 mm. Crops grown in these drought conditions may thus be candidates for irrigation or choice of resistant varieties. It is thus worth examining varietal differences that might minimise yield losses and confer resistance to drought.

1.4. Candidate varietal traits conferring drought resistance

In recent decades, the effect of water availability on winter wheat has been studied in relation to root growth and water uptake (Welbank *et al.*, 1974; Lupton *et al.*, 1974; Barraclough & Leigh, 1984), leaf posture (Innes & Blackwell, 1983), date of ear emergence and crop height (Innes *et al.*, 1985), remobilization of stem carbohydrate reserves (Austin *et al.*, 1977) and ear-bearing capacity (Innes *et al.*, 1981). There are heritable differences in all these traits but in any investigation of varietal differences, it has not been possible to quantitatively apportion the contributions of variation in these traits to variation in grain yield over sites and seasons representing a range of water-stressed environments.

In order to assist wheat growers and their supporting organisations in the selection of varieties for specific environments, the intention at the outset of the Sub-Project was to:

i) suggest ways in which varietal traits may confer tolerance of drought, and
ii) using these suggestions, attempt to prioritise the importance of candidate varietal traits for determining drought performance.

1.4.1. Rooting depth

Welbank *et al.* (1974), Lupton *et al.* (1974) and Barraclough and Leigh (1984) were unable to show significant differences in maximum rooting depth between varieties of winter wheat grown in the UK. However, confidence in measurements is poor and it is possible that differences in maximum rooting depth of 20 cm have gone undetected. Such a difference on a clay loam soil would increase available water by 30 mm. Thus it still may be that varietal differences in rooting would be important in relation to drought performance. For this reason rooting depth was identified as a trait to be investigated during the Sub-Project. Because of the labour involved in root length and dry mass measurements, root activity was measured indirectly by estimating soil water content in the soil profile in the current work. From the pattern of water uptake in experiments throughout the growing season, deductions were made about rooting depth and density within the soil profile to 1.65 m depth (depth of soil water content measurements).

1.4.2. Efficiency of water use

Green *et al.* (1983) reported values for the ratio of total dry-matter accumulation to water use of 3.7 to 5.8 g/m^2/mm (mean 4.9) for four different winter wheat varieties grown in England at different sites and seasons 1973-4 to 1979-80. They suggested that the effect of variety on this ratio was less than that of the environment. Similar estimates were observed by Doyle & Fischer (1979) and Goss *et al.* (1984). Overall, the literature on varietal variation in water use efficiency (WUE) is inconclusive. Small differences have been reported for varieties in individual experiments (Richards, 1983; Innes *et al.*, 1984), but against this Richards (1987) concluded future genetic improvements in water use efficiency were likely to be small.

Work in the current Sub-Project examining data from the NIAB RL trials 1987-91 showed a linear relationship between accumulated actual evapotranspiration from sowing to harvest and grain yield for cvs Avalon and Galahad (Foulkes *et al.*, 1993). In England, it is reasonable to assume that soil evapotranspiration would be small relative to actual evapotranspiration (Ea) (Green *et al.*, 1983), and consequently that Ea would be a good estimate of water transpired by the crop. The varietal difference reported of 0.2 g/m^2/mm between Avalon and Galahad, if real, would relate to a 0.6 t/ha grain yield difference for wheat growing on a finite supply of water equivalent to 300 mm transpired water. At the outset of the current work, there was a need for further clarification in this area. For this reason, WUE was identified as a trait to be measured in Sub-Project experiments.

1.4.3. Green canopy production and survival

Green canopy area is affected by shoot number, the number of leaves per shoot and mean green area per leaf. The total green canopy area is made up of the green leaf lamina area plus the projected green area of stems with their attached leaf sheaths and green ears. It is feasible that varietal differences in coefficients of canopy expansion exist. However, at the outset of current work they did not appear to have been closely investigated. The leaf area ratio (LAR : leaf lamina area m^2 per g above-ground DM) at anthesis is sometimes taken as a crude, composite measure of 'leafiness'. Measurements of LAR for different varieties in England suggest that small differences do exist amongst some recent cultivars (Austin *et al.*, 1980; Thorne *et al.*, 1988). These may have some significance because, in two different drought situations in Western Australia, Richards (1983) controlled leaf area by detillering treatments and observed that the ratio of leaf weight to total plant weight was inversely associated with yield for three wheat cultivars. It was suggested that normal investment in leaves could be excessive. In a similar experiment Islam and Sedgely (1981), using detillering treatments, changed the balance of water use pre-and-post anthesis and increased grain yield and harvest index compared to the control treatment. It may be that genetic (or cultural) modification of leaf area could have important consequences for grain yield in England, where soil water is limited.

At the outset this Sub-Project, reports describing varietal differences for maximum green canopy area amongst currently commercial varieties were scarce. For older varieties, Austin *et al.* (1980) reported leaf area indices for two semi-dwarfs introduced in the late 1970s, Hobbit and Mardler, and one non-dwarf contemporary Maris Huntsman, measured on 22-23 May of 6.3, 7.6 and 8.2, respectively. This suggested potentially meaningful genotypic differences existed about fifteen years ago for wheat varieties, and that semi-dwarfs from the 1970s may have had a tendency towards lower maximum canopy area compared to their predecessors. There has been a paucity of information subsequent to this. Consequently at the outset of this work the varietal range for current varieties was not well defined. Although breeders have certainly reduced the flag leaf area since the early 1980s (cf. Avalon and Riband) (Blackman, personal communication), the relationship between this clearly visible change and total green canopy area is not well documented. At the outset of the experimental programme in 1993-4, there were some grounds to believe that current varieties may differ by *c.* 1.0 to 1.5 GAI unit, and for this reason GAI (green canopy area (m^2) per m^2 ground area) was included as a candidate trait. It was measured for all varieties at GS 31, GS 39, GS 61 and at specific stages during grain filling in Sub-Project experiments.

In addition to varietal effects on canopy production, varietal differences in canopy survival will also be of potential importance for resistance to accelerated senescence with drought. Other than intuitive impressions of wheat breeders that some varieties with better canopy persistence 'finish' better than others (Blackman, personal communication), at the outset of the present work there was little evidence to discriminate between current genotypes in their green area persistence. Nevertheless, to provide a complete picture of the capacity of the canopy for solar radiation interception, it was decided to measure GAI at two stages during grain filling : at GS39+550°Cd (*c.* 14 d after mid-flowering) and GS39+750°Cd (*c.* 28 d after mid-flowering). In addition, the date of complete canopy senescence was also recorded.

1.4.4. Stem carbohydrate reserves

By flowering reserves of carbohydrate have accumulated in the stems and attached leaf sheaths. Maximal amounts are amassed about nine days after GS 61 (Austin *et al.*, 1977). These reserves consist of soluble sugars, stored mostly as fructans, which may be retranslocated during grain filling to buffer premature loss of green area with drought, and also structural stem material, which can be remobilized and then relocated to the grains. The percentage water soluble carbohydrate of stem and leaf sheath dry matter accumulated to about nine days after GS 61 is usually in the range 15 to 30% (Austin *et al.*, 1977; Makunga *et al.*, 1978). At the outset of current work, reports on varietal differences for wheat in the ability to amass these stem sugars were limited. However, loss of stem dry matter from 30 June to maturity was reported to vary between 22 to 48% for six cultivars examined, including tall and semi-dwarf varieties, in a non-drought season (Austin *et al.*, 1977). Allowing for respiratory losses, which may account for up to one-third of stored stem reserves (Stoy, 1966), this approximated to a range of 10 to 20% for percentage stem dry matter accumulated. In preliminary studies at Sutton Bonington in 1992-3, a range of 29 – 36 % WSC was found on 17 June for four recent varieties, Avalon, Apollo, Riband and Haven (Muchingami, 1994). The corresponding range for absolute amount of stem WSC was 2.0 to 3.1 t/ha. By harvest amounts of soluble carbohydrate were low in the range 0.1 - 0.2 t/ha. This evidence, together with the findings of Austin *et al.* (1977), indicated that currently commercial varieties were likely to show sufficient genetic variation in stem reserves to confer differential drought tolerances. Therefore, stem reserves was identified as candidate trait for drought tolerance and stem water soluble carbohydrate was measured at GS 61+75°Cd (*c.* GS 61 + 5d) and at harvest in experiments..

1.4.5. Date of flowering (GS 61)

Differences in date of GS 61 of about 6 d occur between current UK-bred (Blackman, personal communication). With the widespread use of the photoperiod French-bred variety Soissons in recent years this range has been extended to in the order of 10 d. Assuming a transpiration equivalent of 3 mm/d as typical for early June in England (Goss *et al.*, 1984), it can be calculated that varieties representing the extremes of the range currently available to growers may differ in water use to GS 61 by up to 30 mm. This advantage in water conservation for the earlier maturing varietal type might be to some extent offset by the accumulation of less stem carbohydrate reserves in the pre-anthesis period or the development of a less extensive rooting system. Nevertheless, it seems reasonable to assume that, when faced with water-limiting deficits post-anthesis, the use of less water in the vegetative phase may allow for greater water uptake during grain filling. For this reason, flowering date was prioritised as a candidate trait and the development of crops in experiments was characterised by recording the dates of following stages: GS 31, GS 39, GS 61 and GS 87.

1.5. Experimental programme

On the basis of the evidence outlined above,, varieties were selected for testing in irrigation/variety experiments at ADAS Gleadthorpe using an overhead linear irrigator in three seasons, 1993-4, 1994-5 and 1995-6. In addition to candidate traits, facets of growth and development of varieties were monitored using standard growth analysis techniques in an attempt to show the mechanistic relationships between candidate physiological traits and predicted performance under drought. If there were discrepancies between predicted and observed performances, then growth analysis data could be interpreted to attempt to explain why this was the case, and, if necessary, revise and refine the original hypotheses with regard to candidate traits.

2. MATERIALS AND METHODS

2.1. Experimental design and treatments

There was one experiment in each of three seasons, 1993-4, 1994-5 and 1995-6, on the loamy medium sand (Cuckney series) with good drainage at ADAS Gleadthorpe (15° 13' N, 1° 6' W). The same randomized block split-plot design with the same treatments was used in each season. Two irrigation treatments (Unirrigated I_0 and Fully Irrigated I_1) were randomised on mainplots, and six cultivars (Haven, Maris Huntsman, Mercia, Rialto, Riband and Soissons) were randomised on split-plots in three replicates. Plot size was 4 x 18 m. The irrigation treatments were as below:

I_0: Unirrigated
I_1: Water applied using a linear overhead irrigator system to maintain SMD calculated using the ADAS Irriguide model (Bailey & Spackman, 1996) (assuming 1.2 m maximum rooting depth) below 60 mm up to GS61+ 4 weeks and below 75 mm thereafter.

The following amounts of water were applied :

1993-4: 19 May, 25 mm; 11 June, 25 mm; 16 June, 25 mm; 22 June, 25 mm; 27 June, 23 mm; 14 July, 25 mm; 20 July, 15 mm. A total of 163 mm water was applied.

1994-5: 1 May, 19 mm; 6 May, 31 mm; 15 May, 24 mm; 9 June, 25 mm; 19 June, 20 mm; 23 June, 25 mm; 28 June, 25 mm; 5 July, 25 mm; 12 July, 25 mm; 21 July, 14 mm. A total of 233 mm water was applied.

1995-6: 14 May, 27 mm; 24 May, 26 mm; 4 June, 19 mm; 7 June, 25 mm; 17 June, 25 mm; 21 June, 25 mm; 1 July, 25 mm; 9 July, 25 mm; 15 July, 25 mm; 19 July, 25 mm; 26 July, 15 mm. A total of 262 mm water was applied.

The trigger SMD for irrigation was allowed to rise to a higher threshold of 75 mm during the last two weeks of grain filling, since applying excess irrigation water at this stage could potentially interfere with the subsequent ripening process and also predispose the crop to greater risk of lodging.

The soil type in each experimental year was the same, a loamy medium sand over medium sand (Cuckney series) with good drainage. For the loamy medium sand topsoil (0- 35 cm), AWC was 17 mm per 100 mm depth; and, for the medium sand sub-soil below 35 cm, 7 mm per 100 mm depth. The available water capacity to 1.65 m was 151 mm.

Six varieties were chosen for inclusion on the basis of candidate traits. An attempt was made to provide the greatest possible contrast for traits in question within mostly currently commercial varieties.

Table 2.1. *Rationale for variety choice in 1993-4 to 1995-6 experiments at the outset of experimental programme*

	Leafiness	Root depth	Anthesis	Stem reserves	Water Use efficiency	Predicted ability to withstand drought
Haven	Intermediate	*	Late	High	*	Intermediate
M. huntsman	High	*	Intermediate-late	Low	*	Poor
Mercia	High	*	Early-intermediate	*	*	Intermediate-Poor
Rialto	Low-Intermediate	*	Intermediate-late	*	*	Intermediate
Riband	Low	*	Intermediate	Intermediate	*	Intermediate-Good
Soissons	Low-intermediate	*	Early	*	*	Intermediate-Good

Haven (Breeder : PBI, Cambridge)
Haven was first entered into National List Year 1 trials in 1988. It is a feed wheat with high yield potential and soft endosperm texture. It has a slow developmental rate and a erect flag leaf attitude. Its ability to amass reserves of soluble carbohydrate in the stems was shown to be high in preliminary studies at Sutton Bonington (Muchingami, 1994). It is a semi-dwarf with the *Rht2* gene and also possess the 1B/1R rye chromosome translocation associated with high yield potential and poor breadmaking quality (Zeller & Hsam, 1983). It has a normal vernalization requirement for winter wheat. It showed some evidence of being susceptible to early drought based on irrigated variety trials at ADAS Gleadthorpe 1990 and performance in droughted NIAB RL trials 1990-91.

Maris Huntsman (Breeder : PBI, Cambridge)
M. Huntsman was first entered into National List Yearr 1 trials in 1969. It is a feed wheat with low yield potential and soft endosperm texture. Its developmental rate is intermediate within the range relating to currently grown varieties. Its maximum green canopy area was thought to be greater than most currently grown varieties at the outset of current work (Blackman, personal communication). Its flag leaf attitude is semi-recurved. Its ability to accumulate stem reserves was shown to be low in preliminary studies at Sutton Bonington (Muchingami, 1994). It is a tall, non-semi dwarf variety and does not possess the IB/1R rye chromosome translocation. It has a normal vernalization requirement for winter wheat

Mercia (Breeder : PBI, Cambridge)
Mercia was first entered into National List Year 1 trials in 1984. It is a bread-making wheat of low yield potential and hard endosperm texture. Its developmental rate is fast to intermediate within the range relating to current varieties. Its flag leaf attitude is erect to semi-erect. It does not possess the *Rht2* semi-dwarf gene or the 1B/1R rye chromosome translocation. It has a lower vernalization requirement than most current varieties. It was one of two standard varieties across Sub-Project experiments within the overall Project.

Rialto (Breeder : PBI, Cambridge)
Rialto was first entered into National List Year 1 trials in 1992. It is a high yield potential wheat, but with potential for bread-making and hard endosperm texture. Its developmental rate is fast to intermediate; although its ranking relative to other varieties changes within the season . For example, it is generally early to GS 31, but a particularly long period for the main phase of stem extension from GS 31 to GS 39 results in an intermediate date for GS 39 and subsequent stages. Its maximum green canopy area was

thought to be smaller than most currently grown varieties at the outset of the experimental work (Blackman, personal communication). Its flag leaf attitude is erect. It posseses the *Rht2* semi-dwarf gene and the 1B/1R rye chromosome translocation. It has a normal vernalization requirement for winter wheat.

Riband (Breeder : PBI, Cambridge)
Riband was first entered into National List Year 1 trials in 1987. It is a high yield potential variety of soft endosperm texture. It developmental rate is intermediate. Its flag leaf attitude is erect. It was shown to have low to intermediate stem reserves in preliminary studies at Sutton Bonington (Muchingami, 1994). It possesses the *Rht2* semi-dwarf gene but does not possess the 1B/1R rye chromosome translocation common to most other high yield potential feed wheats. It has a normal vernalization requirement. It showed some evidence for being more resistant to early drought compared to Haven based on irrigated variety trials at ADAS Gleadthorpe 1990 and performance in droughted NIAB RL trials 1990-91 (Scott *et al.*, 1994). It was one of two standard varieties in the overall Project.

Soissons (Breeder : Desprez, France)
Soissons's year of introduction was *c.* 1988 (Worland *et al.*, 1994). It is a French-bred variety with moderate yield potential and hard endosperm texture and is suitable for some bread-making processes. It is the fastest developing variety of those currently grown in the UK. Its flag leaf attitude is horizontal. It possesses the *Rht1* semi-dwarf gene, but does not carry the 1B/1R chromosome translocation. It has a normal vernalization requirement, but is photoperiod insensitive and thus can became competent to flower at shorter daylengths than photoperiod sensitive UK-bred genotypes.

2.2. Plot Management

The standard management protocol adopted was outlined in Vol. I, Part 1, Section 6. Details of previous cropping, sowing date, seed rate, applications of N, P, K and Mn fertilizers, PGRs, fungicides, pesticides and harvest date are given in Appendix table 1.

2.3. Growth analysis crop measurements

2.3.1. Sampling times

In 1993-4 and 1994-5, standard growth analysis was performed in all plots in three replicates in one 0.72 m^2 quadrat per plot at seven developmental stages:

- i) beginning of stem extension (GS 31),
- ii) flag leaf emergence (GS 39),
- iii) beginning of flowering (GS 61),
- iv) GS39+550°Cd,
- v) GS39+750°Cd,
- vi) GS 87 (taken as green area index = 0), and
- vii) harvest.

In 1995-6, growth analysis was carried out in all plots in two replicates sampled on 23 April and 15 June and in all plots in three replicates sampled at harvest.

2.3.2. GAI and crop dry mass

GAI and crop dry mass were assessed on the basis of a 10% sub-sample from material within an initial 0.72 m^2 quadrat area as described in Vol. I, Part 1, section 6.

2.3.3. Soluble stem carbohydrate

For all plots in three replicates, percentage water soluble carbohydrate was assessed for six fertile shoots per plot at GS61+75°Cd and at harvest as described in Vol. I, Part 1, Section 6.

2.3.4. Combine yield

For all plots in three replicates, combine yield was assessed in 5 x 3 m plot combine areas on 9 August in unirrigated plots and on 13 August in irrigated plots as described in Vol. I, Part 1, Section 6.

2.4. Environmental measurements

2.4.1. Volumetric soil water content

Volumetric soil water content was measured every 3/4 days from mid-April to harvest in two replicates using a Wallingford Neutron Probe. Readings were taken at each assessment date in one aluminium access tube per plot at 10 cm depth intervals to 1.6 m depth.

2.4.2 Fractional interception of solar radiation

From mid-April to harvest, hourly averages for incident solar radiation above the crop were measured using two tube solarimeters and also below the crop using one tube solarimeter per plot placed at ground level.

2.5. Statistical procedures

Standard analysis of variance and regression analysis was applied to data using the Genstat 5 statistical package.

3. RESULTS

3.1. Weather patterns and soil moisture deficits

1993-4

Rainfall was above the long-term mean during autumn and winter up to the end of March (Fig. 3.1, Appendix table 2), so that on 19 April (beginning of soil water content measurements) SMD was close to zero. Over the winter months and early spring, temperatures were close to the long-term mean overall (Appendix table 2), so that the late sowing date of 4 November with emergence on 3 December resulted in a relatively late date for GS 31 of 21 April. For April and May, rainfall was close to the long-term site mean. In June, however, there was only 8 mm. July rainfall was close to the norm at 43 mm, but 23 mm of this occurred after 23 July. Overall this rainfall pattern resulted in late-season drought in unirrigated plots, the onset of significant stress (assuming SMD > 50% AWC; Bailey, 1990) occurring one week before flowering. GS 61 occurred on a mean date of 21 June for varieties. Mean SMD on 10 June was 73 mm in unirrigated conditions, increasing to 108 mm by 21 June. Thereafter, SMD increased throughout grain filling plateauing at around 155 mm on 18 July. Under irrigation, plots were kept free from stress (SMD > 50% AWC) up until 1 July and free from severe stress (SMD > 75% AWC) up until 19 July, at which point deficits were allowed to rise slightly in order to avoid interfering with the ripening process.

May temperatures were below the site norm, mainly due to a particularly cold, dull period from 20 to 26 May. June and July monthly temperatures were above average overall.

1994-5

The experiment was sown on 14 October and emerged on 28 October. Monthly average temperatures were above the long-term mean for November, December, January, February and March, contributing to an earlier date of GS 31 than in 1994 of 11 April. With April close to the long-term mean for temperature and June above, GS 61 occurred on 14 June (Appendix Table 2). July was also above average for temperature. Incident radiation was close to 1994 values for April and June, but for May and July was greater than in the previous year (Appendix table 2).

Overall, rainfall from September to February was about 50% above the long-term mean (Fig. 3.1, Appendix table 2). In March and April, it was below the site norm at 36 and 18 mm, respectively. Although May rainfall was slightly above average, largely due to 23 mm and 13 mm on 16 May and 24 May, respectively, June and July were dry with only 15 and 9 mm, respectively. This rainfall pattern led to an early onset of drought in May before flowering which was subsequently sustained throughout grain filling (Fig. 3.1). In the unirrigated crop, SMD was > 75 mm for a period of six days from 9 to 15 May and then from 3 June to GS 61, which occurred on a mean date of 14 June for all varieties. Thus, significant stress occurred for a short period around 12 May and from 3 June onwards (Fig. 3.1). Severe stress (SMD > 75% AWC) occurred from 24 June onwards in unirrigated plots. Unirrigated SMD plateaued at around 135 mm on 25 July. The irrigated treatment did not experience SMD > 75% AWC at any time during crop growth, but did experience deficits > 50% AWC from 11 July onwards.

1995-6

The experiment was sown on 9 October, emerging on 19 October. Although monthly average temperatures in November and December were above the norm (Appendix table 2), those for January and February were close to the long-term mean. A cold March with mean maximum temperature of 6.3 °C compared to the norm of 9.4 °C contributed to a relatively late mean date of GS 31 on 24 April. May mean maximum temperature was also low, 13.7 °C , compared to the norm of 15.8 °C, leading to a flag leaf emergence date of 25 May compared to 27 May in 1994 and 17 May in 1995.

September to February rainfall inclusive was 317 mm compared with the site norm of 319 mm (Appendix table 2). From March to July, however, rainfall was consistently below average, 56% below the norm in March, 81% in April, 54% in May, 45% in June and 28% in July. This resulted in pre-and-post anthesis drought in the unirrigated treatment as occurred in 1995. Although the site returned to field capacity in February, on 1 May the unirrigated SMD was 34 mm, about 20 mm less than on the same date in 1995 (Fig. 3.1). No neutron probe measurements were taken in 1996 from 1 May to 11 June. However, the pattern of rainfall (28 mm of rain in May 1996 compared with 66 mm for May 1994 and 56 mm for May 1995) indicated that significant deficits occurred in 1996 from about 20 May to flowering, GS 61, occurring on a mean date of 12 June. At GS 61, the deficit was 116 mm compared with 90 mm at this stage in 1995, indicating that, for the 2 to 3 weeks prior to flowering, water stress was greater in 1996. In 1996, the deficit plateaued at around 145 mm in unirrigated plots on 19 July with severe stress (SMD > 75% AWC) occurred from 18 June onwards. The irrigated plots were maintained free from severe stress throughout, with SMD > 50% AWC occurring only from 16 July onwards.

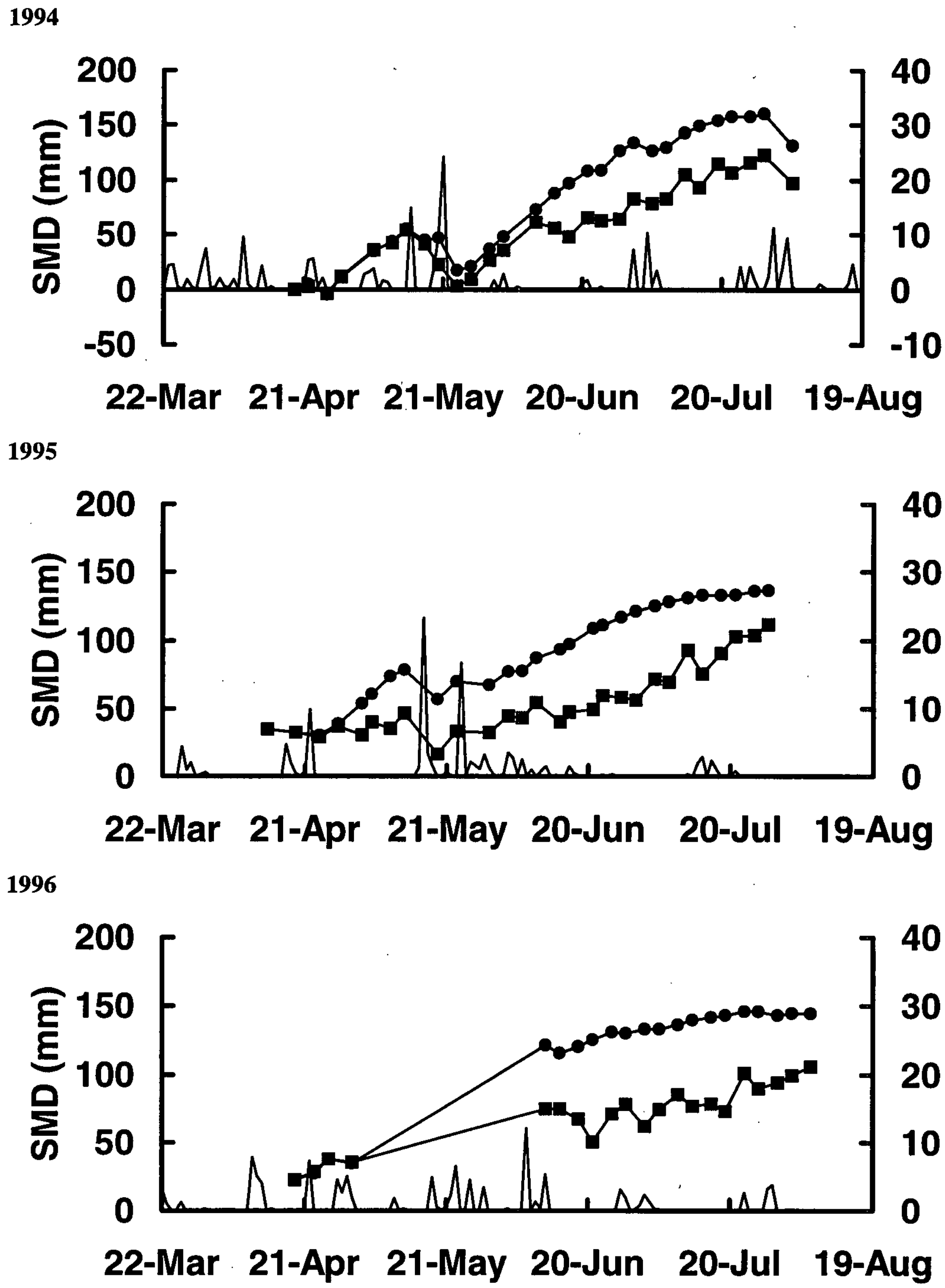


Fig. 3.1. Soil moisture deficits for irrigated (■) and unirrigated (●) treatments and rainfall in 1994, 1995 and 1996.

3.2. Plant establishment and crop development

3.2.1. Plant establishment

Plant number in mid-April was similar in all plots with no consistent differences between treatments designated to be irrigated and unirrigated (Table 3.1). In 93-4, Rialto (268 per m^2) had more plants established than M. Huntsman (212 per m^2) ($P< 0.05$) but all other varietal comparisons were non-significant. In 94-5, Rialto (269 per m^2) had more plants than Mercia (218 per m^2), but other varietal differences were not significant. In 95-6, there were no significant varietal differences; there was, however, a trend for more plants for Soissons (325 per m^2) compared to other varieties in the range 235 - 269 per m^2. Assessments were only taken in two replicates in 95-6 compared with three in preceding seasons and this may have contributed to the lack of statistical significance in 95-6. The irrigation/variety interaction was non-significant in each season.

Table 3.1. Plant number per m^2 measured at GS 31 in 93-4 and 94-5 and 23 April in 95-6.

	1993-4	1994-5	1995-6
Haven	224.5	256.5	316.7
M. Huntsman	248.6	224.5	237.5
Mercia	280.1	225.9	220.8
Rialto	281.0	288.0	266.7
Riband	255.5	253.2	220.8
Soissons	252.3	248.1	320.8
Mean	257.0	249.4	263.9
Haven	228.2	238.9	220.8
M. Hunstman	195.4	234.3	275.0
Mercia	263.2	208.8	279.2
Rialto	254.2	249.5	266.7
Riband	245.8	256.3	250.0
Soissons	259.7	251.9	329.2
Mean	241.1	239.9	270.1
S.E.D. Irr	18.41	11.96	40.97
Prob.	0.290	0.575	0.968
S.E.D. Var	5.60	14.63	32.48
Prob.	0.040	0.023	0.195
S.E.D. Irr*Var	24.08	22.35	58.62
Prob.	0.772	0.493	0.185

3.2.2. Crop development

3.2.2.1. Effect of irrigation

Generally, effects of irrigation on developmental rate were either small or absent (Table 3.2). In 93-4, the largely post-anthesis drought did not affect developmental rate in unirrigated plots for any variety, other than for date of complete canopy senescence and harvest which were delayed by 8 and 2 d, respectively, with irrigation. In the second season, 94-5, with pre-and-post anthesis drought, three varieties, Haven, M. Huntsman and Mercia, were 1 d faster to GS 39 in irrigated conditions. The irrigated crop was on average, however, 4 d slower to GS 61 in this season. In 95-6, where pre-and-post anthesis drought again occurred in unirrigated plots, there was no observed effect of irrigation on any variety, other than for complete canopy senescence and harvest which were delayed with irrigation by 8 and 5 d, respectively.

3.2.2.2. *Effect of variety*

There were clear varietal differences in development rate expressed consistently in 93-4 and 94-5 (date of development stages was not recorded for all irrigation/variety treatment combinations in 95-6). The varietal range for GS 31 was 14 and 13 d in 93-4 and 94-5, respectively. In each season, the earliest varieties to GS 31 were Soissons (French-bred, photoperiod insensitive variety) and Rialto, followed about 3 - 4 d later by Mercia (low vernalization requirement, weaker photoperiod sensitivity than most other UK-bred varieties). The last variety to reach GS 31 in both seasons was Haven, with M. Huntsman and Riband reaching this stage about 3 and 6 d earlier than this, respectively. At GS 39, the range was 12 and 16 d in 93-4 and 94-5, respectively. The ranking order was broadly the same as at GS 31, with the exception of Rialto. This variety was equal earliest to GS 31, but intermediate-to-late within the range at GS 39. It consequently had a longer duration for the stem extension phase compared to other genotypes. At GS 61, the range had narrowed to 7 d in 93-4 and 13 d in 94-5. The ranking order was similar to GS 39. The normal range for GS 61 for the UK-bred varieties would be in the order of 6 d (Foulkes *et al.*, 1993) with Soissons another 3 - 4 d earlier than this. The varietal range currently observed was slightly less than this in 93-4; this may have been due to the late emergence date of 4 December accelerating development, and producing a concertina effect diminishing varietal differences. Conversely, in 94-5, the range at GS 61 was slightly larger than the norm at 7 d for UK varieties, but with the photoperiod insensitive Soissons (Worland *et al.*, 1994) 8 d before this.

3.2.2.3. *Irrigation/variety interaction*

Only for dates of GS 39 and GS 61 in 94-5 was there a differential varietal response to irrigation. At GS 39 the interaction was never greater than one day for any varietal comparisons and probably not important in affecting grain yield responses to drought. Similarly at GS 61, most varieties were delayed by irrigation to a similar degree of about 4 to 5 d with the exception of Soissons, for which irrigation delayed GS61 by 2 d. For date of reaching complete canopy senescence, overall across 93-4 and 94-5, the delay with irrigation was similar for all varieties in the order of 7 to 8 days.

Table 3.2. Dates of developmental stages for irrigation/variety treatment combinations in 93-4 and 94-5 and irrigation treatments in 95-6.

		31	39	61	39 +550°Cd	39+ 750°Cd	87	H'VEST
Haven	94	30/4	05/6	24/6	09/7	22/7	$27/7^{+7}$	$9/8^{+2}$
	95	17/4	$23/5^{-1}$	$16/6^{+4}$	30/6	15/7	$21/7^{+10}$	$3/8^{+5}$
M. H'man	94	30/4	27/5	21/6	05/7	17/7	$28/7^{+6}$	$9/8^{+2}$
	95	16/4	$18/5^{-1}$	$10/6^{+5}$	$30/6^{-1}$	$12/7^{-1}$	$20/7^{+9}$	$3/8^{+5}$
Mercia	94	19/4	24/5	19/6	03/7	15/7	$25/7^{+7}$	$9/8^{+2}$
	95	10/4	$13/5^{-1}$	$08/6^{+5}$	$27/6^{-1}$	$10/7^{-1}$	$27/7^{+4}$	$3/8^{+5}$
Rialto	94	16/4	03/6	24/6	07/7	19/7	$28/7^{+6}$	$9/8^{+2}$
	95	06/4	19/5	$13/6^{+4}$	30/6	12/7	$27/7^{+7}$	$3/8^{+5}$
Riband	94	26/4	29/5	21/6	06/7	18/7	$28/7^{+6}$	$9/8^{+2}$
	95	13/4	21/5	$10/6^{+5}$	01/7	13/7	$23/7^{+11}$	$3/8^{+5}$
Soissons	94	16/4	17/5	17/6	29/6	12/7	$21/7^{+8}$	$9/8^{+2}$
	95	06/4	07/5	$03/6^{+2}$	24/6	07/7	$27/7^{+7}$	$3/8^{+5}$
Mean	94	23/4	27/5	21/6	4/7	17/7	$25/7^{+7}$	$9/8^{+2}$
	95	11/4	$17/5^{-1}$	$10/6^{+4}$	$29/6^{-1}$	$12/7^{-1}$	$23/7^{+8}$	$3/8^{+5}$
	96	25/4	25/5	12/6	5/7	15/7	$24/7^{+8}$	$14/8^{+5}$

Note: i) Dates given in Table are for unirrigtaed plots, differences in days from unirrigtaed plots for the irrigtaed plots are given as superscrpits.
ii) For 1995-6 means relate to the mean of development stages recorded for Soissons and Haven only.

3.3. Combine yield, harvest index and yield components

3.3.1. Effect of irrigation

In summary, there were large yield reductions in each season, the largest reductions relating to those seasons where the onset of drought occurred earlier and duration of stress was extended. In these conditions, ear numbers were affected, in addition to grains per ear and grain weight. It is concluded that a good environmental test-bed was provided within which to look for evidence of differential varietal responses to drought.

Combine grain yield was significantly reduced with drought in all seasons: by 1.83 t/ha in 93-4 ($P< 0.05$), 3.06 t/ha in 94-5 ($P< 0.001$) and 4.55 t/ha in 95-6 ($P< 0.001$) (Table 3.3). Overall, yield reduction in the unirrigated crop was 3.15 t/ha ($P< 0.001$). This was associated with a reduction in harvest index from 0.53 to 0.50 ($P= 0.10$), 0.50 to 0.46 ($P< 0.01$) and 0.53 to 0.45 ($P< 0.001$) in 93-4, 94-5 and 95-6, respectively. Averaged over the three seasons, grains per ear decreased by 13% from 41.2 to 35.7 ($P< 0.001$), although thousand grain weight also decreased by 12% from 43.1 to 38.0 ($P< 0.001$) and ears per m^2 by 8% from 501 to 460 ($P< 0.001$).

The late onset of drought in June in 93-4 did not significantly reduce ear numbers, whereas the earlier onset of drought in May reduced ears per m^2 from 476 to 442 in 94-5 ($P= 0.06$) and from 514 to 437 per m^2 in 95-6 ($P< 0.01$). Grains per ear was less under drought, by 2.9 in 93-4 ($P < 0.05$), by 4.0 in 94-5 ($P < 0.05$) and by 9.6 in 95-6 ($P< 0.01$). The progressively larger decrease in grains per ear mirrored the increased severity of the drought in the 2 to 3 week period prior to GS 61, during which floret survival is largely determined (Hay & Walker, 1989). Thousand grain weight also decreased under drought each year ($P< 0.05$) : by 3.9 g with late drought in 93-4 and 7.3 g and 4.2 g with earlier onset of drought in 94-5 and 95-6, respectively.

3.3.2. Effect of variety

Overall, across the three seasons, there were varietal differences for combine yield and all yield components ($P< 0.001$) (Table 3.3). With irrigation, the grain yield potential of the different varieties was broadly expressed and reflected their performance on the Recommended List (NIAB, 1997 and preceding publications). Thus, within the group of modern high yield potential varieties, Haven (10.9 t/ha) outyielded Riband (10.4 t/ha) and Rialto (10.3 t/ha). The low yield potential of the older feed wheat M. Huntsman and the more recent bread-making variety Mercia was reflected in their irrigated yields of 9.2 and 9.4 t/ha, respectively. Soissons, the modern French-bred milling variety with intermediate yield potential, yielded 9.6 t/ha.

There were consistent varietal differences in yield structure in the irrigated crop, with varieties falling into three broad categories. Firstly, there were the high yield potential, semi-dwarfs Haven, Riband and Rialto. These generally had fewer ears in the range 445 - 460 per m^2, but more grains per ear in the range 44 - 48 and heavier grain in the range 0.042 - 0.045 g. Secondly, there were the modern low-to-intermediate yield potential varieties, Mercia and Soissons. These generally had more ears in the range 567 - 635 per m^2, but with fewer grains per ear with values in the range 33 - 38 and slightly lighter grain from 0.039 to 0.040 g. The third category was represented by the low yield potential, non-semi-dwarf M. Huntsman. In all seasons, compared to the second group, this variety had fewer ears (448 per m^2), similar grains per (39), but heavier grains (0.049 g). The overall effect was for M. Huntsman to have lower irrigated grain yield compared to Soissons and Mercia. The responses to drought of the three broad yield structure types and more specifically the six varieties to drought is discussed in 3.3.3 below.

3.3.3. Irrigation/variety interaction

Overall, across seasons, varieties responded differently to drought for grain yield ($P< 0.05$). Rialto and Mercia lost relatively less yield *c.* 2.7 t/ha under drought compared with Haven and Riband *c.* 3.5 t/ha. Yield losses for M. Huntsman and Soissons were intermediate. In absolute amounts, Rialto performed the best in 94-5 and 95-6 in unirrigated conditions and second highest after Haven in 93-4. On average, unirrigated yield was greatest for Rialto (7.4 t/ha) followed by Haven (7.2 t/ha), Riband (6.9 t/ha) and other varieties with values in the range 6.6 - 6.1 t/ha. The high yield of Haven with late drought in 93-4 was not maintained with the earlier onset of drought in 94-5 and 95-6.There was no clear effect for any of the three yield structure types to perform relatively better or worse than any another with drought.

With late drought in 93-4, the irrigation/variety interaction was not significant for grain yield ($P=0.18$), ears per m^2 ($P=0.51$), and grains per ear ($P=0.43$). For grain weight, it was significant, with Rialto maintaining individual grain weight better than Riband, M. Huntsman and Haven ($P< 0.05$). In absolute terms, although the yield interaction was not significant, ranking order did change with and without drought. The main differences were than Riband and M. Huntsman ranked lower under drought and the converse for Soissons and Rialto. Haven (9.82 t/ha) and Rialto (9.54 t/ha) yielded best under drought with lower yield for Riband at 8.71 t/ha. Such a differential response for these three varieties would be of interest if consistently expressed, since their performance on the RL shows them to be more comparable, giving no indication of Riband's apparently poorer drought resistance. In 93-4, there was a trend for greater yield loss for M. Huntsman compared to other varieties, associated with its proportionately greater reduction in grain weight under drought. M. Huntsman has a large grain weight under optimal conditions (NIAB 1997 and

and preceding publicatons); and this was the component of yield most affected by late drought in 93-4.

With earlier onset of drought in 94-5 in May, the interaction was significant for grain yield ($P< 0.05$), ears per m^2 ($P< 0.05$), grains per ear ($P< 0.05$) and grain weight ($P< 0.001$) (Table 3.3). Whereas with irrigation yields related to the broadly expected pattern of yield potential with values in the range 8.1 - 9.8 t/ha, there was a levelling of performance with drought. Yields varied from 5.5 to 6.3 t/ha. Rialto and Mercia performed relatively better than Riband and Haven with drought. In absolute terms, Rialto yielded highest with drought and again outyielded Riband by 0.21 t/ha similar to its performance in 93-4. The high absolute yield of Haven with drought in 93-4 was not observed in 94-5 where its yield was no better than the mean for all the varieties examined. The significant interaction for ear number ($P< 0.05$) was almost entirely explained by the maintenance of proportionately more ears under drought for Soissons (actually gaining 46 ears per m^2 under drought) compared to other varieties, which had in the region of 50 ears per m^2 fewer. This probably resulted from more pronounced secondary tillering for Soissons in unirrigated crops, the reduction of canopy with drought during stem extension allowing increased radiation intensity at the level of the secondary tiller buds. Presumably all varieties were subjected to a similar increase in radiation intensities in unirrigated crops, but Soissons responded differently to the others. Also, as Soissons was the most rapid developing variety, drought escape associated with the earlier phasing of the tiller survival period may have contributed to some extent to better maintenance of ear numbers. Rialto maintained grains per ear better under drought than other varieties; and the interaction was significant ($P< 0.05$). Soissons showed particularly poor maintenance of grains per ear, probably associated with its better maintenance of ear numbers compared to other varieties under drought. Individual grain weight showed the most significant irrigation/variety interaction ($P< 0.001$). The reduction was greater for Haven and Riband compared to Mercia, Soissons and Rialto. In summary, the slightly greater yield with drought of Rialto compared to other varieties in 94-5 was explained by maintaining grains per ear particularly better than other genotypes, by maintaining grain weight better than most varieties, but by maintaining ear number no better than other varieties.

In 95-6, with early onset of drought similar to 94-5, varieties again performed broadly in line with their known yield potentials under irrigated conditions with values in the range 9.7 - 11.2 t/ha, but there was again a levelling of performance with drought. Yields were in the range 5.2 - 6.2 t/ha. As in 94-5, Rialto performed relatively better than Haven under drought and Rialto again had greater absolute yield than Haven and Riband. Thus, the high yield of Haven with drought detected in 93-4 was not found in 95-6. Additionally, Soissons performed relatively well, similar to Rialto, and M. Huntsman relatively worse, similar to Haven, under drought. There was a significant interaction for grain weight ($P< 0.05$), due to proportionately greater loss for Mercia and Soissons compared to other genotypes, particularly Riband. The greater yield for Rialto under drought was mainly due to more surviving grains per ear (42) compared to other varieties in the range 28 - 38. In the irrigated crop, Rialto also had more grains per ear than other varieties; therefore the irrigation/variety interaction for grains per ear wasn't significant (P=0.32). There may be other mechanisms accounting for Rialto's drought resistance in addition to those affecting 'sink' size (number of grain sites set per unit area). This is suggested by the fact that Rialto, averaged across seasons, was able to maintain grain size relatively better than all other varieties under drought, even though it had more grain sites with drought. Thus, some feature of this variety enabled it to maintain assimilate supply better under drought compared to other genotypes. It follows that factors affecting the 'source' of assimilate as well as 'sink' must be invoked to fully explain the consistently better yield performance of Rialto under drought.

Table 3.3. Grain yield (t/ha 85% DM), harvest index, ears/m², grains/ear and 1,000 grain weight (g 100% DM) 1993-4 - 1995-6

	1993-4					1994-5					1995-6					Mean 1993/4 - 5/6				
	Yd t/ha	HI	Ear/ m²	Grn/ Ear	TGW g	Yd t/ha	HI	Ear/ m²	Grn/ Ear	TGW g	Yd t/ha	HI	Ear/ m²	Grn/ Ear	TGW g	Yd t/ha	HI	Ear/ m²	Grn/ Ear	TGW g
Irrigated																				
Haven	11.59	0.55	478	40.4	46.8	9.77	0.51	435	45.2	44.4	11.21	0.54	462	46.5	43.2	10.86	0.54	458	44.0	44.8
M. H'man	9.89	0.51	450	36.9	48.4	8.08	0.48	417	36.9	49.5	9.71	0.52	475	39.9	48.1	9.23	0.50	448	37.9	48.6
Mercia	10.11	0.53	621	34.6	39.6	8.22	0.48	503	40.4	39.2	9.67	0.52	576	37.4	38.6	9.34	0.51	567	37.5	39.1
Rialto	10.81	0.52	472	44.0	41.9	9.12	0.49	445	47.1	41.5	10.81	0.54	421	52.2	42.4	10.25	0.52	446	47.8	41.9
Riband	11.28	0.56	451	47.5	45.5	9.81	0.52	419	45.8	43.6	10.19	0.54	482	45.9	42.3	10.43	0.54	450	46.4	43.8
Soissons	9.41	0.51	600	29.9	42.5	9.34	0.51	638	33.4	39.6	10.01	0.52	668	36.9	38.4	9.59	0.51	635	33.4	40.1
Mean	10.52	0.53	512	38.9	44.1	9.06	0.50	476	41.5	43.0	10.27	0.53	514	43.1	42.2	9.95	0.52	501	41.2	43.1
Unirrigated																				
Haven	9.82	0.51	488	39.4	41.0	6.01	0.46	385	40.5	33.4	5.87	0.46	399	32.9	39.9	7.23	0.48	424	37.6	38.1
M. H'man	7.55	0.48	455	33.5	43.3	5.52	0.42	386	33.4	42.4	5.31	0.42	393	28.9	44.1	6.13	0.44	434	31.9	43.3
Mercia	8.40	0.49	628	30.9	36.0	6.05	0.45	462	34.4	34.1	5.24	0.42	451	32.3	32.4	6.56	0.46	513	32.5	32.4
Rialto	9.54	0.51	428	41.9	40.7	6.34	0.48	377	48.1	35.2	6.21	0.47	395	41.8	38.3	7.37	0.48	400	43.9	38.1
Riband	8.71	0.52	407	42.6	40.8	6.13	0.46	359	44.8	35.1	5.87	0.48	388	37.6	40.9	6.90	0.49	384	41.6	39.0
Soissons	8.13	0.50	607	27.8	39.2	5.93	0.46	684	23.5	34.4	5.83	0.44	597	27.7	31.9	6.63	0.47	629	26.3	35.2
Mean	8.69	0.50	502	36.0	40.2	6.00	0.46	442	37.5	35.8	5.72	0.45	437	33.5	37.9	6.80	0.47	460	35.7	38.0
SED Irr	0.232	0.009	10.1	0.66	0.51	0.231	0.004	8.3	0.69	0.43	0.079	0.001	14.9	0.50	0.56	0.112	0.003	6.6	0.36	0.29
Prob	0.016	0.099	0.429	0.048	0.016	0.006	0.009	0.055	0.028	0.004	<0.001	<0.001	0.036	0.003	0.017	<0.001	<0.001	<0.00	<0.00	<0.001
SED Var	0.288	0.007	19.8	0.98	0.66	0.251	0.008	15.8	1.40	0.44	0.229	0.006	22.4	1.78	0.66	0.149	0.004	11.3	0.82	0.34
Prob	<0.001	<0.011	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.00	0.001	<0.001
SED I*V	0.438	0.013	27.5	1.43	0.99	0.398	0.011	22.0	1.94	0.71	0.306	0.008	32.6	2.35	1.02	0.195	0.006	16.0	1.12	0.53
Prob	0.175	0.311	0.508	0.429	0.028	0.023	0.076	0.021	0.016	<0.001	0.197	0.036	0.397	0.317	0.010	0.023	0.050	0.159	0.402	<0.005

3.4. Fertile shoots per m^2

3.4.1. Effect of irrigation

With late drought in 93-4, shoot numbers, averaged across irrigation treatments, were maximal at GS 31 (1056 per m^2), declining to 645 per m^2 (GS 39) and then 543 per m^2 (GS 61), remaining broadly stable thereafter to harvest (Fig. 3.2; Table 3.4). The irrigation effect was not significant at any sample time, except for GS 61 when there were fewer shoots (P< 0.05) in the unirrigated (536 per m^2) than irrigated (550 per m^2) crop. This reflected a short period of incipient water stress shortly after GS 39 in unirrigated plots causing tiller death to occur marginally faster in these plots. The final ear number at harvest was, however, similar with irrigation (512 per m^2) and under drought (502 per m^2).

In 94-5, overall shoot numbers at GS 31 were 873 per m^2, and fewer than at this stage in 93-4. They declined thereafter to 485 (irrigated) and 435 (unirrigated) per m^2 at GS 61. Shoot numbers did not differ significantly at GS 31, but did thereafter with fewer under drought at GS 39 (P< 0.01), GS 61 (P< 0.01), GS 39+550°Cd (P< 0.09), GS 87 (P< 0.07) and harvest (P< 0.06). This was consistent with the onset of early drought in May affecting tiller survival. At harvest, ear number was 476 and 442 per m^2 in irrigated and unirrigated crops, respectively.

In the third season, 95-6, assessments were only undertaken on 23 April, 15 June and at harvest. Maximum numbers in April were not significantly different between irrigation treatments with a mean of 1083 per m^2 (Table 3.5). On 15 June, there was a trend for more shoots with irrigation (516 per m^2) than under drought (443 per m^2) (P=0.16), consistent with early drought. Measurements were only taken in two replicates on 15 June, and this may have contributed to the lack of statistical significance. At final harvest, when assessments were taken in three replicates, shoot numbers were similar to GS 61, 514 (irrigated) and 437 (unirrigated) per m^2, and the difference was significant (P< 0.05).

The lower maximum shoot population in April 94-5 compared to the other two seasons may have related to greater overwinter rainfall in this season (December – February inclusive was 232 mm in 94-5 compared to the site norm of 155 mm). This could have contributed to low soil N availability in spring due to increased leaching. Plant establishment was broadly stable across the three test seasons and could not have accounted for these differences (Table 3.1).

3.4.2. Effect of variety

3.4.2.1. Tiller production

In each season, there were varietal differences in maximum shoot number in mid-April (Tables 3.4 & 3.5; Fig. 3.2). Soissons and Mercia had consistently fewer shoots than Haven and Riband at this stage. In 93-4 and 94-5, Soissons (874 per m^2) thus had fewest and then Mercia (911 per m^2) with other varieties with values in the range 981 - 1011 per m^2 (Table 3.6). It was noticeable that the two most rapidly developing varieties generally had lowest maximum shoot numbers in April. This probably related to their earlier stem extension at which point further development of tiller buds into growing tillers is largely suppressed by the effect of competition for assimilate from newly extending shoots.

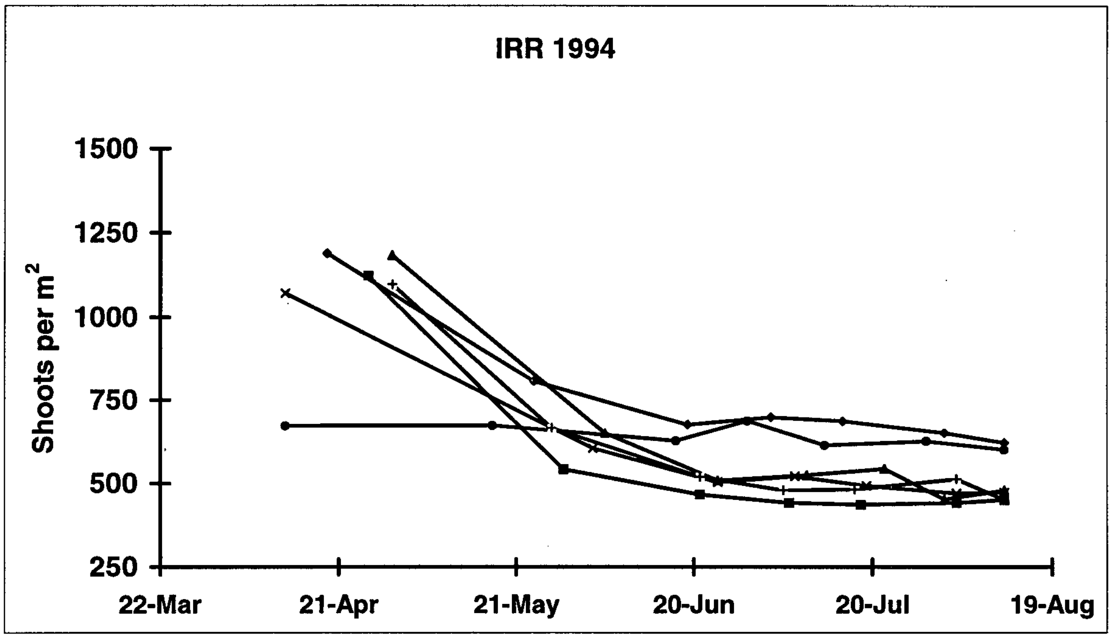
3.4.2.2. Tiller survival

The variety ranking order for final shoot number at harvest was different to that in April. In both irrigated and unirrigated conditions, over the three experiments, Soissons and Mercia consistently had more ears at harvest compared to other varieties. It follows that tiller survival differed amongst the six varieties examined. Broadly, Soissons and Mercia exhibited low tiller production but high tiller survival, whereas Haven, Riband, Rialto and M. Huntsman produced more tillers with fewer surviving.

3.4.3. Irrigation/variety interaction

In 93-4, the irrigation/variety interaction was not significant at any sample time consistent with the onset of drought stress coinciding approximately with GS 61, by which time final ear number per m^2 is largely determined. In 94-5, the interaction was significant at harvest ($P< 0.05$), with a trend for a significant interaction also at GS 39 and GS 61. At GS 39, Rialto maintained proportionately more shoots than other varieties in the unirrigated crop, and the converse for Haven. This may have related to drought avoidance, in that Rialto, together with Soissons, was the earliest variety to GS 31 and Haven the latest. These effects were again apparent as trends at GS 61, where Soissons, due to late production of secondary tillers under drought, also showed a trend for relatively more shoots in the unirrigated crop. The significant interaction observed at harvest 94-5 was largely due this phenomenon of secondary tillering for Soissons. In 95-6, fertile shoots were only counted on 23 April, 15 June and final harvest. The interaction was non-significant at all sample times.

Although there are dangers in summarising across seasons with different timings of drought, the varietal interaction overall for 93-4 and 94-5 was not significant at any stage. In summary, varietal differences in shoot populations were generally consistently expressed across irrigation treatments. In 94-5, early onset of drought appeared to lead to relatively earlier tiller death for the late developing varieties, but by final harvest only Soissons was responding differently to drought. This seemed to be due to a greater capacity for secondary tillering rather than any drought avoidance effects *per se.*



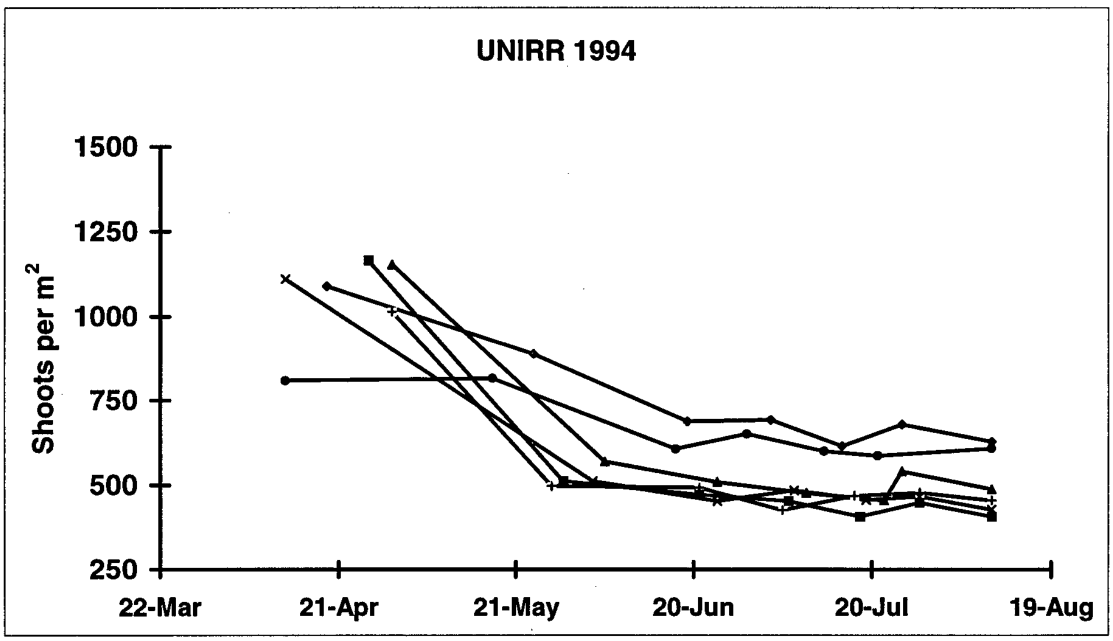
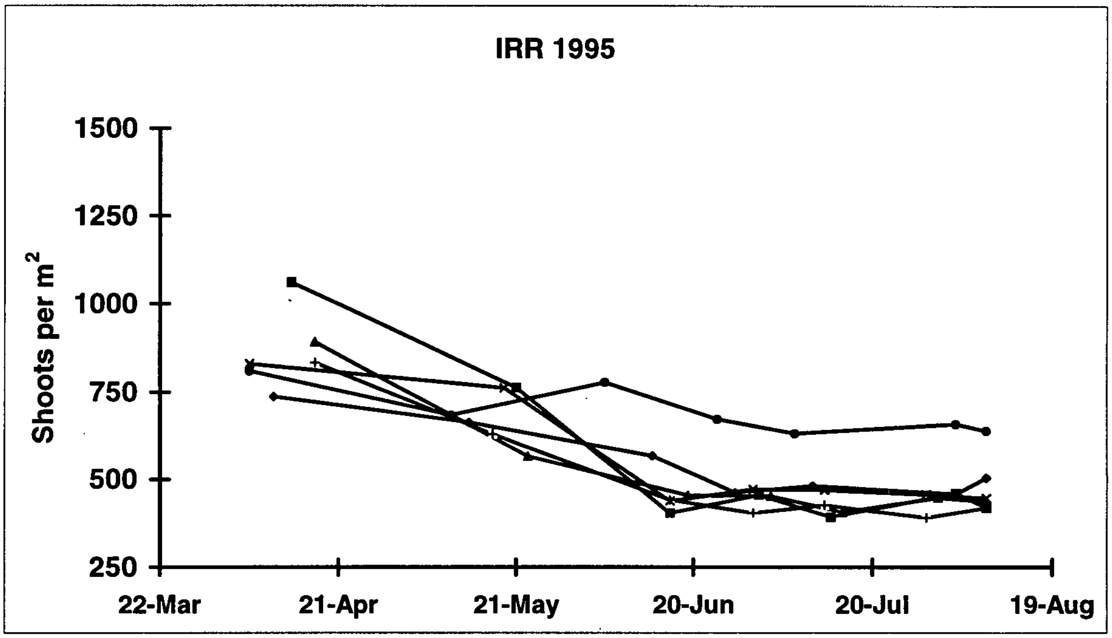


Fig. 3.2.a Potentially fertile shoots per m^2 for Haven (■), M. Huntsman (+), Mercia (◆), Rialto (X), Riband (▲) and Soissons (●) wheat crops at GS 31, GS 39, GS 61, GS 39+550°Cd, GS 39+750°Cd, GS 87 and pre-harvest.



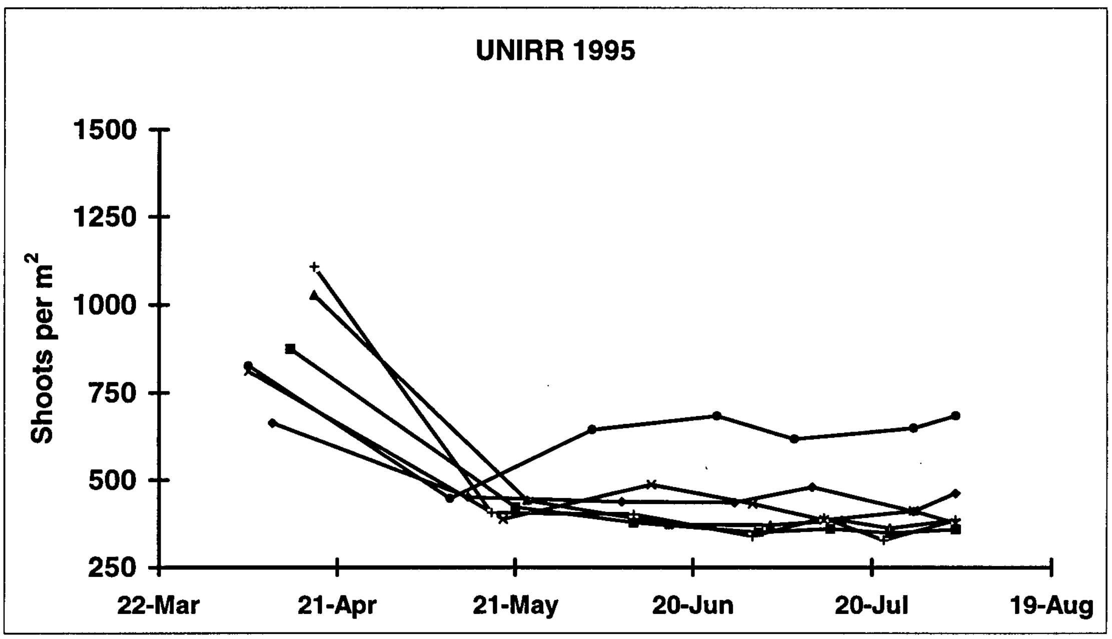


Fig. 3.2.b Potentially fertile shoots per m^2 for Haven (■), M. Huntsman (+), Mercia (◆), Rialto (X), Riband (▲) Soissons (●) wheat crops at GS 31, GS 39, GS 61, GS 39+550°Cd, GS 39+750°Cd, GS 87 and pre-harvest.

Table 3.4. Standard errors of the difference of the means and probabilities for a) potentially fertile shoots per m², b) GAI and c) above-ground dry mass (g/m²) in 1993-4 and 1994-5.

a) Potentially fertile shoots per m²

			GS 31		GS 39		GS 61		GS39+550°Cd		GS39+750°Cd		GS 87		Harvest	
		DF	SED	Prob	SED	Prob	SED	Prob	SED	Prob	SED	Prob	SED	Prob	SED	Prob
1994	Irr	2	75.1	0.993	26.9	0.437	2.7	0.039	28.4	0.132	15.2	0.098	21.1	0.862	19.8	0.429
	Var	20	76.8	0.003	52.7	<0.01	30.5	<0.001	11.3	<0.001	23.6	<0.001	29.2	<0.001	10.1	<0.001
	Irr/Var	20	124.4	0.657	73.1	0.066	39.5	0.902	38.4	0.848	34.0	0.500	43.2	0.267	27.5	0.508
1995	Irr	2	113.3	0.851	26.7	0.011	5.5	0.008	16.0	0.088	19.2	0.244	17.1	0.073	8.3	0.055
	Var	20	72.5	0.005	46.4	0.429	34.6	<0.001	32.9	<0.001	19.5	<0.001	32.4	<0.001	15.8	<0.001
	Irr/var	20	147.0	0.067	65.6	0.126	44.9	0.118	45.4	0.549	31.7	0.404	45.2	0.695	22.0	0.021

b) GAI

			GS 31		GS 39		GS 61		GS 39+550°Cd		GS 39+750°Cd	
		DF	SED	Prob	SED	Prob	SED	Prob	SED	Prob	SED	Prob
1994	Irr	2	0.474	0.254	0.071	0.035	0.190	0.040	0.087	0.003	0.082	<0.001
	Var	20	0.155	<0.010	0.328	<0.001	0.374	<0.001	0.239	0.025	0.247	0.002
	Irr/Var	20	0.205	0.533	0.429	0.256	0.519	0.649	0.320	0.084	0.329	0.296
1995	Irr	2	0.163	0.879	0.111	0.008	0.075	0.006	0.113	0.004	0.059	<0.001
	Var	20	0.103	<0.001	0.165	<0.001	0.220	0.017	0.222	0.005	0.172	0.088
	Irr/var	20	0.210	0.440	0.240	0.065	0.294	0.003	0.308	0.269	0.229	0.862

c) Crop dry matter (g/m²)

			GS 31		GS 39		GS 61		GS 39+550°Cd		GS 39+750°Cd		GS 87		Harvest	
		DF	SED	Prob	SED	Prob	SED	Prob	SED	Prob	SED	Prob	SED	Prob	SED	Prob
1994	Irr	2	4.5	0.435	26.9	10.561	9.8	0.942	9.9	0.015	46.4	0.063	63.0	0.086	18.4	0.007
	Var	20	7.3	<0.001	33.5	<0.001	32.9	<0.001	34.2	<0.001	54.1	0.004	50.0	0.070	47.3	0.011
	Irr/Var	20	10.4	0.346	50.9	0.702	43.5	0.251	45.3	0.299	83.8	0.885	90.1	0.637	63.7	0.087
1995	Irr	2	10.1	0.918	19.4	0.228	38.3	0.028	38.3	0.028	11.4	<0.001	40.9	0.008	37.7	0.009
	Var	20	6.6	<0.001	20.7	<0.001	62.2	0.019	62.2	0.019	52.8	0.007	64.8	0.590	56.6	0.413
	Irr/var	20	13.2	0.500	33.0	0.006	53.0	0.411	89.0	0.522	69.2	0.152	93.1	0.396	82.3	0.393

Table 3.5. Potentially fertile shoots per m^2 on 23 April and 15 June 1995-6

	23 April		15 June	
	Irr	Unirr	Irr	Unirr
Haven	1218	1197	412	388
M. Huntsman	793	766	609	533
Mercia	1087	1105	476	488
Rialto	831	1063	521	350
Riband	1232	1494	463	389
Soissons	1113	1090	615	549
Mean	1046	1119	516	443
S.E.D. Irr		35.1		19.1
Prob.		0.284		0.163
S.E.D. Var		136.8		55.1
Prob.		0.023		0.030
S.E.D. Irr/Var		180.1		73.7
Prob.		0.777		0.793

Table 3.6. Cross season analysis for PF shoots per m^2, GAI and crop dry mass (g/m^2) 1993-4 - 1994-5

	PF Shoots per m^2							GAI				Biomass g/m^2 (100% DM)					
	GS 31	GS 39	GS 61	GS 39+ 550°Cd	GS 39+ 750°Cd	GS 87	Har	GS 39	GS 61	GS 39+ 550°Cd	GS 39+ 750°Cd	GS 39	GS 61	GS 39+ 550°Cd	GS 39+ 750°Cd	GS 87	Har
Irrigated																	
Haven	1001	609	481	488	474	449	457	4.66	4.72	4.18	2.40	696	1201	1551	1725	1732	1677
M. H'man	984	650	480	441	453	451	434	5.05	5.33	4.16	2.82	547	1065	1348	1564	1696	1589
Mercia	900	734	622	578	583	554	562	4.67	4.99	4.44	3.29	514	1056	1281	1526	1670	1632
Rialto	980	683	470	495	490	462	458	4.06	4.23	3.90	2.47	648	1223	1471	1761	1799	1721
Riband	1018	652	435	447	414	450	435	4.48	4.65	3.78	2.79	654	1038	1361	1598	1727	1680
Soissons	870	679	702	680	622	641	619	3.86	4.84	4.04	2.88	489	1037	1370	1588	1648	1571
Mean	959	668	532	522	506	501	494	4.46	4.79	4.08	2.77	592	1096	1397	1627	1712	1645
Unirrigated																	
Haven	1021	505	441	423	420	451	436	3.73	3.46	2.57	0.08	661	1060	1340	1392	1431	1331
M. H'man	1148	451	446	382	429	402	420	3.89	4.79	2.39	0.53	495	991	1197	1390	1420	1327
Mercia	922	669	563	564	547	544	545	4.26	4.10	2.73	0.71	516	961	1222	1345	1372	1304
Rialto	982	449	469	457	421	427	402	3.16	3.32	2.10	0.22	640	1095	1282	1483	1409	1386
Riband	988	462	425	401	383	398	383	3.31	3.96	2.38	0.46	578	975	1222	1351	1387	1288
Soissons	877	631	625	667	608	618	646	3.55	3.44	2.71	0.71	503	888	1198	1299	1316	1264
Mean	990	528	495	482	468	473	472	3.65	3.84	2.48	0.45	566	1003	1243	1377	1389	1317
SED Irr	75.6	18.9	3.1	9.8	12.3	13.6	6.6	0.066	0.102	0.071	0.051	16.6	5.8	19.8	23.9	37.5	23.3
Prob	0.709	0.002	<0.001	0.016	0.036	0.109	0.028	<0.001	<0.001	<0.001	<0.001	0.192	<0.001	<0.001	<0.001	<0.001	<0.001
SED Var	59.4	35.1	23.0	21.7	15.3	21.8	12.7	0.185	0.217	0.163	0.150	19.8	37.0	35.3	37.8	40.9	39.6
Prob	0.036	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.012	<0.001	<0.001	<0.001	<0.001	<0.001	0.066	0.035
SED I*V	107.7	49.1	29.9	29.7	23.3	31.3	17.6	0.248	0.298	0.223	0.201	30.4	48.5	49.9	54.3	64.8	56.2
Prob	0.660	0.051	0.141	0.759	0.491	0.790	0.028	0.104	0.355	0.598	0.817	0.206	0.462	0.242	0.247	0.784	0.706

3.5. Green area index (GAI)

3.5.1. Effect of irrigation

With irrigation, GAI was maximal either at GS 39 or GS 61 and in the region of 5.0 having increased from about 1.5 at GS 31 (Fig. 3.3). Onset of the rapid phase of senescence occurred shortly after GS 61, from when green area progressively decreased to values close to zero at end of grain filling. Irrigation effects were not significant at GS 31 (Table 3.4; Fig. 3.3) in any season, consistent with the onset of drought occurring after this stage.

In 93-4, GAI in mid-April was 1.5. It was maximal at GS 39, and smaller under drought (4.8) than with irrigation (5.2) ($P< 0.05$). Thereafter, although green area decreased overall, differences between irrigation treatments became progressively greater and were always significant ($P< 0.05$). At GS 39+750°Cd (*c.* GS 61 + 28 d), the irrigation effect was maximal, with GAI of 2.7 (irrigated) and 0.6 (unirrigated). Drought advanced date of complete canopy senescence by 7 d from 1 August to 25 July.

In 94-5, onset of drought was earlier. Overall, GAI was generally slightly lower than in 93-4, with maximal values occurring slightly later at GS 61 (Fig. 3.3). Thus, irrigated maximum GAI (4.5) was smaller than in the previous season (5.2.) For the unirrigated crop, the maximum was 3.5 compared to 4.8 in the preceding season. The effect of irrigation was always significant after GS 31 ($P< 0.01$), and corresponding differences were greater than in 93-4. By GS 39+750°Cd (*c.* GS 61 + 28 d), GAI was reduced from 2.8 in the irrigated crop to 0.3 under drought. The advancement in complete canopy senescence with drought was 8 d from 31 to 23 July. In summary, GAI for irrigation treatment levels in 93-4 and 94-5 could be classified into three groups. Greatest areas occurred for the irrigated crop in 93-4. The second group of intermediate GAI comprised the irrigated crop in 94-5 and the unirrigated crop in 93-4. The third group with smallest GAI corresponded to the unirrigated crop in 94-5.

In 95-6, assessments were only taken on 23 April and 15 June. On 15 June, irrigated GAI was broadly similar to GAI at GS 61 in previous seasons at 4.8; the unirrigated crop, however, was lower than in previous years at 2.8. This reflected greater SMD in the 2 - 3 week period prior to anthesis in 95-6 than in other seasons. The advancement in complete canopy senescence was similar to other seasons at 8 d from 1 August to 24 July. Overall, reduction in GAI was greatest in 94-5 and 95-6. This clearly corresponded to the effects of the more severe pre-and-post anthesis droughts in these latter two seasons.

3.5.2. Effect of variety

For 93-4 and 94-5, there were varietal differences at all sample times in each season ($P< 0.05$), with the exception of GS 39+750°Cd in 94-5 (P=0.09) (Table 3.4; Fig. 3.3). Varietal effects were also significant when data was analysed across seasons (Table 3.6). At GS 31 overall there was greater GAI for Haven and Maris Huntsman compared to Soissons, Mercia and Rialto at GS 31 ($P< 0.05$); this was explained by the longer duration for growth for these slower developing varieties. By maximum GAI (occurring overall at GS 61), the irrigated varietal range was 4.2 - 5.3. Maris Huntsman (5.3) and

Mercia (5.0) had larger GAI than Rialto (4.2) ($P< 0.01$), with intermediate values for other varieties. At GS 39+750°Cd, the ranking order had changed slightly. Poorer canopy persistence for Haven and better canopy persistence for Soissons led to Haven producing lowest GAI and Soissons having amongst the highest at this stage. The high GAI of Mercia at GS 61 was, however, maintained through to GS 39+750°Cd. There were also consistent effects in duration from GS 61 to complete canopy senescence. For both irrigated and unirrigated crops, this period was about 10 d longer for Soissons and Mercia compared to Haven, with intermediate durations for Riband, M. Huntsman and Rialto (Table 3.2). In relation to the three broad categories of yield structure described (see Section 3.3.2), there was a tendency for the high yield potential, semi-dwarfs, Haven, Riband and Rialto, to have lower GAI compared to the two other categories.

In 95-6, with assessments on 23 April and 15 June (Table 3.7), there were no significant varietal differences on 23 April. On 15 June in the irrigated crop, M. Huntsman (5.3) and Mercia (5.3) had larger green area indices than Rialto (3.9) ($P<0.05$), with intermediate green canopy areas for other varieties. (Table 3.4; Fig. 3.3), corroborating effects observed in the previous seasons.

3.5.3. Irrigation/variety interaction

In summary, the variety ranking order was generally similar in irrigated and unirrigated crops, with little evidence for large interactions. One exception to this was flag leaf emergence in seasons with early drought, where there was some evidence that early developing varieties may have maintained GAI better under drought. There was also some evidence in both 93-4 and 94-5 experiments that Haven's (late flowering) rate of senescence was more accelerated under drought compared to Soissons (early flowering).

Overall, from the cross-season analysis of variance for 93-4 and 94-5, the interaction was not statistically significant at any sample time (Table 3.6). There was a trend ($P= 0.10$) at GS 39 for Soissons and Mercia, the two most rapid developing genotypes, to lose relatively less green area under drought compared to Haven and M. Huntsman, and this trend was also detected during the latter stages of grain filling. Dealing with the individual experiments, in 93-4 the interaction was not significant at any sample time. In 94-5, the interaction was significant at GS 61 ($P< 0.01$) with a trend also at GS 39 for an interaction ($P=0.07$), but not at other sample times. At GS 39, GAI was on average lower by 1.3 units with drought. Green area reduction, however, was relatively less for the earlier developing varieties, Soissons, Mercia and Rialto, compared to the later developing Haven and Riband (Fig. 3.3; Table 3.4). At GS 61, a similar interaction was observed in respect of Rialto and Haven. For 95-6, the interaction was not statistically significant at any sample time (Table 3.7).

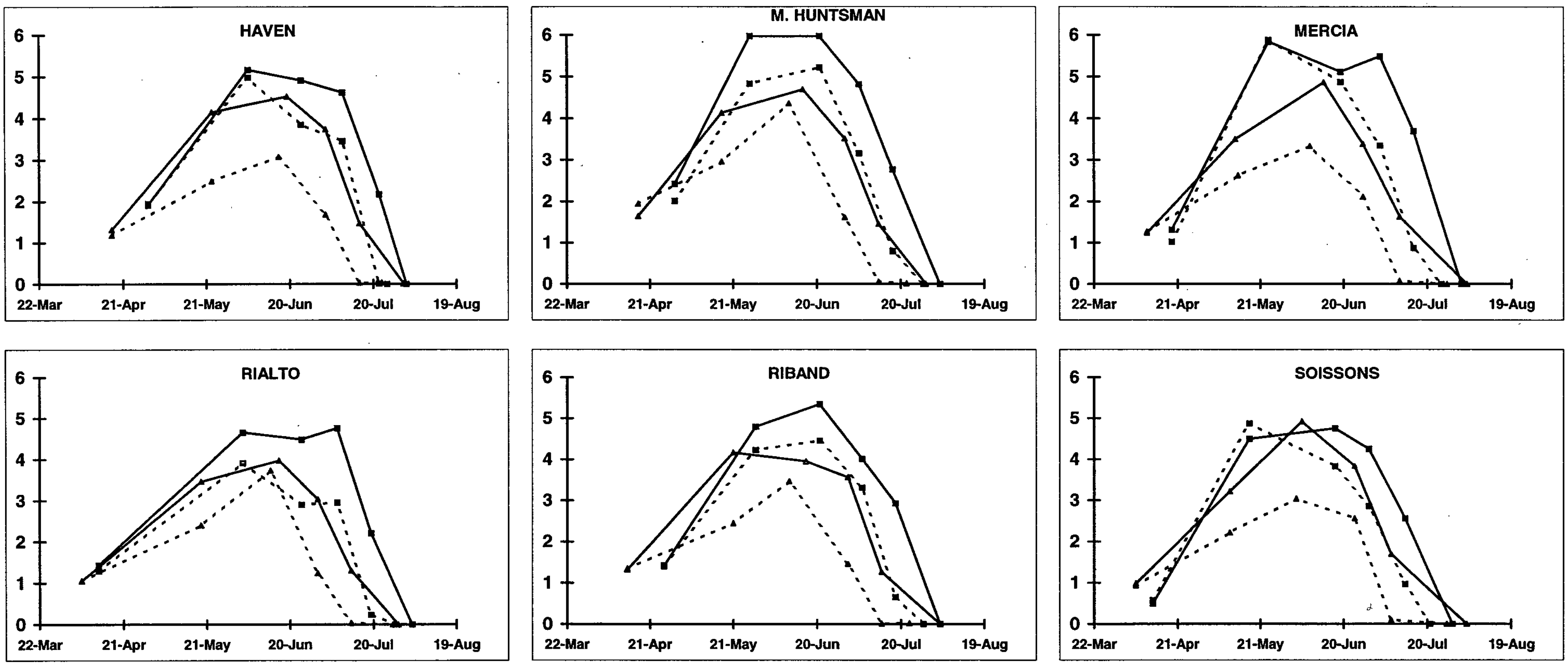


Fig. 3.3 Green area index for 1993-4 (■) and 1994-5 (▲) for irrigated (—) and unirrigated (......) wheat crops at GS 31, GS 39, GS 61, GS 39+550°Cd, GS 39+750°Cd, GS 87 and pre-harvest.

Table 3.7. Green area index on 23 April and 15 June 1995-6

	23 April		15 June	
	Irr	Unirr	Irr	Unirr
Haven	1.36	1.55	4.88	2.71
M. Huntsman	1.60	1.66	5.30	2.61
Mercia	2.00	2.15	5.32	4.00
Rialto	1.52	1.79	3.93	2.35
Riband	2.08	1.79	4.50	2.79
Soissons	1.91	1.97	4.59	2.34
Mean	1.74	1.82	4.75	2.80
SED Irr		0.180		0.379
Prob		0.745		0.122
SED Var		0.242		0.357
Prob		0.177		0.026
SED Irr/Var		0.360		0.597
Prob		0.881		0.464

3.6. Above-ground crop dry mass

3.6.1. Effect of irrigation

In summary, the effects of the earlier onset of drought in 94-5 and 95-6 on dry mass were much larger than the late drought in 93-4, leading to reductions in the order of 4 to 5 t/ha at harvest rather than about 2 t/ha.

In 93-4 with late drought, there were no differences at GS 39 and GS 61. At GS 39+550°Cd (*c.* GS 61 + 14 d), dry mass was reduced under drought (13.4 t/ha) compared with irrigation (14.3 t/ha) ($P< 0.05$). Subsequently, irrigation effects were always significant at the 10% significance level: a reduction with drought of 1.8 t/ha at GS 39+750°Cd (P=0.06), 1.9 t/ha at GS 87 (P= 0.09) and 2.2 t/ha (P=0.09) at harvest. Dry mass was maximal at GS 87, decreasing by 1.3 t/ha during the ripening phase up to harvest.

In 94-5, with earlier onset of drought, at GS 39 dry mass was smaller in the unirrigated (4.9 t/ha) than the irrigated (5.2 t/ha) crop, but the difference was not significant. By GS 61, there was a strong trend (P=0.07) for a reduction in dry mass with drought (8.9 vs 11.1 t/ha). Thereafter, the reduction was always significant ($P< 0.05$) and became progressively larger through grain filling. At GS 87, drought decreased dry mass by 4.4 t/ha from 16.9 t/ha to 12.5 t/ha. By harvest after ripening the reduction with drought was again 4.4 t/ha.

In 95-6, again with pre-anthesis drought but where unirrigated SMD was slightly greater in the 2 - 3 wks preceding anthesis, on 15 June there was a non-significant reduction in dry mass of 1.0 t/ha from 10.8 to 9.8 t/ha. At harvest, irrigated dry mass was greatest of any season at 17.3 t/ha, and there was a 5.3 t/ha loss with drought ($P<$ 0.001). Unirrigated harvest dry mass at 12.0 t/ha was similar to that in 94-5.

3.6.2. Effect of variety

The variety effect was significant at all sample times in 93-4 and 94-5 (Table 3.4.; Fig. 3.4) ($P< 0.01$), with the exception of GS 87 93-4 ($P=0.07$) and GS 87 ($P=0.59$) and harvest ($P=0.41$) 94-5. Differences at GS 31, GS 39 and GS 61 generally reflected development rates: for example, at GS 39 93-4, Soissons (5.4 t/ha) and Mercia (6.1 t/ha) with more rapid development had smaller dry mass than Rialto (7.7 t/ha) and Haven (7.5 t/ha) ($P< 0.05$). In 95-6, varietal differences were significant on 23 April with the more advanced varieties, Soissons and Rialto, showing greater crop dry mass compared to all others. Differences were not significant at GS 61. Harvest crop dry mass, when analysed across the three seasons, was greater ($P< 0.05$) for Rialto (15.5 t/ha) compared to all other varieties and particularly compared to Mercia (14.2 t/ha). Amongst other varieties, it was more difficult to detect consistent effects. Haven showed a trend for greater dry mass with irrigation in all seasons and also under drought in 93-4. But with early drought in 94-5 and 95-6, its dry mass at harvest was lowest and second lowest, respectively

3.6.3. Irrigation/variety interaction

When 93-4 and 94-5 data was analysed across seasons, the interaction was non-significant at all sample times. For the individual experiments, in 93-4 the interaction was not significant at any sample time. There was a trend at harvest for relatively smaller dry mass with drought for Riband, and the converse for Haven. In 94-5, the interaction was only significant at GS 39 ($P< 0.05$). Here, dry mass loss with drought was relatively smaller for the three most rapid developing varieties, Soissons, Mercia and Rialto, compared to others examined. In 95-6, the interaction was not significant on 23 April and 15 June.

In summary, evidence pointed to a lack of statistically significant interactions between irrigation and variety for above-ground dry mass. Different responses to early drought between the faster and slower developing varieties in 94-5 early in the season were not sustained during the later grain filling period. At harvest, the range was from Rialto which maintained 80% of irrigated biomass under drought to Haven which maintained only 75%.

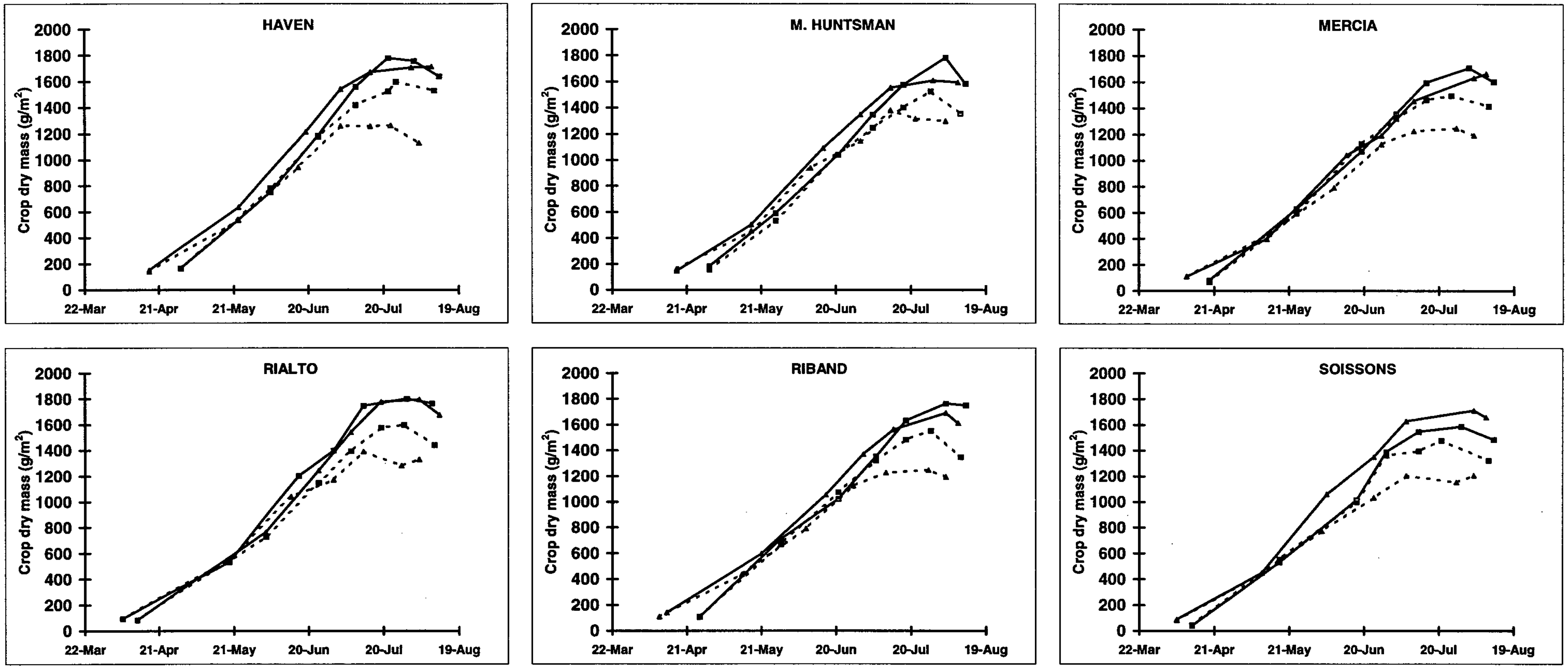


Fig. 3.4. Crop dry mass (g/m^2) for 1993-4 (■) and 1994-5 (▲) for irrigated (—) and unirrigated (......) wheat crops at GS 31, GS 39, GS 61, GS 39+550°Cd, GS 39+750°Cd, GS 87 and pre-harvest.

Table 3.8. Dry mass (g/m^2) on 23 April and 15 June 1995-6

	23 April		15 June	
	Irr	Unirr	Irr	Unirr
Haven	143	148	1121	951
M. Huntsman	125	145	1064	912
Mercia	155	155	1046	1032
Rialto	158	177	1120	1028
Riband	127	146	1004	948
Soissons	167	167	1099	978
Mean	146	156	1076	975
SED Irr		9.7		31.0
Prob		0.478		0.191
SED Var		9.0		33.9
Prob		0.014		0.118
SED Irr/Var		15.2		53.6
Prob		0.694		0.267

Table 3.9. Harvest dry mass (g/m^2) 1993-4 - 1995-6

		93-4	94-5	95-6	93-4 – 95-6
Irrigated	Haven	1640	1714	1712	1689
	M. Huntsman	1585	1593	1755	1645
	Mercia	1601	1663	1595	1620
	Rialto	1676	1766	1720	1721
	Riband	1750	1611	1739	1700
	Soissons	1484	1657	1832	1658
Mean		1623	1667	1725	1672
Unirrigated	Haven	1532	1130	1129	1263
	M. Huntsman	1356	1298	1187	1280
	Mercia	1416	1193	1077	1228
	Rialto	1443	1330	1350	1374
	Riband	1348	1228	1249	1275
	Soissons	1322	1206	1205	1244
Mean		1403	1231	1199	1278
SED, Prob Irr		18.4, < 0.01	37.7, <0.01	30.6, < 0.01	18.6, < 0.001
SED, Prob Var		47.3, < 0.01	56.5, 0.413	44.8, < 0.01	30.4, 0.005
SED, Prob Irr/Var		63.7 ,< 0.087	82.3, 0.393	65.4, 0.114	43.4, 0.709

3.7. Water uptake and water use efficiency

3.7.1. Water uptake

Table 3.10. Crop water use (mm) from 17 April (1994), 13 April (1995) and 19 April (1996) to end of grain filling (GS87)

Year		1994	1995	1996			
		334.0	302.1	353.4			
Irr		Irr	Unirr				
		425.6	234.1				
Variety		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
		333.5	324.5	323.0	336.4	337.4	324.1
Year/Irr		1994	1995	1996			
	Irr	398.6	406.8	471.4			
	Unirr	269.4	197.5	235.4			
Irr/Var		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
	Irr	434.8	422.2	418.6	423.2	434.3	420.4
	Unirr	232.1	226.9	227.4	250.0	240.6	227.9
Year/Var		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
	1994	343.3	318.4	340.9	341.8	338.9	320.7
	1995	315.9	298.8	291.2	303.5	305.5	298.0
	1996	341.2	356.5	336.8	364.4	367.9	353.7
Year/Irr/Var		Haven	Hunstman	Mercia	Rialto	Riband	Soissons
	Irr 94	410.6	399.4	412.4	392.0	394.7	382.5
	Unirr 94	275.9	237.4	269.5	291.6	283.1	259.0
	Irr 95	438.4	390.8	385.0	405.7	414.4	406.4
	Unirr 95	193.3	206.8	197.4	201.4	196.5	189.5
	Irr 96	455.5	476.5	458.4	471.9	493.8	472.3
	Unirr 96	227.0	236.4	215.2	256.9	242.1	235.2

S.E.D. : Irrigation 6.64 (D.F.=3, P< 0.001); Variety 7.21 (D.F.=30, P=0.160); Irr/Var 11.43 (D.F.=30, P=0.477).

3.7.1.1. Effect of irrigation

With drought, water uptake from mid-April to end of grain fill (taken as GAI = zero) was 269 mm (93-4), 198 mm (94-5) and 235 mm (95-6). The lower uptake in 94-5 corresponded to a SMD in the order of 30 mm in mid-April (at onset of soil water content measurements) compared with negligible deficits at this time in the two other seasons. Averaged across seasons, water uptake was 192 mm less under drought (234 mm) than with irrigation (426 mm) (P< 0.001) (Table 3.10). This represented the additional water availability and capacity for uptake due to applied irrigation. The respective differences were 119 mm (93-4), 209 mm (94-5) and 236 mm (95-6). The greater differences in 94-5 and 95-6 compared to the earlier season reflected their earlier onset of more extended drought.

3.7.1.2 Effect of variety

Averaged across seasons, differences amongst varieties were not significant (P=0.16) (Table 3.10). The range, averaged across irrigation treatments, was 323 - 337 mm. There was a tendency overall for the shorter life cycle, lower yield potential varieties, Soissons and Mercia, to take up slightly less water than the slower developing, higher yield potential varieties, Riband, Rialto and Haven. There was also a non-significant trend for the older, non-dwarf feed M. Huntsman to take up less water than the modern feed varieties of similar developmental pattern but greater yield potential.

3.7.1.3. Irrigation/variety interaction

Overall, combining data across the three seasons, the irrigation/variety interaction was not significant (P=0.48). Taking into account the way in which water use was calculated, there are grounds for attaching more weight to varietal rankings under drought than those with irrigation. This is because the calculation assumed all irrigation water entered the soil system and that none was lost either to direct evaporation of water intercepted on the canopy surface or to surface run-off. The average droplet size of applied water is smaller than rainfall and thus it is more susceptible to interception by the canopy (McEwen *et al.*, 1981). Therefore, considering the unirrigated crop only, the varietal range was 227 - 250 mm. Rialto had greatest water uptake, showing consistently greater uptake than the rapid developing varieties, Soissons and Mercia, in each season. Of the other varieties, Riband had consistently moderate-to-high uptake. M. Huntsman had lowest uptake in 93-4 (20 mm lower than any other variety), but this apparent trend was not observed in 94-5 or 95-6, where, in each case, it was one of the higher ranking varieties. Haven generally showed a trend for lower uptake compared to the other high yield potential varieties, Riband and Rialto, but differences, in absolute amounts, were only in the order of 10 mm.

In summary, although differences were not statistically significant, there was trend for Rialto to take up more water than other genotypes in drought-affected crops, particularly compared to the more rapid developing varieties. Soil water content was only assessed in two replicates, and this may have contributed, in part, to the lack of statistically significant effects.

3.7.1.4. Temporal phasing of water uptake pre- and post-flowering

The balance of total water use from mid-April to GS 61 and from GS 61 to end of grain filling (GAI = zero) for 93-4 and 94-5 is shown in Fig. 3.5. There were varietal differences in water use up to GS 61 (P< 0.001). In the unirrigated treatment, the range was 149 - 176 mm. As expected, rapid developing varieties with less days from mid-April to GS 61 generally used less water up to this stage; thus, Soissons (149 mm) and Mercia (156 mm) used less water than Rialto (176 mm), Riband (168 mm) and Haven (174 mm). These effects in the drought-affected treatments were consistently expressed in the two seasons.

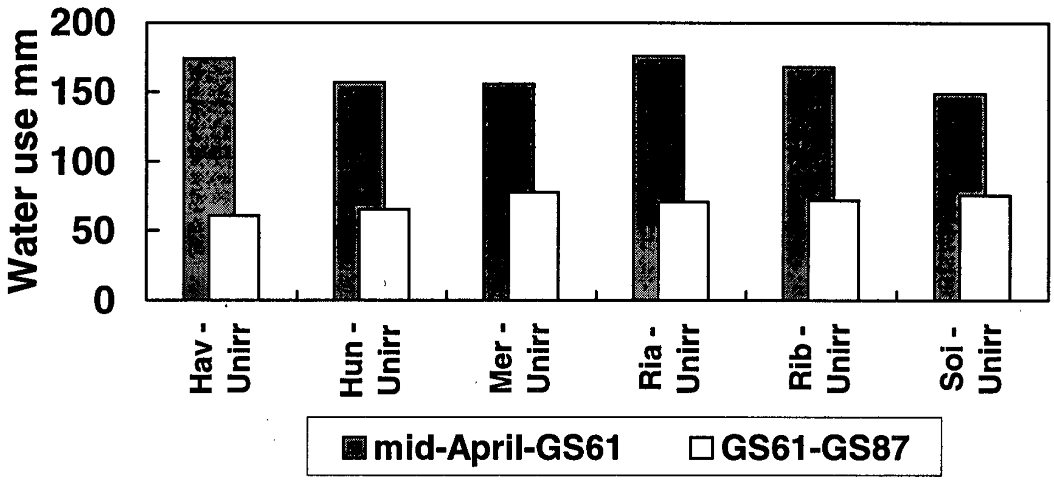


Fig. 3.5. Crop water use (mm) from 17 April (1994), 13 April (1995) and 19 April (1996) to GS 61 and from GS 61 to end of grain fill (GS 87) averaged for 1993-4 and 1994-5.

There were also differences in water use during grain filling (GS 61 - zero GAI) (Fig. 3.5) ($P < 0.05$). Under drought, the range was 61 - 78 mm. As expected, varieties which used least water from mid-April to GS 61, theoretically conserving water for use during grain fill, subsequently used most during grain filling. Thus, Soissons (76 mm) and Mercia (78 mm) used more than Haven (61 mm), M. Huntsman (65 mm), Rialto (71 mm) and Riband (72 mm). With the exception of Haven, however, these differences were smaller than the respective differences in water use up to GS 61. For example, Rialto which used 27 mm more water than Soissons up to GS 61 only used 5 mm less during grain filling. Similarly, Riband, which used 12 mm more than Mercia up to GS 61, only used 6 mm less during grain filling. Larger amounts of water use in the vegetative phase seemed not to compromise water uptake greatly during grain filling. This was because total water uptake was generally greater for the slower developing varieties. Possibly more water uptake up to GS 61 was correlated with greater below ground investment in roots (Barraclough & Leigh, 1984). Furthermore, it is likely that a proportion of additional water use up to GS 61 for the slower developing varieties could potentially have contributed to higher stem carbohydrate. The case of Haven was, however, more in line with the original hypothesis. In the early drought seasons, its water use during grain filling was least of all the varieties. This suggested that late flowering still may be detrimental in early drought seasons, although early flowering may not necessarily confer a significant advantage over varieties of intermediate flowering date under UK drought.

In summary, the mechanism of earlier flowering as a strategy for drought resistance seems to be of marginal benefit in the UK environment. The more rapid developing varieties did take up more water during grain filling, but their total water seasonal uptake was generally lower. Against this, it should be noted that at the corresponding developmental stages through grain filling the more rapid developing genotypes may have encountered slightly less severe water stress; this may have had consequences for rate of canopy senescence. Indeed, there was some evidence for a longer period from GS 61 to complete canopy senescence for Soissons compared to later flowering varieties, e.g. Haven, under drought in 94-5 (Table 3.2).

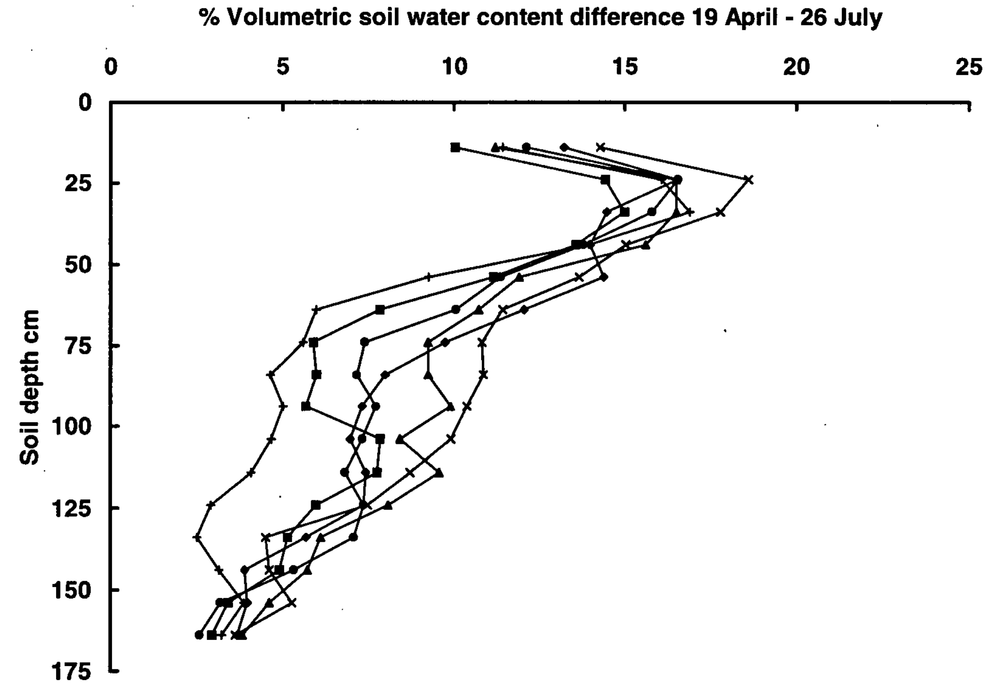
3.7.1.5. Distribution of water uptake with soil depth

The difference between soil water stored in the profile in mid-April and then at end of grain fill is shown for varieties in unirrigated conditions in each season in Fig. 3.6.

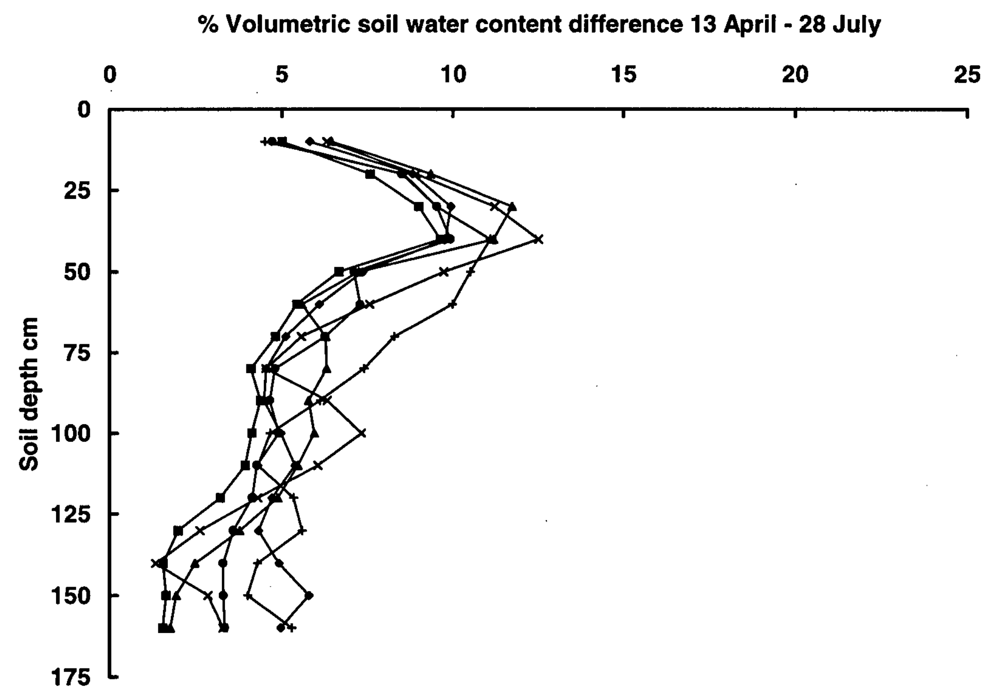
In summary, varietal differences detected in total water use related to greater extraction at all depths within the profile from *c.* 20 to 120 cm rather than deeper maximum rooting depth. Thus, Rialto, which showed greatest water uptake, extracted more water at all depths from *c.* 20 to 120 cm, but showed no trend for greater uptake below this depth compared to other genotypes. Similarly, a smaller uptake for M. Huntsman in 93-4 related to uniformly poorer extraction at depths from about 50 to 120 cm rather than shallower rooting depth. There may have been an effect of developmental rate here. Maximum rooting depth is largely determined by GS 61 and the period of maximum crown root proliferation takes place from GS 31 to GS 61 (Barraclough & Leigh, 1984). Therefore, Rialto with an extended phase from GS 31 to GS 61 compared to other genotypes may have been predisposed to greater water uptake under drought due to a longer period for proliferation of crown.

In summary, apparent varietal trends in seasonal water uptake with drought related to uniformly greater extraction within the profile to about 120 cm depth rather than deeper rooting. It should be noted that direct measurements of root dry mass and root length per unit volume would ideally be required to strengthen current conclusions, but, due to the labour-intensive nature of these assessments, they could not be undertaken in the current study.

1994



1995



Figs 3.6a & b Difference in volumetric water content (%) between mid-April and end of grain filling for unirrigated crops in 1994 and 1995 for Haven (■), M. Huntsman (+), Mercia (◆), Rialto (X), Riband (▲) and Soissons (●) wheat crops.

1996

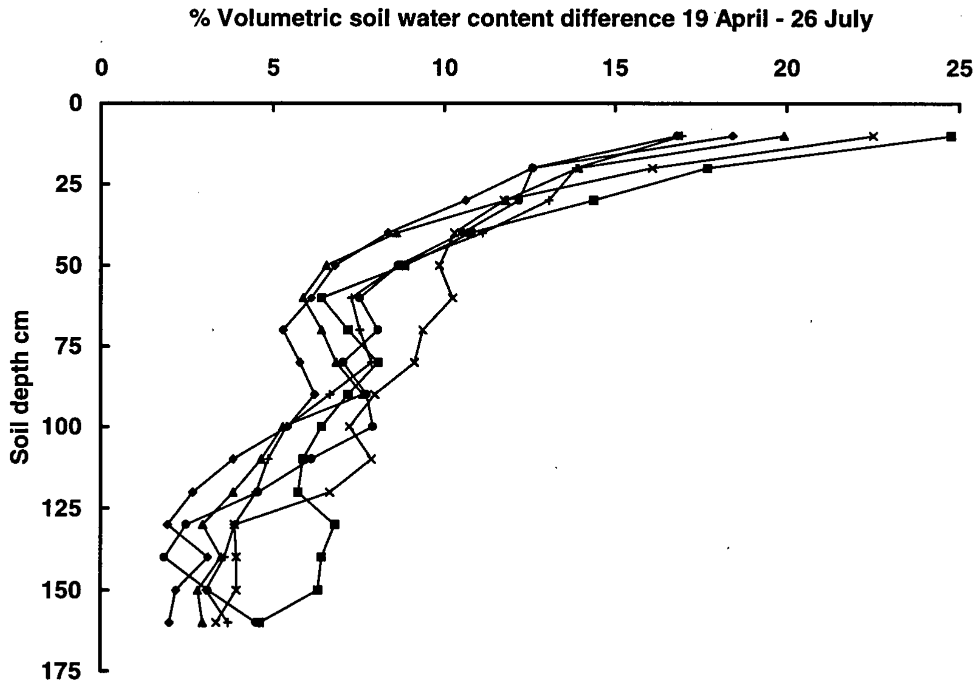


Fig. 3.6c Difference in volumetric water content (%) between mid-April and end of grain filling for unirrigated crops in 1996 for Haven (■), M. Huntsman (+), Mercia (◆), Rialto (X), Riband (▲) and Soissons (●) wheat crops.

3.7.2. Water use efficiency

Because dry mass was only assessed at three sample times in 95-6, linear regressions of cumulative dry mass on cumulative water use could only be calculated for 93-4 and 94-5 data. Cumulative water use was estimated from daily records of rainfall and measurements of volumetric soil water using the neutron probe. It was assumed that no water was lost to drainage from the start of measurements. The slope of the linear regression was taken as the water use efficiency in $g/m^2/mm$. Cumulative water use efficiencies over the six sample times from mid-April to GS 87 were calculated for each plot in each experiment and subjected to analysis of variance.

3.7.2.1. *Effect of irrigation*

Table 3.11. Crop water use efficiency (g/m²/mm) from the linear regression of cumulative dry mass on cumulative water uptake at six sequential sampling times from GS 31 to GS 87 in 1993-4 and 1994-5

Year		1994	1995				
		4.81	5.00				
Irr		Irr	Unirr				
		4.10	5.71				
Variety		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
		4.88	5.13	4.86	4.94	4.83	4.79
Year/Irr		1994	1995				
	Irr	4.23	3.96				
	Unirr	5.39	6.04				
Irr/Var		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
	Irr	4.08	4.06	3.99	4.41	3.98	4.06
	Unirr	5.68	6.21	5.72	5.46	5.68	5.52
Year/Var		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
	1994	5.02	5.19	4.70	4.65	4.63	4.68
	1995	4.74	5.08	5.02	5.22	5.02	4.91
Year/Irr/Var		Haven	Hunstman	Mercia	Rialto	Riband	Soissons
	Irr 94	4.43	4.18	4.06	4.42	4.23	4.08
	Unirr 94	5.62	6.20	5.33	4.89	5.04	5.29
	Irr 95	3.73	3.94	3.91	4.40	3.72	4.04
	Unirr 95	5.75	6.22	6.12	6.04	6.31	5.77

S.E.D. : Irrigation 0.316 (D.F. = 2, P = 0.036); Variety 0.205 (D.F. = 20, P=0.619); Irr/Var 0.412 (D.F. = 20, P=0.338).

WUE was 1.61 g/m²/mm higher on average in the unirrigated crop (5.71 g/m²/mm) than with irrigation (4.10 g/m²/mm) (*P*< 0.05) (Table 3.11). This difference related to the higher leaf temperature under drought acting to decrease the internal concentration of water vapour in leaves, such that the difference between ambient concentration of water vapour and internal concentration of leaf water vapour will have been less than that for the irrigated crop. In general, the estimates of water use efficiency were of the same order as those previously reported for winter wheat in the UK, e.g. the ranges of 3.7 - 5.8 g/m²/mm (Green *et al.* ,1983) and 4.1 - 6.0 g/m²/mm (Goss *et al.* , 1984).

3.7.2.2. *Effect of variety*

Averaged across irrigation treatments and seasons, variety differences were not significant (*P*=0.62) with values in the range 4.83 - 5.13 g/m²/mm. Five of the varieties were very similar in the range 4.83 - 4.94 g/m²/mm, with only M. Huntsman showing a tendency for greater efficiency (5.13 g/m²/mm). Under drought, the range was 5.52 - 6.21 g/m²/mm. Again, with the exception of M. Huntsman, varieties fell within a narrow range of 5.46 - 5.68 g/m²/mm. The trend for M. Huntsman depended on particularly low uptake in one replicate in 93-4 and may have been an artefact of the low levels of replication of soil water measurements (in only two replicates) rather than the representation of a real effect.

This would be in agreement with the most of the previous literature on this subject, e.g. Richards (1987), showing little consistent evidence for differences in WUE among wheat varieties.

3.7.2.3. Irrigation/variety interaction

Consistent with the lack of discernible differences amongst the varieties themselves, the interaction was not significant for combined 93-4 and 94-5 data (P=0.34).

3.8 Solar radiation interception and conversion efficiency

3.8.1 Solar radiation interception

Table 3.12. Intercepted solar radiation (MJ/m^2) from GS 31 to GS 39+750°Cd in 1993-4 and 1994-5

Year		1994	1995				
		1042	1007				
Irr		Irr	Unirr				
		1052	997				
Variety		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
		998	1001	1033	1104	996	1015
Year/Irr		1994	1995				
	Irr	1067	1041				
	Unirr	1021	972				
Irr/Var		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
	Irr	1043	1027	1057	1137	1015	1035
	Unirr	954	976	1010	1071	976	995
Year/Var		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
	1994	1002	1019	1050	1148	1008	1030
	1995	994	984	1017	1062	982	1001
Year/Irr/Var		Haven	Hunstman	Mercia	Rialto	Riband	Soissons
	Irr 94	1043	1031	1071	1176	1015	1045
	Unirr 94	961	1007	1028	1115	1002	1014
	Irr 95	1042	1023	1042	1098	1015	1026
	Unirr 95	947	944	991	1026	950	975

S.E.D. : Irrigation 13.0 (D.F. = 2, P= 0.051); Variety 14.9 (D.F. = 20, P<0.001); Irr/Var 23.2 (D.F. = 20, P=0.551)

3.8.1.1. Effect of irrigation

Averaged across seasons, there was a reduction in intercepted radiation in the unirrigated compared to the irrigated crop (P= 0.05), in the order of 50 and 70 MJ/m^2 in 93-4 and 94-5, respectively (Table 3.12). In the unirrigated crops, there was 49 MJ/m^2 more radiation interception in 93-4 than 94-5. The smaller interception in 94-5 related to earlier onset of drought and greater reduction in canopy area. Amounts of intercepted radiation (Table 3.12) refer to the combined interception by the green and dead canopy area. Since the unirrigated treatment will have had proportionately more dead area than the irrigated treatment, differences with respect to that interception by green area alone would be expected to be proportionately larger than values reported here. Variety differences in green canopy area with drought would, however, be expected to be reflected in total canopy area, and it is thus still worth examining varietal differences in radiation interception shown in Table 3.12.

3.8.1.2. Effect of variety

Overall, there were significant varietal differences in radiation interception, with Rialto accumulating more than all other varieties Mercia (P< 0.001) (Table 3.12). This effect was observed in both seasons. Rialto, with an early date for GS 31 but an intermediate-to-late date for GS 61, had a longer period from GS 31 to end of grain fill than other genotypes. It thus had more calendar days to intercept radiation. The greater harvest dry mass for Rialto compared to other varieties (Table 3.9) was associated with this developmental pattern. The trend for Mercia also to have high interception was, however, more due to a generally large maximum GAI (Fig. 3.4) and good canopy persistence (Table 3.2) rather than a prolonged duration for interception.

3.8.1.3. Irrigation/variety interaction

The irrigation/variety interaction was not significant (P=0.55), varieties generally performing similarly in proportional terms in both irrigated and unirrigated conditions. This was consistent with non-significant interactions for both GAI (Table 3.4) and dates of development stages (Table 3.2).

3.8.2. Solar radiation use efficiency

3.8.2.1. Effect of irrigation

Solar radiation use efficiency (g/MJ) (RUE) was calculated from the slope of the linear regression of cumulative dry mass on cumulative radiation interception in 93-4 and 94-5. Averaged across experiments, RUE was lower at 1.28 g/MJ under drought than with irrigation at 1.47 g/MJ (P< 0.05) (Table 3.13). The explanation for this, in part at least, was that, after the canopy began to senescence around GS 61, proportionately more radiation was intercepted by dead canopy in the unirrigated than irrigated crop. In addition, RUE was probably also reduced in the unirrigated crop due to water stress effects: plasmolysis damage to mesophyll cells occurring when water supply to green tissues became restricted. The reduction in RUE with drought in 94-5 (0.24 g/MJ) was greater than 93-4 (0.13 g/MJ) associated with the more extended drought in 94-5.

3.8.2.2. Effect of variety

Across seasons and irrigation treatments, there was a strong trend for varietal differences in conversion efficiency (P= 0.08) (Table 3.13). Rialto and Haven (1.41 g//MJ) had a greater efficiency than Soissons (1.40 g/MJ) and M. Huntsman, Riband and Mercia in the range 1.31 - 1.35 g/MJ. The greater efficiency for Rialto was associated with greater dry mass and lower maximum green canopy area compared to other varieties. However, absolute differences in maximum GAI between Rialto and some varieties, e.g. Riband and Soissons, were only marginal. There was a tendency for lower efficiency for M. Huntsman compared to other varieties, with M. Huntsman having highest green canopy area but only mid-range harvest dry mass. The tendency may also have been associated with M. Huntsman's semi-recurved flag-leaf attitude (NIAB, 1996b) and consequently high extinction coefficient, leading to the flag leaves being light saturated during periods of high incident radiation. Such periods will have occurred frequently in these drought-affected seasons.

3.8.2.3. Irrigation/variety interaction

The interaction, from the analysis of variance combining 93-4 and 94-5 data, was not significant (*P*=0.15). Although there was a trend for Rialto and Haven to have relatively greater RUE than other varieties in irrigated compared to unirrigated crops.

Table 3.13. Solar radiation use efficiency (g/MJ) from the linear regression of cumulative dry mass on cumulative radiation interception at five sequential sampling times from GS 31 to GS 39+750 °Cd in 1993-4 and 1994-5.

Year		1994	1995				
		1.40	1.34				
Irr		Irr	Unirr				
		1.47	1.28				
Variety		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
		1.41	1.31	1.34	1.41	1.35	1.40
Year/Irr		1994	1995				
	Irr	1.47	1.46				
	Unirr	1.34	1.22				
Irr/Var		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
	Irr	1.55	1.37	1.38	1.52	1.44	1.52
	Unirr	1.28	1.26	1.30	1.31	1.26	1.27
Year/Var		Haven	Huntsman	Mercia	Rialto	Riband	Soissons
	1994	1.48	1.27	1.40	1.43	1.42	1.43
	1995	1.34	1.36	1.28	1.40	1.28	1.36
Year/Irr/Var		Haven	Hunstman	Mercia	Rialto	Riband	Soissons
	Irr 94	1.57	1.34	1.43	1.50	1.48	1.52
	Unirr 94	1.40	1.20	1.37	1.36	1.36	1.35
	Irr 95	1.53	1.39	1.34	1.55	1.41	1.51
	Unirr 95	1.16	1.32	1.22	1.25	1.16	1.21

S.E.D. : Irrigation 0.029 (DF=2, *P*=0.025); Variety 0.059 (DF=20, *P*=0.075); Irr/Var 0.058 (DF=20, *P*=0.152).

3.9 Water soluble stem carbohydrate

In each season, percentage water soluble carbohydrate stem content was assessed in six shoots per plot at GS 61+75°Cd, when amounts are close to maximal (Austin *et al.*, 1977) and at harvest. In 93-4 and 94-5, stem dry mass at GS 61+75°Cd was calculated from linear interpolation of the stem dry mass measured at GS 61 and GS 39+550°Cd. Water soluble stem carbohydrate dry mass was calculated as the product of i) % WSC and ii) interpolated stem dry mass. In 95-6, stem dry mass per m^2 at GS 61+75°Cd was calculated from the product of i) stem dry mass per shoot (taken from the six shoots sampled for water soluble carbohydrate analysis themselves) and ii) shoots per m^2 (from growth analysis samples at harvest). Water soluble stem carbohydrate dry mass was calculated as the product of i) % WSC and ii) stem dry mass. At harvest, WSC stem dry mass was then calculated as the product of i) %WSC and ii) stem dry mass from harvest growth analysis assessments.

3.9.1. GS 61+75°Cd

3.9.1.1. Effect of irrigation

The effect of irrigation on soluble stem carbohydrate was not significant in 93-4, with only a 0.01 t/ha decrease in the unirrigated crop (Table 3.14). In both 94-5 and 95-6, there was a trend for less stem reserves with drought, a 0.36 (P= 0.06) and 0.30 t/ha (P=0.24) decrease, respectively. Since a large proportion of stem reserves is accumulated between flag leaf emergence and the end of flowering (Schnyder, 1993), the reduction in reserves in the unirrigated crop in the latter two seasons was consistent with early onset of drought in these experiments.

3.9.1.2. Effect of variety

There were varietal differences in all seasons (P< 0.001) (Table 3.14). For the two seasons where the methodology was comparable (93-4 and 94-5), the varietal range with irrigation was 2.31 - 3.48 t/ha and under drought 2.24 - 2.89 t/ha. The variety ranking order was consistent from season to season. Averaged across irrigation treatments, Haven and Rialto had greatest reserves at 3.18 and 3.00 t/ha, respectively, compared with Mercia (2.28 t/ha), M. Huntsman (2.36 t/ha), Riband (2.43 t/ha) and Soissons (2.49 t/ha). In 95-6, where there was slightly more variation in the data, the same broad varietal differences were detected (P=0.12) in the range 2.49 - 3.59 t/ha with irrigation and 2.13 - 3.33 under drought. In summary, meaningful varietal differences in the order of 1.00 t/ha were detected in each season. Rialto and Haven were the varieties consistently with highest reserves, Mercia and M. Huntsman with the lowest, and intermediate amounts for Soissons and Riband.

3.9.1.3. Irrigation/variety effect

The interaction was non-significant in all cases (Table 3.14) reflecting a similar ranking for varieties in both unirrigated conditions, where reserves were reduced with early drought, and in irrigated conditions.

Table 3.14 Percentage water soluble carbohydrate in stem dry mass and stem soluble carbohydrate dry mass (g/m²) at GS 61+75 °Cd

	1993-4		1994-5		1995-6		1993-4 - 94-5	
	%WSC	WSC g/m²	%WSC	WSC g/m²	%WSC	WSCg/m²	%WSC	WSC g/m²
Irrigated								
Haven	41.2	332	42.8	363	38.1	359	41.9	348
M. H'man	26.0	191	37.0	298	29.3	249	31.5	244
Mercia	29.9	210	34.0	252	29.7	254	32.0	231
Rialto	37.8	314	39.4	329	33.1	278	38.6	317
Riband	33.0	233	33.0	278	30.8	280	33.0	241
Soissons	34.4	246	35.1	273	33.1	357	34.8	259
Mean	33.7	253	36.9	294	32.3	296	35.3	273
Unirrigated								
Haven	39.5	299	43.0	278	39.8	293	41.3	289
M. H'man	29.7	205	37.3	251	33.9	281	33.5	228
Mercia	29.3	219	39.1	229	37.3	213	34.2	224
Rialto	39.3	294	40.0	272	40.1	333	39.6	283
Riband	35.4	256	38.6	235	36.1	252	35.8	246
Soissons	39.5	253	39.3	225	34.8	278	37.2	239
Mean	34.9	254	39.5	258	37.0	275	38.2	251
SED Irr	0.36	5.3	0.897	12.1	0.399	12.8	0.48	6.6
Prob.	0.089	0.771	0.098	0.064	0.007	0.239	<0.017	0.030
SED Var	1.84	14.3	1.954	18.7	1.902	35.9	1.34	17.3
Prob.	<0.001	<0.001	0.016	<0.001	0.014	0.115	<0.001	<0.001
SED Irr/Var	2.40	19.3	2.677	27.0	2.487	48.1	1.78	16.5
Prob	0.726	0.442	0.519	0.474	0.677	0.389	0.616	0.131

3.9.2. Harvest

Amounts of soluble stem carbohydrate remaining at harvest were always very low and averaged across experiments and varieties were 0.10 t/ha in both irrigated and unirrigated conditions (Table 3.15). Combining data for the three experiments, trends for differences amongst varieties (*P*=0.07) did not relate to meaningful differences in amounts of soluble stem carbohydrate dry mass accumulated.

Table 3.15 Percentage water soluble carbohydrate in stem dry mass and soluble carbohydrate dry mass (g/m^2) at harvest

	93-4		94-5		95-6		93-4 - 95-6	
	%WSC	WSC g/m^2	%WSC	WSCg/m^2	%WS	WSCg/m^2	%WSC	WSC g/m^2
Irrigated								
Haven	2.99	14	3.36	17	1.07	5	2.48	12
M. H'man	0.52	3	3.96	23	0.67	4	1.72	10
Mercia	0.95	5	3.95	21	0.94	5	1.95	10
Rialto	1.90	9	2.86	16	0.67	3	1.81	9
Riband	1.04	5	3.10	15	0.40	2	1.51	7
Soissons	2.09	11	2.87	15	1.48	9	2.15	12
Mean	1.58	8	3.35	18	0.87	5	1.94	10
Unirrigated								
Haven	1.28	6	3.41	13	2.54	8	2.42	9
M. H'man	1.42	6	6.14	31	2.26	8	3.27	15
Mercia	0.85	4	3.45	14	1.21	5	1.84	7
Rialto	0.90	4	3.64	16	3.47	14	2.67	11
Riband	0.67	3	3.64	15	1.48	6	1.93	8
Soissons	0.85	4	5.23	21	1.06	5	2.38	10
Mean	1.00	4	4.25	18	2.00	8	2.42	10
SED Irr							0.217	0.9
Prob							0.068	0.972
SED Var							0.321	1.5
Prob							0.118	0.070
SED I*V							0.468	2.1
Prob							0.099	0.051

3.9.3 Temporal phasing of stem dry mass loss with onset of drought

Fig. 3.7 shows the varietal mean for total above-ground dry mass in irrigated and unirrigated crops and components of total dry mass in 93-4 and 94-5 through the season.

In 93-4, even though total dry mass was less under drought during grain filling, ear dry mass remained similar in irrigated and unirrigated crops up until GS 39+750°Cd (*c.* GS 61+28 d). It was only during the last two weeks of grain fill that ear dry mass with drought became significantly smaller, decreasing by in the order of 1.5 t/ha at GS 87. For the drought-affected crop, maintenance of assimilate supply to grains in amounts comparable to irrigated crops was associated with greater loss of stem dry mass up to this point. This strongly implied that stem reserves were involved in this buffering process. Between GS 39+550°Cd (*c.* GS61+14 d) and GS 39+750°Cd (*c.* GS 61+28 d), the loss of dry mass from stems was 1.2 t/ha with irrigation but 2.0 t/ha under drought. This indicated that soluble carbohydrate stored in stems was remobilized earlier in response to drought. During the latter stages of grain fill, from GS 39+750°Cd to zero GAI, loss of dry matter from stems was 2.0 t/ha in the irrigated crop compared to 0.6 t/ha in the drought-affected crop. Again this suggested earlier remobilization with drought, but also implied reserves may have been important in maximizing yield in the unstressed crop as well as buffering grain filling with drought. Amounts of soluble carbohydrate initially accumulated in stems at GS 61+75°Cd were similar in both irrigated and unirrigated crops (Table 3.14), in the region of 3 t/ha. Amounts remaining at harvest both with and without irrigation were about 0.1 t/ha. It is possible that in the irrigated crop the later loss of stem sugars during late grain filling may have been associated with proportionately greater respiratory losses, but the extent of any respiratory losses were not quantified in the present study.

In 94-5, similar effects were observed to those in 93-4. Ear dry mass in the unirrigated crop again broadly maintained parity with irrigated ear growth up to GS 39+750°Cd, with only a 0.5 t/ha reduction with drought at this time. During latter grain fill from GS 39+750°Cd to GS 87, the increase in ear dry mass was 3.6 t/ha with irrigation compared to only 0.6 t/ha in unirrigated conditions. Again there was evidence for an earlier utilisation of stem reserves in drought-affected crops, indicated by greater stem dry mass loss from GS 39+550°Cd to GS 39+750°Cd of 1.6 t/ha in unirrigated crops compared to 1.1 t/ha in irrigated crops. Stem dry mass loss during late grain filling from GS 39+750°Cd to GS 87 again suggested that stem reserves may have a role in maximizing yields under unstressed conditions in addition to buffering yield under drought; the loss was 2.0 t/ha in the irrigated crop compared with only 0.7 t/ha in unirrigated conditions.

a) 1993-4

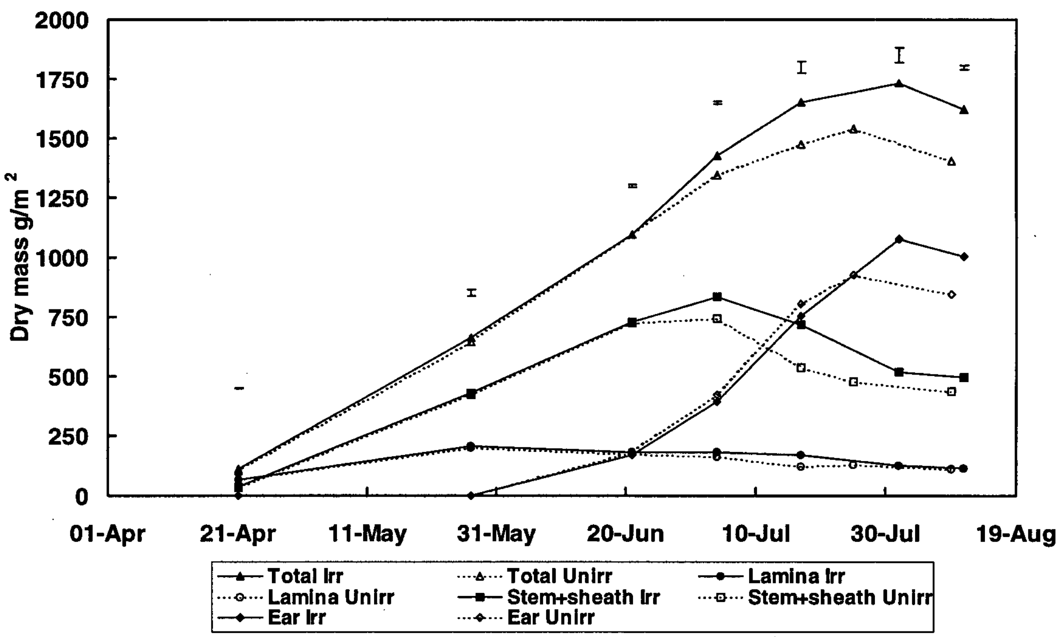


Fig. 3.7a Varietal mean for irrigated and unirrigated total dry mass and components of total dry mass in 1993-4.

b) 1994-5

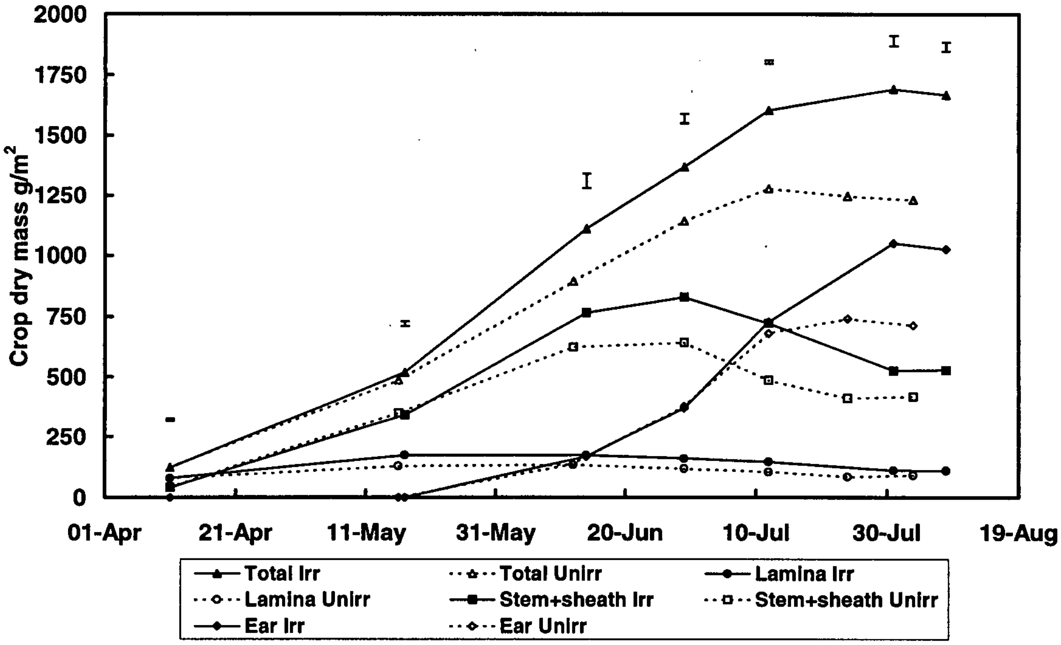


Fig. 3.7b Varietal mean for irrigated and unirrigated total dry mass and components of total dry mass in 1994-5.

4. DISCUSSION

4.1. Grain yield performance with drought

Irrigated yields were generally high and representative of performance in optimum UK growing conditions more usually associated with heavier soil types than the current experimental site. This was reflected in relative performance of varieties which mirrored closely their known yield potential under broadly stress-free conditions, as described on the RL (NIAB, 1996a and preceding publications). Over the three seasons, there was a significant irrigation/variety interaction. Rialto and Mercia lost relatively less grain yield under drought (*c.* 2.7 t/ha) compared with Haven and Riband (*c.* 3.5 t/ha), with intermediate losses for M. Huntsman and Soissons. Growers are concerned more with absolute yield levels under drought than comparative performances. In absolute terms averaged across the three seasons, Rialto yielded 0.14 t/ha (2%) better than Haven and 0.47 t/ha (7%) better than Riband under drought. These three varieties have been competitors in the feed wheat market in recent years and according to the RL (NIAB, 1996a) the fungicide-treated yield performance for Rialto and Haven was the same with these two genotypes performing better than Riband by 2%. Thus, present findings would indicate that Rialto performed better than its average on the RL under drought and Riband worse. In relative terms, Mercia performed better in unirrigated crops than with irrigation over the three test years. It was outyielded by Rialto by 11% in these experiments compared with 15% according to the RL (NIAB, 1996a). But Mercia was still lower yielding than Rialto with drought by 0.79 t/ha in the present study, and thus could not be designated a drought resistant variety solely on the basis of its grain dry mass production. A further examination of drought effects on grain quality characteristics for Mercia would be necessary to show an economic advantage for Mercia. This grain quality analysis was not undertaken in the present study.

The above conclusions relate to overall effects averaged across the three seasons. With regard to the individual seasons, there was late drought in 93-4 and earlier onset of drought in early May in 94-5 and mid-May in 95-6. The late drought in 93-4 may be more representative of the types of droughts most commonly incurred by the majority of UK growers on soil types with AWC in the order of 175 – 225 mm (Foulkes *et al.*, 1993). In 93-4 where yield was reduced on average by 1.83 t/ha, yield was 9.82 t/ha for Haven, 9.54 t/ha for Rialto and 8.71 t/ha for Riband. This order of difference between Rialto and Haven or Riband would not be indicated by their RL performance in recent NIAB Cereal Variety Handbooks.

In general, in the two seasons with early onset of drought, there was a levelling up of performance in unirrigated conditions compared with differences observed under irrigation. In these early-drought seasons, Haven no longer outperformed Riband as it did under late drought but yielded comparably, 0.1 t/ha less in 94-5 and the same in 95-6. Rialto, however, maintained its drought resistance observed in 93-4, outperforming both Riband and Haven in each season by *c.* 0.30 t/ha. When growers select varieties, the timing of any future drought will not be known. Thus, a drought resistant variety must, in practice, be resistant to both early and late onset of droughts. On current evidence, this seems to exclude Haven from categorisation as a drought resistant variety, because it performed no better than other varieties in early drought years. However, evidence suggested that Rialto may possess the desirable combination of physiological traits for resistance to both early and late drought. The Haven type may nevertheless be of some use to growers on medium-to-heavy soil types, who may infrequently encounter early droughts but more often suffer water stress late in the season. If climate change is leading to an increased frequency of dryer seasons, it may be beneficial for UK farmers to select a variety with some capacity for maintaining grain filling and buffering the effects of late-season drought even if they are not on particularly drought-susceptible soil types. Of course, growers on lighter land would be the group to potentially benefit most from current research, by growing types resistant to both early and late onset of drought, such as Rialto.

M. Huntsman, the older tall, non-dwarf variety, widely grown in the early-to-mid 1970s, showed no evidence for drought resistance in any of the three test seasons. This seems to run counter to some of the 'folklore' current at the outset of the Project, suggesting older taller, non-semi-dwarf types were more drought resistant than modern shorter, semi-dwarfs. M. Huntsman was lowest yielding overall in both irrigated and unirrigated conditions. As a percentage of the mean of all varieties, its yield was 93% (irrigated) and 90% (unirrigated). Soissons, the rapid developing, French-bred variety, which is photoperiod insensitive (Worland *et al.*, 1994), showed no strong evidence either for drought susceptibility or resistance. As a percentage of the mean of all varieties, it yielded 96% irrigated and 97% unirrigated with an overall yield reduction of 2.96 t/ha similar to the average for all varieties. This suggested that early flowering of itself was not sufficient to confer drought resistance to the types of droughts encountered in the temperate UK climate.

4.2. The relationship between physiological traits and yield performance

4.2.1. Development rate

Developmental stages are potentially useful traits for variety testers to work with because they are relatively easy to measure and show a high degree of consistency from site to site (Kirby, 1994). At the outset of Project work, no developmental stages were recorded routinely in UK RL winter wheat trials, other than ripening date. The original hypothesis was that varieties with earlier flowering dates would be more drought resistant due to conservation of water in the vegetative phase of growth up to flowering which could be more profitably used during grain filling in late drought environments.

Varietal differences were consistently expressed in the three seasons. The earliest varieties to onset of stem extension (GS 31) were Soissons and Rialto, followed, in sequence, by Mercia, Riband, M. Huntsman and Haven. This order was broadly maintained through subsequent developmental stages, the only significant change being that Rialto moved from earliest at GS 31 to mid-to-late within the varietal range at GS 39 and later stages. Rialto consequently had a longer period from GS 31 to GS 39. Rapid development for the French-bred Soissons is associated with the *Ppd1* gene (Worland *et al.*, 1994) conferring photoperiod insensitivity and an ability to flower in shorter daylengths. Mercia's earliness is associated with a lower vernalization requirement than other varieties tested and a slightly weaker photoperiod sensitivity than the other four UK varieties examined here (Worland *et al.*, 1994). Across the three seasons, effects of drought on development were neglible, with the exception of date of complete canopy senescence and harvest, which were delayed by *c.* 7 d with irrigation for all varieties.

The two earliest varieties, Soissons and Mercia, generally had lowest maximum shoot numbers. Conversely, Haven, the latest variety, had the greatest maximum shoot number. Soissons and Mercia exhibited low tiller production with high tiller survival, whereas other varieties tillered more profusely but had poorer tiller survival. Irrigation/variety interactions for shoot numbers were only transitory if present in all three seasons. When they did occur, they did not translate into large effects on dry mass growth at GS 61 and later grain filling. The evidence was that earlier phasing of tiller survival, broadly GS 31 to GS 39, did not lead to relatively more ears at harvest under drought. Indeed, there were indications that slower developing varieties aborted tillers at a relatively earlier stage in their development terms and this may have limited resources wasted in tillers destined to die (Thorne, 1982).

For green canopy area at GS 31, consistently greater GAI for the slower developing varieties (Haven and Maris Huntsman) was observed compared to earlier types (Soissons and Mercia). This was explained by their greater duration for crop growth up until this developmental stage. Maximum green area was not, however, strongly correlated with developmental rate; effects of partitioning and tiller survival also acted to affect canopy area production. In contrast, canopy persistence during grain fill did appear, at least at the varietal extremes, to be correlated with developmental rate. Persistence was consistently poorer for the late developing Haven and better for the early developing Soissons compared to other varieties. It follows that the period from GS 61 to complete canopy senescence was normally about 7-8 d longer for Soissons than Haven both with and without drought, with intermediate durations for other varieties, e.g. M. Huntsman and Rialto.

Varietal differences in development rate up to GS 39 largely accounted for observed differences in dry mass at this stage, those with more rapid development having smaller biomass. There were also consistently expressed varietal differences in total crop dry mass at harvest. Harvest dry mass was greater ($P < 0.05$) for Rialto compared with all other varieties, both with and without irrigation, and particularly compared with Mercia. Rialto with an early date for GS 31 but an intermediate-to-late date for GS 61 had a longer lifecycle. It thus had more calendar days to intercept radiation than other varieties.

In terms of water use, the more rapid developing varieties with less days from mid-April to GS 61 used less water during this period under drought. Thus, Soissons and Mercia used *c.* 20 - 25 mm less water up to flowering than Rialto, Riband and Haven. Differences in water use post-flowering during the grain filling period were relatively smaller than differences up to flowering. For example, Rialto which used 27 mm more water than Soissons up to GS 61 under drought only used 5 mm less during grain filling. The original hypothesis stated that earlier flowering varieties would be more drought resistant than later types because they used less water in the vegetative phase, and, under conditions of terminal post-anthesis drought, would conserve limited water for more profitable use during grain filling. Experiments in Australia have shown faster developing varieties to have improved yield through drought escape (Richards, 1987). In the current Project, with the exception of Haven (latest flowering variety), increases in post-flowering water use for early flowering varieties were only marginal compared to later genotypes. Additionally, it is likely that a proportion of the additional water use up to GS 61 for the slower types could contribute to the formation of soluble stem carbohydrate reserves. In summary, for the UK environment, results suggested that early flowering only marginally improved later water uptake during grain filling over varieties of intermediate flowering date. Total water uptake was greater for the later flowering varieties, probably associated with greater below-ground investment in roots in the longer period up to GS 61. However, the extreme late flowering type, as exemplified by Haven, did appear to show meaningfully reduced uptake during grain filling in early drought seasons compared to both early and intermediate flowering types.

In summary, the evidence was that early flowering was only marginally advantageous for drought resistance compared to intermediate flowering date types, but that extreme late flowering could be detrimental with early drought. Results suggested that flowering date should still be included as one of the indicative traits defining varietal ability to perform under drought, but perhaps at a lower order of priority than originally envisaged at the outset of the current work. Protocols have been written for recording date of GS 61 in NIAB RL winter wheat trials and tested for their feasibility by variety testers in NIAB RL trials in 94-5 and 95-6 as a part of the current Project (see Vol. V, Part 2). Present results suggested that it would be worth adding the date of GS 61 permanently to the list agronomic characters routinely recorded by variety testers in the UK winter wheat RL trials series as an indicator of susceptibility to late season stress.

4.2.2. Leafiness: green canopy area production

The original hypothesis was that normal investment in leaves may be excessive in late drought situations, and that restricted maximum canopy green area may confer drought resistance by conserving water during the vegetative phase of growth for later grain filling. This assumed that there would be meaningful varietal differences for maximum green area amongst currently grown varieties; and that these differences would be accentuated, in terms of water uptake, at GAI < *c*. 3, since there is a positive linear relationship between the fraction of potential evapotranspiration actually transpired by the crop and GAI at GAI 0 – 3 (Kristensen, 1974).

In the irrigated crop, GAI was generally maximal at *c*. 5. Averaged across 93-4 and 94-5, the varietal range was 4.2 - 5.3 (irrigated) and 3.3 - 4.8 (unirrigated). With irrigation, M. Huntsman (5.3) and Mercia (5.0) had largest areas, followed by Soissons (4.8), Haven (4.7), Riband (4.7) and Rialto (4.2). Whereas variety effects were highly significant ($P< 0.001$), the interaction was not; and the variety ranking order was broadly the same with and without drought. Varietal water use mid-April - GS 61 did not correlate strongly with varietal differences in maximum green area. Under drought, uptake to GS 61 was greatest for Rialto (247 mm) and least for Soissons (224 mm), with intermediate uptakes for Riband, Haven, M. Huntsman and Haven. Clearly, with Rialto (greatest pre-GS 61 water use) having smallest maximum green area, there was no obvious relationship such that restricted 'leafiness' was associated with reduced water use during vegetative growth. Presumably varietal differences for extinction coefficient, rooting characteristics, duration of the phase of canopy expansion and possibly also photosynthetic efficiency will have combined to interact with maximum canopy green area in ultimately determining water uptake for the varieties currently examined.

In summary, the varietal differences in maximum green area detected were relatively small, in the order of 1.0 GAI units at the extremes, and not well correlated with water use in the pre-flowering period. It therefore seems that the original hypothesis should be revised and other physiological traits and processes associated with leafiness perhaps examined more closely. Rialto, the variety with the smallest green area, showed consistently good yield performance under drought. Conversely, M. Huntsman with the largest maximum green area showed consistently poor drought performance. These effects perhaps owed more to an increase in the fraction of total assimilate partitioned to stems associated with restricted leafiness than conservation of water use *per se*. For example, varieties with smallest canopies might be those tending to partition more assimilate to stem reserves. In Australia, where droughts are more severe than those experienced in the UK and wheat is grown largely on stored water, maximum GAI may be in the order of only 3 and yields as low as 3 - 4 t/ha. In this environment restricted leafiness has been associated with improved drought performance (Islam & Sedgely, 1981). Present results indicate the original hypothesis stated at the outset of the Project may have more relevance for guiding growers in these more extreme environmental conditions than in the UK temperate climate in their choice of varieties

In summary, it seems that maximum canopy area may not be a trait for current prioritisation by variety testers. There is also the consideration that it is relatively time consuming to measure and it may not be feasible to characterise large numbers of variety in testers' plots cost effectively. To record maximum green area accurately involves the use of a leaf area meter and sampling plant material within quadrats. Quicker, in-field assessment methods have been developed for estimating GAI, involving counting shoot numbers in defined row lengths, numbers of leaves per main stem and associated leaf lengths and widths (HGCA, 1998a; Project Report 151), but these methods are not currently variety specific. On the basis of the relationship between canopy size and water uptake pre-flowering, the current recommendation to UK testers would be that maximum GAI should not be prioritised for recording in UK RL trials with regard to predicting drought resistance.

4.2.3. Maximum rooting depth

The hypothesis under test was that varieties with greater maximum rooting depth perform relatively better under drought due to accessing a larger amount of soil water. In the current Project, root dry mass, root length per unit volume and maximum rooting depth were not measured directly. Root activity was, however, assessed indirectly from estimates of water uptake within the profile to 1.65 m depth throughout the season. Soil water profiles in unirrigated conditions are considered chiefly here, due to problems associated with unaccounted for direct evaporation of intercepted irrigation water from the canopy surface in irrigated plots (see 3.7.2). In all three years in the unirrigated crop, varietal differences detected in total water use generally related to greater extraction uniformly within the profile to *c.* 1.2 m rather than greater maximum rooting depth. Thus, Rialto with greatest uptake showed a trend for greater uptake at all depths to *c.* 1.2 m, but no trend for greater maximum rooting depth as would be indicated by greater uptake from 1.2 to 1.6 m. Since crown root proliferation largely occurs from GS 31 to GS 61 (Barraclough

& Leigh, 1984), the developmental pattern of Rialto, with an extended phase from GS 31 to GS 61, appeared to fit with greater acquisition of water compared to other genotypes. The earlier phasing of the GS 31 – GS 61 period for Soissons, similarly, appeared to be consistent with its lower water uptake. In summary, amongst the six varieties examined, there was no evidence for differences in maximum rooting depth. Differences in uptake between varieties thus generally related to greater uptake per unit soil volume at equivalent depths within the profile to c. 1.2 m rather than deeper maximum rooting depth.

Only six varieties were examined in the present experiments and there is a danger in deriving conclusions from these results and then applying them to the whole range of wheat varieties cultivated in the UK. It may be that other varieties not investigated would have shown greater differences. Present results were associated with large standard errors and differences were not statistically significant. In future experiments, replication would ideally be increased above the two replicates of the current exercise. In summary, the preliminary conclusion is that maximum rooting depth should not be a trait prioritised for routine incorporation in NIAB RL winter wheat trials. Direct measurement of maximum rooting depth would be impractical with regard to rapidity and labour costs. Indirect methods, e.g. radiometry techniques measuring canopy temperature, have been proposed and tested in Australia and Mexico (Clarke & McCraig, 1982), but as yet these methodologies are untested in UK conditions and it is not certain that they would be precise enough to detect the marginal differences suggested in the present data set. It is thus concluded that maximum rooting depth should not be prioritised as trait indicative of UK drought performance at the present time.

4.2.4. Water use efficiency

The original hypothesis proposed that varieties with greater water use efficiency would be more efficient types under drought, in that dry mass production would be proportionately greater per unit water transpired in drought conditions; and, assuming harvest index is conserved, proportionately greater grain yield would result. The hypothesis assumed that there were meaningful varietal differences amongst current UK-grown genotypes, and that expression of differences was independent of expression for other physiological traits: for example, that greater water use efficiency was not simply a consequence of shallower rooting depth leading to equivalent dry mass production from a decreased water uptake.

Averaged across the two seasons, 93-4 and 94-5, water use efficiency was 1.61 g/m^2/mm greater in the unirrigated crop (5.71 g/m^2/mm) than with irrigation (4.10 g/m^2/mm) ($P<$ 0.05). Part of this difference may have been due to direct evaporation of irrigation water intercepted by the canopy in the irrigated crop, the extent of which was not quantified in the experiments. For this reason, efficiencies under drought are principally considered here. Overall, averaged across the two seasons, the varietal range under drought was 5.52 - 6.21 g/m^2/mm, but the variety effect was not significant (P=0.62). With the exception of M. Huntsman, varieties fell within a narrow range of 5.46 - 5.68 g/m^2/mm. The overall range was 4.89 - 5.62 in 93-4 and 5.75 - 6.31 in 94-5. Although, M. Huntsman did show a tendency for greater efficiency in both seasons, this was associated with lower water uptake rather than more efficient dry mass production from equivalent water uptake. The lower uptake for M. Huntsman in 93-4 was associated with slightly less water in the profile at the beginning of measurements in April and May. This effect was largely dependent on the measured uptake in just one plot and may, to some extent, have been a consequence of the low level of replication for soil water assessments in two replicates. In general, with the exception of this trend for M. Huntsman, there was little evidence to support differences for water use efficiency amongst currently grown UK varieties. This would be in agreement with most of the previous literature, which points to a general paucity of evidence for intra-species differences for water use efficiency, e.g. Richards (1987).

Only six varieties were examined in the present study and it may be that other varieties not investigated would have shown up greater differences. Nevertheless, on the basis of these results, it is concluded that water use efficiency was not a physiological trait likely to affect performance with drought for currently commercial varieties in the UK environment. It follows that this trait should not be prioritised for routine assessment in NIAB RL trials. It may be worth, however, recording efficiencies over a wider range of genotypes in future experiments in order to corroborate the lack of effects currently detected. This could possibly be done by utilising the method of ^{13}C isotope discrimination described by Farquhar & Richards (1984), where an inverse linear relationship between ^{13}C discrimination and water use efficiency was found. If in further experiments varietal differences were in fact detected, then this methodology could potentially be introduced into the RL trials system with the necessary rapidity to deal with large numbers of field plots. On the basis of present results, however, the preliminary conclusion would be that water use efficiency should not be prioritised as an indicative physiological trait for drought resistance in winter wheat UK RL trials.

4.2.5. Stem reserves

During stem extension, leaf, stem and ear tissues are in direct competition for available carbohydrate assimilate. During the latter stages of stem extension, from GS 37 onwards, the demand for assimilate from the non-soluble, structural stem tissues (mainly lignin, cellulose and hemi-cellulose) and leaf tissues decreases rapidly, and proportionately more is available for partitioning to the pool of soluble carbohydrate around the developing ear in the upper internodes of the plant. Percentage soluble carbohydrate of stems and leaf sheaths is maximal at about 30 - 35% (HGCA, 1998b) at around nine days after GS 61 (Austin *et al.*, 1977), with soluble carbohydrate in excess of about 5% of dry weight being stored as fructan (Schnyder, 1993). As the green canopy senesces and the source of assimilate declines, the mobilization of stem and leaf sheath soluble carbohydrate maintains the translocation of assimilate to the grain. This process generally starts at about the mid-to-late grain fill stage. Redistribution of dry matter, however, may be induced at an earlier stage by factors contributing to accelerated senescence, such as drought. Accumulation and depletion of reserves is reflected in changes in stem dry mass after anthesis, reduction in dry mass helping to maintain a constant rate of grain growth during grain filling. The original hypothesis at the outset of the Project proposed that there were meaningful varietal differences in the ability to amass and relocate stem reserves and that these differences related to differential ability to tolerate the effects of premature canopy senescence due to late-season drought.

In the seasons where the methodology was most precise and comparable, 93-4 and 94-5, there were varietal differences for assessments at the end of flowering ($P < 0.001$). The overall range with irrigation was 2.31 - 3.48 t/ha and without irrigation 2.24 - 2.89

t/ha. The varietal ranking order was consistent between seasons and irrigation treatment levels. Overall, Haven and Rialto amassed greatest reserves at 3.18 and 3.00 t/ha, respectively, followed in order by Soissons (2.49 t/ha), Riband (2.43 t/ha), M. Huntsman (2.36 t/ha) and Mercia (2.28 t/ha). In 95-6, where stem dry mass was estimated on the basis of ten shoots per plot rather than full quadrat growth analysis, the same broad varietal differences were detected (P=0.12). Late drought had no effect on stem reserves in 93-4, but early drought in the two following seasons resulted in a trend for reduced amounts under drought by *c.* 0.30 t/ha in each season. The irrigation/variety interaction was non-significant in all seasons. In summary, meaningful and consistent varietal differences were detected in all experiments. Rialto and Haven were the varieties consistently with greatest reserves, Mercia and M. Huntsman the lowest, and intermediate amounts for Soissons and Riband. At harvest, amounts of stem reserves remaining were invariably very small. The varietal range averaged across irrigation treatments and seasons was 0.08 - 0.13 t/ha. These differences indicated that drought tolerance for this trait related predominantly to maximum amounts of reserves accumulated rather than the difference between the maximum amount and the residue at harvest.

There was a good correlation between varietal differences in soluble stem carbohydrate and differences in performance with drought in the three seasons. In 93-4, when amounts accumulated in the unirrigated crop were largest, yield of Rialto and Haven (> Riband by *c.* 1 t/ha) corresponded to their greater accumulation of reserves. Furthermore, the poor performance of M. Huntsman under drought in this season was associated with low reserves. In the early drought years of 94-5 and 95-6, Rialto performed best under drought and had highest stem reserves. The large reserves of Haven in these seasons, however, did not translate into greater unirrigated yield compared to other genotypes. The accelerated canopy senescence for Haven compared to other varieties with early drought apparently counteracted any advantage gained from greater stem reserves in these seasons. Rialto with better canopy persistence than Haven may have been better adapted to exploit larger reserves in seasons with early drought. There was also some evidence that Rialto maintained its ability to amass stem reserves relatively better than Haven in early drought seasons. The poor performance of Riband compared to Rialto and Haven overall with drought was associated with its consistently lower reserves.

Up to about 25% of soluble carbohydrate accumulated may be lost in respiratory processes, either due to maintenance respiration or respiratory losses incurred in the transport of soluble carbohydrate to the grain (Stoy, 1966). The percentage lost to respiration was not quantified in the present study. Therefore, it could be argued that, even though there was a good correlation between varietal stem reserves and unirrigated yield, it was not definitively proved that reserves contributed directly to these yields. There was strong evidence in the data, however, to support the contention that stem reserves were actually remobilized in response to drought and actively contributing to grain filling. In both 93-4 and 94-5, loss of stem dry mass after GS 61 occurred earlier under drought than it did in the irrigated crop (Fig. 3.7). Between GS 39+550°Cd (c. GS 61+ 14 d) and GS 39+750°Cd (c. GS 61 + 28d), stem dry mass loss was in the region of 1 t/ha with irrigation but 2.0 t/ha with drought. This strongly implied that reserve buffering was phased earlier where rates of senescence were greater. Also, in these seasons, ear dry mass growth was broadly comparable in both irrigated and unirrigated conditions up until about four weeks after GS 61, and it is improbable that this would have been the case if all grain filling up to this stage had been from current photosynthesis.

In summary, the original hypothesis was strongly supported by evidence in present experiments. Varietal differences were large, over 1 t/ha, and consistently expressed and well correlated with unirrigated yield. The varietal ranking order and respective differences were corroborated by the results from parallel Project Typing Trials (see section Vol. V, Part 1). It is therefore proposed that this physiological trait is worthy of continued further attention by variety testers. Stem reserves can be measured relatively easily by sampling about ten shoots per plot, drying them at 100°C for two hours, and then submitting dried stems for chemical analysis at a convenient date. It is concluded that it would be advantageous to add measurement of stem water soluble carbohydrate at GS 61+75°Cd to the agronomic characters presently recorded in the winter wheat RL. A protocol for assessing stem reserves has been written and tested for its feasibility within the current Project and was used by variety testers on a trial basis at three NIAB regional centres in 1995-6 (see Vol. V, Part 2). The varietal range and ranking order detected for stem reserves in these NIAB trials corroborated differences reported in present experiments. Stem reserves has subsequently be measured at these same three NIAB sites in 1996-7 and this information made available to growers in the Cereal Variety Handbook. These assessments were again undertaken by NIAB testers in 1997-8, and information will be made available in future Cereal Variety Handbooks. It is interesting to note that there were very little reserves remaining at harvest in irrigated crops as well as in unirrigated crops. This implied that reserves may be utilised to maximise yield performance even in optimal grain filling conditions without significant late-season stress. If this were the case, a correlation between yield potential of varieties and their ability to accumulate stem reserves would be expected. Such a relationship was detected in parallel Project Variety Typing Trials (see relevant discussion, Vol. V, Part 1).

4.3 Changes in prioritisation of candidate physiological traits since the outset of the Project

At the outset of the Project, an attempt was made to prioritise candidate traits (Foulkes *et al.*, 1993). A sensitivity analysis indicated that potential grain yield in late-drought seasons was little affected by variation in water use efficiency and stem carbohydrate reserves, moderately affected by variation in rooting depth and anthesis date, but much affected by variation in leafiness. Although this sensitivity analysis related exclusively to responses to late-season drought, and in two of the three years at Gleadthorpe onset of drought occurred in May before anthesis, current results would suggest that this initial prioritisation of traits should be revised.

Stem reserves were found to vary significantly amongst varieties in the range 2.0 to 3.5 t/ha and to be strongly correlated with yield under late-season drought in 93-4. In the sensitivity analysis (Foulkes *et al.*, 1993), stem reserves were set to vary within a narrower range of only 15 - 25% stem dry mass broadly equivalent to 1.5 to 2.5 t/ha. Thus, the observed varietal range for stem reserves was approximately 50% greater than that predicted at the outset of the Project, and consequently this trait now assumes greater importance. Indeed of the all traits examined, it was the one most strongly correlated with yield.

Leafiness was predicted to exert most influence on drought resistance with respect to late season drought. Our experimental evidence did not bear this out. The range in maximum GAI under drought was relatively small (*c.* 1.0 GAI units compared with the range in the model of *c.* 2.0 GAI units). It was assumed in the model that conservation of water through restricted leafiness and generation of less biomass up to flowering would have no consequences for rooting depth or density. Experimental evidence suggested that this was probably not a correct assumption and where biomass was reduced at anthesis, for example for the early-developing Soissons, slightly poorer total seasonal water extraction was observed. Thus the assumption that variation in leafiness and rooting depth were independent was probably invalid. Experimental evidence did indicate, however, that at the varietal extremes lower maximum GAI was associated with better drought performance; but this was accounted for more by an association between reduced leafiness and greater partitioning to stem reserves than conservation of water use *per se*. Thus, the influence of leafiness on drought performance is predicted to be less now than at the outset of the Project. Restricted leafiness would, nevertheless, still be included, at a lower order of priority and for slightly different reasons to that originally postulated, as an element of the varietal ideotype best suited to maintain performance under drought.

Predictions in relation to the prioritisation of the other traits (water use efficiency, rooting depth and flowering date; Foulkes *et al.*, 1993) were broadly in line with their observed associations with yield performance under drought in the experiments over the three test seasons. That is, variation in flowering date was shown to have a greater influence on varietal responses to drought than either rooting depth or water use efficiency.

4.4 Problems of examining effects of physiological traits within confounded varietal backgrounds

The associations described between traits and performance in this Sub-Project were detected using a range of different varieties, having high or low expression for the target trait, but otherwise having very different genetic backgrounds. Effects of trait expression on yield formation will depend on interactions between the trait and the whole range of other background traits. Therefore there is an inherent danger in drawing conclusions about effects of traits on drought performance based on evidence from a limited number of genotypes, as the effects of the individual traits may be unduly affected by the particular varietal backgrounds in which they happen to occur. It could be argued that the value of a trait cannot be proved definitively by interaction experiments examining with relatively few varieties. In order to overcome this potential criticism and to prove more definitely the value of a target trait, a number of follow-up strategies are possible.

Firstly, isogenic lines could be produced for target characteristics in well adapted material, using modern parents. This technique would only be possible for traits under the control of one or else a small number of major genes. Examining performance of these isogenic lines (differing only in expression of a single gene controlling the trait examined) across different environments could be used to more precisely quantify the effect of a trait. A second and broadly similar approach could be to produce near homozygous F_6 lines contrasting for the trait in question (by single seed descent in a relatively few years) and to test these lines across a range of different environments.

The third method that could be adopted to overcome the effect of confounding in varietal backgrounds would be to test a very large number of varieties, say 30-40, for trait expression and grain yield performance across different environments. In such experiments, it is likely that interactions between the target traits and other traits would broadly cancel each other out when averaged across all varieties and that correlations between trait expression and yield response to environmental treatments would thus be reasonably robust and meaningful.

4.5 Conclusions and future work

- Over the three test seasons, there was a significant irrigation/variety interaction for grain yield. Rialto and Mercia lost relatively less grain yield under drought (*c.* 2.7 t/ha) compared with Haven and Riband (*c.* 3.5 t/ha). In terms of absolute yield under drought, Rialto overall yielded 0.14 t/ha better than Haven and 0.47 t/ha better than Riband.

- In 93-4 with late drought, yield was reduced on average by 1.83 t/ha, and Haven (9.82 t/ha) and Rialto (9.54 t/ha) showed drought resistance compared to Riband (8.71 t/ha). In 94-5 and 95-6 with early onset of pre-flowering drought, where yield was reduced by 3.06 and 4.55 t/ha, respectively, Haven no longer outperformed Riband but yielded comparably. Rialto, however, maintained its drought resistance, outperforming both Riband and Haven in each season by *c.* 0.30 t/ha.

- Maris Huntsman, the older tall, non-dwarf variety, widely grown in the early-to-mid 1970s, showed no evidence for drought resistance in any of the three test seasons. Indeed, its yield performance indicated it to be marginally drought susceptible compared to the average performance of the other varieties. Soissons, the rapid developing, French-bred variety, showed no consistent evidence either for drought susceptibility or resistance.

- Earlier phasing of the tiller survival phase (GS 31 to GS 39) did not lead to relatively better maintenance of ears at harvest under early drought. Indeed, there was some evidence to suggest that slower developing varieties aborted tillers at a relatively earlier developmental stage and this may have restricted dry mass lost in aborted tillers for these genotypes.

- For GAI production and crop dry mass growth, at respective developmental stages, variety differences were nearly always highly significant ($P < 0.01$), but the irrigation/variety interaction was usually not.

- Varietal differences in maximum green area were relatively small, in the order of c. 1.25 units at the extremes, and were not well correlated with water use in the pre-flowering period. The original hypothesis that normal investment in leaves may be excessive in UK drought situations, and that restricted maximum canopy area could conserve water for grain filling with late drought, was not supported by current results.

- There were consistent varietal differences in total crop dry mass at harvest in the range 1228 to 1374 g/m^2 unirrigated and 1620 - 1721 g/m^2 irrigated. Harvest dry mass was greater ($P< 0.05$) for Rialto compared to all other varieties, both with and without irrigation, and particularly compared to Mercia. The greater dry mass for Rialto was, in part, explained by its higher radiation use efficiency than other varieties.

- There was little evidence to support differences for water use efficiency amongst the six varieties examined.

- Averaged across seasons, Rialto and Haven amassed greatest stem reserves at 3.00 and 3.18 t/ha, respectively, followed by Soissons (2.49 t/ha), Riband (2.43 t/ha), M. Huntsman (2.36 t/ha) and Mercia (2.28 t/ha). With early drought, amounts overall were *c.* 0.3 t/ha less with drought but the varietal ranking order remained unaffected compared to irrigated controls. There was a strong correlation between varietal ability to amass stem reserves differences and performance under drought.

- In summary, the consistent drought resistance of Rialto appeared to be associated with a greater capacity for growth *per se* than other varieties at respective growth stages coupled with an ability to partition relatively more of this growth into stem soluble carbohydrate reserves. The greater growth was due to both high radiation use efficiency (dry mass g/MJ) and more calendar days for growth (largely due to an extended period from GS 31 to GS 61 compared to other varieties). Greater growth during GS31 to GS 61 was also associated with a greater capacity for seasonal water uptake, possibly linked with the development of a more extensive rooting system compared to other varieties. It appears this ideotype may provide a combination of physiological traits desirable for resistance to both early (onset pre-flowering) and late UK droughts.

- Drought resistance for Haven with late drought was associated with high stem reserves. Its drought resistance was not maintained in response to earlier onset of drought; this was associated with poorer maintenance of stem growth, stem reserves, total seasonal water uptake and harvest dry mass under these conditions compared to other varieties. The reasons for this response are still being investigated, but appear to relate to a particularly acute susceptibility to water stress during late stem extension manifested in a large reduction in stem dry mass during this period compared to other genotypes.

- Future work could concentrate on examining effects of traits in the absence of confounding effects of the different varietal backgrounds (see 4.4 above). This could be done by working with very large numbers of varieties, say 30-40, and characterising trait expression and grain yield performance across different irrigation treatments. An alternative approach might be to develop isogenic lines for genes controlling target traits in well adapted material and to examine trait expression and yield performance of these lines over a range of environments contrasting for their extent of drought.

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Appendix table 1 - Meterological data

ADAS Gleadthorpe

Monthly mean air temperature (°C)

	1993-4	1994-5	1995-6	Long-term mean 1952-94
Sep	9.9	12.3	13.6	12.9
Oct	8.0	9.4	12.5	9.8
Nov	1.0	8.9	7.7	6.0
Dec	2.4	5.8	1.9	4.1
Jan	4.7	4.2	3.6	3.1
Feb	2.2	6.1	2.6	3.2
Mar	7.6	5.4	3.8	5.4
Apr	8.3	8.7	7.9	7.6
May	10.2	11.1	8.8	10.7
Jun	14.6	13.7	13.5	13.6
Jul	17.6	18.6	16.2	15.5
Aug	15.5	17.7	-	15.2

Rainfall (mm)

	1993-4	1994-5	1995-6	Long-term mean 1953-95
Sep	110.3	140.8	76.7	56.0
Oct	72.1	46.2	24.5	52.8
Nov	50.3	61.9	66.0	56.0
Dec	95.0	78.6	63.9	57.5
Jan	54.9	97.3	33.0	54.6
Feb	53.1	55.7	52.9	42.5
Mar	45.1	35.6	26.4	47.0
Apr	35.9	18.2	37.6	46.6
May	66.3	56.3	27.7	50.8
Jun	8.8	15.2	25.0	55.7
Jul	45.0	9.3	14.5	51.6
Aug	62.6	4.7	50.0	53.4

Radiation ($MJ/m^2/day$)

	1993-4	1994-5	1995-6	Long-term mean 1953-95
Sep	n/a	n/a	n/a	n/a
Oct	n/a	n/a	n/a	n/a
Nov	n/a	n/a	n/a	n/a
Dec	n/a	1.83	n/a	n/a
Jan	n/a	2.09	n/a	n/a
Feb	n/a	4.35	n/a	n/a
Mar	12.28	9.20	n/a	n/a
Apr	11.60	12.63	10.93	n/a
May	12.68	15.27	13.95	n/a
Jun	16.31	15.07	17.68	n/a
Jul	17.06	20.10	17.84	n/a
Aug	14.81	18.29	n/a	n/a

Appendix table 2 - Site details

a) ***ADAS Gleadthorpe 1993-4***

Soil series		Cuckney
Soil texture		Loamy medium sand over medium sand
Soil analysis	pH	7.8
	P index	3 (43 mg/l)
	K index	2 (167 mg/l)
	Mg index	2 (100 mg/l)
	Organic matter (%)	1.6
Sowing date		3 November 1993
Emergence date		3 December 1993
Seed rate	Haven	150 kg/ha
	M. Huntsman	164 kg/ha
	Mercia	124 kg/ha
	Rialto	146 kg/ha
	Riband	160 kg/ha
	Soissons	136 kg/ha
Drainage		Good
Previous crop	1993	Maincrop potatoes
	1992	Onions
	1991	Peas
Cultivations	1 November	Chisel ploughed, ploughed and furrow-pressed
Fertilizer	10 February	76 kg/ha K (as muriate of potash)
	11 March	40 kg/ha N (as ammonium nitrate prill)
	22-23 April	130 kg/ha N (as ammonium nitrate prill)
Herbicide	3 November	Prebane 500 SC 3 l/ha
Fungicide	30 April	Sportak 45 0.9 l/ha
	30 April	Tern 750 EC 0.75 l/ha
	1 June	Folicur 1 l/ha
	23 June	Folicur 1 l/ha
Pesticide	24 January	Dursban 4 1.5 l/ha
	30 June	Aphox 0.28 kg/ha
Growth regulator	18 April	New 5C Cyclocel 1.75 l/ha
	30 April	New 5C Cyclocel 0.75 l/ha
Trace elements	11 April	7 kg/ha $MnSO_4$
Harvest date	Unirrigated plots	9 August
	Irrigated plots	13 August

b) *ADAS Gleadthorpe 1994-5*

Soil series		Cuckney
Soil texture		Loamy medium sand over medium sand
Soil analysis	pH	6.7
	P index	4 (47 mg/l)
	K index	1 (92 mg/l)
	Mg index	3 (106 mg/l)
	Organic matter (%)	1.4
Sowing date		14 October 1994
Emergence date		28 October 1994
Seed rate	Haven	150 kg/ha
	M. Huntsman	164 kg/ha
	Mercia	124 kg/ha
	Rialto	146 kg/ha
	Riband	160 kg/ha
	Soissons	136 kg/ha
Drainage		Good
Previous crop	1994	Maincrop potatoes
	1993	Onions
	1992	Sugar beet
Cultivations	12 October	Chisel ploughed
	13 October	Ploughed and furrow-pressed
Fertilizer	25 February	76 kg/ha K (as muriate of potash)
	13 March	40 kg/ha N (as ammonium nitrate prill)
	25 April	80 kg/ha N (as ammonium nitrate prill)
	28 April	60 kg/ha N (as ammonium nitrate prill)
Herbicide	15 October	Prebane 500 SC 3 l/ha
	15 May	Starane 2 1 l/ha
Fungicide	28 April	Sportak 45 0.9 l/ha
	24 May	Tern 750 EC 0.75 l/ha
	15 June	Silvacur 1 l/ha
	15 June	Hinge 1 l/ha
Pesticide	30 November	Cyperkill 10 0.25 l/ha
	21 June	Aphox 0.28 kg/ha
Growth regulator	4 April	New 5C Cyclocel 1.7 l/ha
	14 April	New 5C Cyclocel 0.75 l/ha
Trace elements	11 April	7 kg/ha $MnSO_4$
Harvest date	Unirrigated plots	3 August
	Irrigated plots	8 August

c) *ADAS Gleadthorpe 1995-6*

Soil series		Cuckney
Soil texture		Loamy medium sand over medium sand
Soil analysis	pH	6.8
	P index	3 (38 mg/l)
	K index	0 (58 mg/l)
	Mg index	2 (94 mg/l)
	Organic matter (%)	1.59
Sowing date		9 October1995
Emergence date		19 October 1995
Seed rate	Haven	160 kg/ha
	M. Huntsman	181 kg/ha
	Mercia	140 kg/ha
	Rialto	150 kg/ha
	Riband	158 kg/ha
	Soissons	144 kg/ha
Drainage		Good
Previous crop	1995	Maincrop potatoes
	1994	Calabrese
	1993	Carrots
Cultivations	3 October	Chisel ploughed
	4 October	Ploughed and furrow-pressed
Fertilizer	19 February	70 kg/ha K (as muriate of potash)
	11 March	40 kg/ha N (as ammonium nitrate prill)
	16 April	138 kg/ha N (as ammonium nitrate prill)
Herbicide	11 October	Prebane 500 SC 3 l/ha
Fungicide	30 April	Sportak 45 0.9 l/ha
	30 April	Tern 750 EC 0.75 l/ha
	3 June	Folicur 750 E 1 l/ha
	26 June	Silvacur 1 l/ha
Pesticide	Nil	
Growth regulator	4 April	New 5C Cyclocel 1.7 l/ha
	14 April	New 5C Cyclocel 0.75 l/ha
Trace elements	9 April	6 kg/ha $MnSO_4$
Harvest date	Unirrigated plots	14 August
	Irrigated plots	19 August

EXPLOITATION OF VARIETIES FOR UK CEREAL PRODUCTION

(VOLUME II)

PART 2. VARIETAL RESPONSES TO ROTATIONAL POSITION
by

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Summary

This work examined the potential for identifying varietal physiological traits that may confer tolerance of take-all root loss in second or successive wheats. At the outset of the work, the prioritised varietal traits, hypothesised to confer relatively better performance in non-first wheat environments, were : i) high economy of tillering (low production of destined-to-die shoots, restricting water and radiation lost in aborted shoots), ii) earlier flowering date (escape of late-season stress) and iii) larger stem soluble carbohydrate reserves (yield buffering). In each of three seasons (1993-4, 1994-5 and 1995-6), an experiment was conducted at two sites, ADAS Boxworth (high take-all risk) and ADAS Boxworth (low take-all risk), with rotational position as the main plot treatment in a factorial split-plot design. In 1993-4 and 1994-5 there were two main plot treatments (first and second wheats) and in 1995-6 there were three (first, second and third wheats). Eight varieties (Brigadier, Cadenza, Lynx, Rialto, Riband, Soissons, Spark and Zentos), chosen to contrast for prioritised traits, were randomised within main plots. Boxworth experiments consistently showed low take-all levels. Although final disease levels were always higher at Rosemaund, none of the seasons could be classed as a high take-all season. At Rosemaund, rotational position differences for take-all were not significant in 1993-4. In 1994-5, however, non-first wheats had significantly more disease than first wheats (take-all index, 16.7 vs 10.2) and also in 1995-6 (take-all index 23.0 vs 9.9). At only three of the six site-seasons (Boxworth 93-4: 0.30 t/ha, Rosemaund 94-5 : 0.50 t/ha and Rosemaund 95-6 : 0.85 t/ha) was yield loss as a non-first wheat > 0.2 t/ha. Averaged across these site-seasons, there were trends for varieties to respond differently to rotational position. As a non-first wheat, Soissons lost on average only about 0.40 t/ha grain yield compared with Spark and Brigadier which lost about 0.75 t/ha. Rialto also performed consistently well as a non-first wheat in terms of its absolute yield performance. At the extremes of the varietal range for responses to rotational position, varietal traits correlated with observed yield responses. For example, there was a consistent relationship between economy of tillering, as measured in dry matter lost in aborted shoots, and relative variety performance. Performance of those varieties losing least dry matter (Soissons) and most dry matter (Brigadier) correlated with relatively better and worse maintenance of yield as a non-first wheat, respectively. With regard to flowering date, although Soissons (early flowering, 8 June) and Spark (late flowering, 20 June) performed relatively better and worse, respectively, as non-first wheats, overall flowering date did not consistently predict response to rotational position well. Of the varietal characteristics recorded, the amount of stem soluble carbohydrate reserves at the end of flowering had the greatest and most consistent effect on non-first wheat performance. The overall varietal range, averaged across rotational positions, was from 2.42 (Spark) to 3.38 (Rialto) t/ha, and variety ranking was consistent across site-seasons. It is concluded that the ability to accumulate soluble stem carbohydrate is an important component of the varietal type best suited to maintaining yield performance in conditions with high take-all root loss. In summary, the combination of desirable characteristics for tolerance of take-all root loss appeared to be high stem carbohydrate reserves, high economy of tillering and to a lesser extent early flowering. The varietal traits discussed above, however, are most probably not of equal importance. In this work, soluble carbohydrate reserves appeared to have had the largest influence on variety performance. The take-all results, expressed as an index accounting for both incidence and severity, consistently showed no effect of variety on take-all level. Thus, varietal resistance to the disease was not a factor in the currently reported work.

Contents

PART 2 : ROTATIONAL POSITION SUB-PROJECT

PART 2 : VARIETAL RESPONSES TO ROTATIONAL POSITION

1. INTRODUCTION

1.1. General

A significant proportion of the wheat grown in the UK is grown following another cereal crop. The exact proportion varies between seasons and is affected by changes in agricultural policy such as the introduction of set-aside. Over the period 1989 to 1996 non-first wheats have accounted for between 36 and 59 % of the UK crop; the proportion has been lower in the years 1994 and 1995 following the widespread introduction of set-aside (Table 1.1). Although the situation in terms of the proportion of the national wheat crop which is not first wheats appears to be improving, within those crops now classed as first wheats those following set-aside are included (Table 1.1, footnote). As a large proportion of set-aside is in the form of natural regeneration, which is not a complete take-all break (Jones *et al.*, 1996), a larger proportion than at first sight is still at risk of take-all infection.

Table 1.1 Occurrence of non-first wheats following another cereal crop. Source:- Winter wheat disease survey, R.W. Polley, unpublished data.

Number surveyed	*1989*	*1990*	*1991*	*1992*	*1993*	*1994*	*1995*	*1996*
First wheats	*108*	*123*	*200*	*190*	*182*	*217**	*207**	*204**
Non first wheats	*144*	*180*	*169*	*171*	*150*	*136*	*116*	*132*
% non first wheats	*57*	*59*	*46*	*47*	*45*	*39*	*36*	*39*
% crops with take-all symptoms	*33.7*	*32.2*	*25.9*	*28.4*	*37.4*	*17.5*	*22.2*	*13.0*

* includes wheat after set-aside; 1994 -30 crops, 1995 - 24 crops, 1996 - 29 crops

Non-first wheats are widely recognised as being lower yielding than first wheats. Nix (1995) assumes second wheats are 12.5% lower yielding than first, and that third wheats may be 10 to 15% lower yielding than seconds. The lower yield of non-first wheats is due to a number of factors, namely; lower fertility than following high residue break crops, increased stem base disease and increased take-all. The impact of the first two of these can to a large extent be minimised through careful crop husbandry, accurate accounting for mineral N residues in deciding on fertiliser N applications, and control of stem base disease through varietal resistance and early season fungicide application. The situation with take-all is however different: It has frequently been reported that varietal resistance to take-all can not be found, e.g. Hollins *et al.* (1986), and furthermore that the identification of resistance in wheat allowing breeding of resistant varieties is unlikely (Scott *et al.*, 1989). There are currently no really effective, commercially available means of chemical control of the disease. Other novel methods of control such as Biological Control Agents have proved unreliable. Currently, the most effective method of minimising the impact of the disease through husbandry is delaying drilling of the crop, which may also directly reduce the yield potential of the crop.

The importance of take-all in reducing the yield of non-first wheats can be seen in work done at ADAS Rosemaund in the 1982-3 to 1984-5 seasons where crops were grown in factorial combinations of early and late drilling over successive second and third wheat crops. In each season there was a significant relationship between take-all index measured during the winter and the yield of the crops. Over all three seasons a similar relationship was observed, an increase in take-all index of 10 (0 - 100 scale) reduced final crop yield by nearly 0.9 t/ha, the take-all index alone accounting for 82% of the variation in crop yield (Fig. 1.1). Vaiydanathan *et al.* (1987) reported that overall, in non-first wheat crops after discounting the effects of N, mean yield loss due to take-all was in the order of 1 t/ha. There is, however, a wide range in the yield loss due to take-all reported, the interpretation of which is not helped by the number of different methods of scoring the disease that are used (Table 1.2).

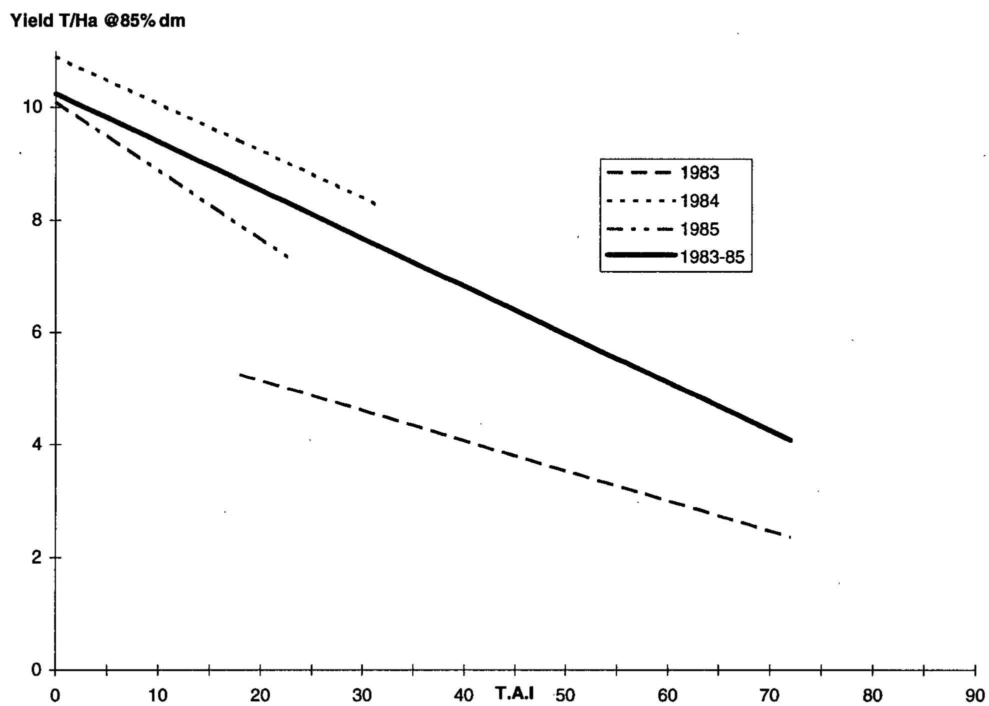

Figure 1.1 ADAS Rosemaund 1983-1985, Relationship between winter take-all index and final crop yield. 1983-85 yield = -0.0856(take-all index) + 10.2461 (r^2=0.8164, p=0.001)

Table 1.2. Measures of take-all severity and the yield loss caused from: Hornby and Bateman (1991)

Assessment method	Yield loss	Scale	Reported by
% plants infected	0.4% per 1% increase		SW, RES,
% tillers infected	0.35% per 1% increase		Rosser and Chadburn (1968)
	0.6% per 1% increase		Slope and Etheridge (1971)
% roots infected	0.44% per 1% increase		SW, RES.
take-all rating	1.4 t/ha per 100 TAR units	0 - 300	Gutteridge *et al* (1987)
take-all index	0.56 t/ha per 10% TAI	0-100	Clare *et al.* unpublished

The level of take-all infection in susceptible crops varies between years as does the appearance of visible symptoms (stunting and premature ripening) in the crop (Table 1.1). The environmental conditions which promote development of the disease and its expression in the crop have not been conclusively determined (Hornby & Bateman, 1991). There are from various reviews of take-all infection and yield of crops certain generalities which seem to hold true. Namely the disease develops when soil conditions are warm and moist (the disease will not grow in wheat tissue which has a water potential below about -45 bars); the extent of yield reduction then depends on dry conditions later in the growing season for the reduction in crop root function to be expressed (Hornby & Bateman, 1991).

Although there are no reports in the literature of consistent varietal differences in susceptibility to take-all root loss, the capacity of varieties to tolerate root loss may not be the same. There have been in the past varieties identified through grower experience as not performing well when grown as non-first wheats. For example, in the early 1980s Brock had the reputation of performing poorly as a non-first wheat. Although at the time there were suggestions that this poor performance was due to increased susceptibility to take-all, this was never proven in experiments and was based purely on its field performance (Rosemary Bayles, Pers. Comm.). There has been more recent evidence that varietal rankings may change in different rotational positions, for example the ADAS Crop Centre trial series of 1991-2. In these experiments, Talon, Brigadier and Riband lost relatively little yield (0.3 t/ha) while Spark lost on average over 1 t/ha when grown as a second wheat. It is on this basis that an explanation is sought for interactions between variety and rotational position, over and above those attributable directly to nutrition and above-ground disease or pest effects, in the current work. This Sub-Project therefore examined the potential for identifying varietal physiological traits that may confer tolerance of root loss due to take-all infection in second or successive wheats.

Table 1.3 Performance of varieties in ADAS Crop centre trial series in 1991-2, when grown as first or second wheats.

Variety	No. of sites	Mean yield as first wheats (t/ha)	Mean yield as second wheats (t/ha)	Yield difference (t/ha)
		8	8	
Talon		7.83	7.84	-0.01
Brigadier		8.67	8.46	0.21
Riband		8.12	7.85	0.27
Haven		8.93	8.31	0.62
Cadenza		8.67	7.67	1.00
Soissons		8.74	7.72	1.02
Apollo		8.55	7.49	1.06
Spark		8.24	7.10	1.14

1.2. Candidate varietal traits conferring tolerance of take-all

Once a take-all infection becomes well established its action is in effect to sever the root it is infecting. The main consequence of this is to reduce water and nutrient uptake by the crop. As the stage of development of the crop progresses and nitrogen uptake nears completion the effect of the disease shifts more towards limitation of water uptake. It is reasonable, therefore, to expect some commonalty between varietal traits conferring tolerance to root loss through take-all infection and those conferring tolerance of drought (See Part 1, Section 1.4).

1.2.1. Rate of development

Field experience in eastern England strongly suggests that take-all development is arrested in dry soil conditions from April onwards (Hornby & Bateman, 1991). From a study of a 33 year data set at Rothamsted, prevalence of take-all has also been associated with warm, dull springs (Hornby, 1978). Yield losses due to take-all tend to be greatest in summers where a sudden dry spell in late May and June follows a warm, wet spring, for example in 1987 (Cook & Polley, 1990). If root function of a plant is destroyed completely prior to grain filling, then 100% yield loss can occur, but similar disease severity achieved during grain filling is not likely to cause such severe yield loss (Hornby & Bateman, 1991). It follows that a faster developing variety may be better adapted to tolerate take-all, because i) it reduces the probability of total grain loss due to severe take-all pre-flowering (GS 61) and ii) the onset of severe take-all is more likely to occur later in the grain filling period with less yield loss.

Varietal variation in flowering date for current UK-bred winter wheat varieties from a common October sowing date is in the order of seven days (Foulkes *et al.*, 1993). Assuming a transpiration rate equivalent to 3 mm/day as typical for early June in England (Goss *et al.*, 1984), it can be calculated that the total presence or absence of a functional root system for seven days will result in varietal extremes differing in water use during grain filling by up to 21 mm. Assuming a water use efficiency of 5 $g/m^2/mm$ (Green *et al.*, 1983), this relates to a potential difference in grain yield production of > 1 t/ha. It can thus be postulated that earlier flowering varieties may be better adapted to tolerating take-all root loss, and that this trait is worthy of examination. The advantage of short lifecycle varieties in improving performance through drought escape has been well documented in dryland climates (Fischer & Wood, 1979; Richards, 1987). There is also some evidence for better performance in response to UK droughts associated with earlier date of ear emergence (Innes *et al.*, 1985).

1.2.2. Economy of tillering

As many as two-thirds of the shoots produced in a winter wheat crop may fail to survive and form ears and yield grain (Prew *et al.*, 1985). Tiller production and tiller survival are both varietal traits (Hay & Kirby, 1991; Kirby, 1994). Varieties with high vernalization requirements and long daylength requirements tend to produce greater numbers of tillers (Kirby, 1994). Varieties with more erect flag leaves tend to exhibit better tiller survival (HGCA, 1995).

The presence of shoots that are not going to survive may be deleterious in terms of total grain productivity, especially in growing conditions where water uptake is restricted, as is the case in second and subsequent wheats where take-all kills many roots. Competition between dying tillers and the ear-bearing tillers adversely affects the developing ears. Developing ears have a large relative growth rate which can be restricted by small absolute changes in assimilate supply, giving a consequent reduction in the number of grains per ear (Brooking & Kirby, 1981; Fischer, 1985). More importantly, excessive production of tillers, which are subsequently lost, effectively wastes water resources, since the dry matter contained in dead tillers is not redistributed to surviving plant tissues (Thorne & Wood, 1987).

It has been reported that for cv. Avalon sown in October the amount of dry matter in all dead shoots on 1 June was 1.39 t/ha (Thorne & Wood, 1987). Our current experiments testing a broad range of varieties, including Avalon, have indicated that current varieties may differ from Avalon by 25% in the dry matter lost in dead shoots. This relates to a difference of 14 mm in the amount of water used in producing dead tillers, again assuming a water use efficiency of 5 g/m^2/mm (Green *et al.*, 1983). The varietal type most economic in tillering is likely to show low tiller production coupled with high tiller survival. It is currently postulated that economy of tillering is a varietal characteristic better suited to second or subsequent wheats and that consequently this trait is of potential importance in determining varietal response to high and low take-all environments.

1.2.3. Stem carbohydrate reserves

During later stem extension, from GS 37 onwards, demand by the non-soluble, structural stem tissues and leaf tissues for assimilate decreases rapidly. Proportionately more is then available for partitioning to soluble carbohydrate in the upper internodes of the plant (Brooking & Kirby, 1981). Most soluble carbohydrate accumulating in the peduncle occurs after GS 61 (Schnyder, 1993). Soluble carbohydrate accumulation, expressed as a percentage of stem and leaf sheath biomass, is maximal at about 30 to 35%, and this stage is reached approximately nine days after GS 61 (Austin *et al.*, 1977), with soluble carbohydrate in excess of about 5% of dry weight being stored as fructan (Kubach & Thome, 1989). This relates to actual amounts of soluble carbohydrate stored in stems and leaf sheaths nine days after flowering in the order of 2 to 3 t/ha for an average winter wheat crop in the UK (HGCA, 1995).

As the green canopy senesces and the source of assimilate declines, mobilisation of carbohydrate reserves stored in leaf sheaths and stems maintains translocation of assimilate to the grains (Thorne, 1982; Makunga, 1978). This process generally starts at about the mid-to-late grain fill stage. Redistribution of dry matter will, however, be induced at an earlier stage by factors contributing to accelerated senescence, such as restricted water availability due to drought (Bidinger *et al.*, 1977) or reduced capability for water and N uptake with take-all. Effectively all soluble carbohydrate is lost by harvest both in stressed and unstressed wheat crops and amounts remaining at harvest are rarely greater than 0.25 t/ha (HGCA, 1998). Due to respiratory losses, the contribution of stem reserves to grain is generally in the order of 25% less than the total amounts accumulated (Stoy, 1966).

At the outset of Sub-Project work there was evidence for significant differences between current UK varieties in the maximum amount of stem reserves accumulated. Foulkes *et al.* (1994) reported a range of 30 to 39% for soluble carbohydrate concentration in stems plus sheaths at GS 61 in five UK cultivars. In previous work, Thorne (1982) reported that amount of ^{14}C moving from the stem to the grain between anthesis and maturity was about 50% greater in the semi-dwarf variety Hobbit than in the taller variety Maris Huntsman. It was therefore hypothesised at the outset of current work that differences in capacity to accumulate stem reserves existed for currently, commercial varieties and that these were correlated with the ability to buffer effects of accelerated senescence with take all. Capacity to accumulate stem reserves was therefore prioritised as a target varietal trait in the current Sub-Project. This trait has also been shown to be advantageous in buffering grain yield under drought (Bidinger *et al.*, 1977) (see Part 1, Section 1.4).

2. MATERIALS & METHODS

2.1. General

A phased experiment (see below) was conducted at two sites with rotational position as a main plot treatment in a replicated and randomised experiment. The sites were chosen, on past evidence, to produce either relatively high (ADAS Rosemaund) or relatively low (ADAS Boxworth) levels of take-all infection. Immediately prior to the establishment of the first test season of the experiment it appeared likely that a chemical means of controlling the take-all fungus would be commercially available in the foreseeable future. In order to assess the likely implications of this for the outcome of the project, each main plot was divided and a standard seed treatment applied in one half and a standard seed treatment plus the experimental product applied in the other. Eight varieties of winter wheat - chosen to represent a range of reported performance when grown as non-first wheats, as well as a range in the candidate physiological traits - were randomised within each sub-plot.

2.2. Experimental details

2.2.1. Experimental sites

In choosing sites for the experiments a number of criteria had to be met: the sites should be representative of a significant proportion of the UK wheat area, there should be high enough levels of take-all to cause significant yield loss, and the disease should not be so severe as to cause complete crop loss. Of the ADAS farms, Boxworth on a Hanslope soil series is representative of the single largest arable soil series in the UK : 2.4% of the total land area of England and Wales (Mackney *et al.*, 1983). Wheat grown on this soil type is, however, relatively insensitive to yield loss due to a second wheat position. Historic yield figures for Boxworth show that second wheats yield on average 6% less than first wheats. On the other hand, Rosemaund in Herefordshire has probably the highest yield loss of the ADAS arable farms at 14% (Hornby & Bateman, 1991).

Further details of the two sites selected are :

ADAS Boxworth (low take-all risk). The soil is a grey clay containing chalk fragments over an impervious sub-soil, and is of the Hanslope series, derived from chalky boulder clay. It has a water holding capacity of about 200 mm in the top 1.2 m of the profile. The site ranges from 25 to 67 m above sea level. The long term annual rainfall of 550 mm is typical of the locality, the farm being mid-way between Cambridge and Huntingdon.

ADAS Rosemaund (high take-all risk). The soil is a fertile, stoneless silty clay loam of the Bromyard series, which is derived from Old red sandstone. It has a water holding capacity of about 220 mm in the top 1.2 m of the profile. The site ranges from 80 to 100 m above sea level. Despite its westerly location just north east of Hereford, it has a long term average annual rainfall of only 660 mm, which is fairly evenly distributed throughout the year.

2.2.2. Experimental design

Design: Randomised split-split plot.
Replicates: 3.

Example of the phasing of the experiment for 1 block at ADAS Rosemaund:

Main plot	1992-3	1993-4 Test season 1	1994-5 Test season 2	1995-6 Test season 3
1	Ww	Oats	ww 1	ww 2
2	Ww	ww 2	spring osr	ww 1
3	Oats	ww 1	ww 2	ww 3

<u>Main plots: Rotational position</u>

1 First wheat
2 Second wheat
3 Third wheat (1995-6 only)

<u>Sub-plots: Seed treatment</u>

1 Panoctine (+ Birlane 1993-4 only)
2 Panoctine (+ Birlane 1993-4 only) + experimental take-all control chemical

<u>Sub-sub plots: Variety</u>

1 Brigadier
2 Cadenza
3 Lynx
4 Rialto
5 Riband
6 Soissons
7 Spark
8 Zentos

Sub-sub plot size: 12 x 2 m duplicated for combining and sampling

2.2.3. Crop management

All pesticides, PGRs and fertilisers were using a prophylactic approach to exclude any external pest or disease interference (see Vol. I, Part 1.6). The aim was to exclude differential residual nitrogen levels from the comparison of different rotational positions. To this end, the nitrogen inputs to the break crops preceding each first wheat were targeted to leave a similar residue to a wheat crop. All crop residues were baled and removed, in an attempt to minimise any differential mineralisation of N in the spring or summer of the test crop. To assess the success or otherwise of this approach the mineral nitrogen level in the stubble preceding each test crop was measured (Table 2.1). On only one occasion was there a difference in N residues large enough and consistent enough across the experiment to warrant intervention. This was at Rosemaund for the 1995-6 crop where 40 kg N/ha was applied to the stubble in the autumn of 1995 to the areas destined to be second and third wheat crops the following year (Appendix table 2).

Table 2.1. Soil mineral N (Kg N/ha) measured between 0-90 cm, in the stubble preceding the test crops, ADAS Rosemaund.

	1994-5	1995-6
FIRST	52.67	78.21
SECOND	67.33	52.92
THIRD	-	44.59

2.3. Rationale for choice of varieties tested

Following the desk study carried out at the beginning of the Sub-Project (Foulkes *et al*, 1994) some information existed on the yield performance of varieties grown as first and non-first wheats from ADAS and NIAB variety trials. Availbale information on the candidate physiological characteristics for a wide range of varieties had also been collated. On the basis of both these sources of information eight varieties were chosen to contrast the range of yield performance and/or physiological characteristics.

Brigadier	Shown in the desk study to perform well as a non-first wheat in ADAS federated variety trials in 1991-2.
Cadenza	Low vernalisation requirement, rapid development with good early vigour, and 'solid' stems which may indicate large reserves of soluble carbohydrate, to buffer grain filling in non-first wheats.
Lynx	Short strawed and high yield potential, but shown in the desk study to perform poorly as a second wheat in Cambridge Plant Breeders' trials.
Rialto	New variety with both high yield potential and grain quality. Allows a cross-over to look at the trade-off of take-all on yield potential and grain N%.
Riband	High yield potential feed variety, shown in the desk study to have a relatively better performance as a non-first wheat in NIAB RL trials 1986-7 to 1990-1.
Soissons	French, bread-making variety with rapid development. Awned ear and shy tillering indicate potential drought tolerance and also potential to tolerate root loss due to take-all, poor resistance to eyespot may mitigate against non-first wheat use.
Spark	Low yield potential, bread-making wheat, shown in the desk study to perform poorly as a second wheat in ADAS federated variety trial 1991-2.
Zentos	German bread wheat, very slow developing and late to ripen. Tall in comparison with English varieties, may be associated with poor stem reserves. Thought to be unsuited to non-first wheat position.

2.4. Assessments

2.4.1. Take-all

Take-all was assessed using the index method. This involves the removal of 20 plants from random locations within the plot to account for the inherent variation of the disease. The roots of each plant are washed and the proportion of the root system which is showing visible symptoms of the disease recorded in one of five categories:

0= no disease
1= 1-10% of root system infected
2= 10=25% "
3= 25-50% "
4=50-75% "
5=75-100% "

a take-all index is then calculated;

$$\text{index} = \frac{1*n1 + 2*n2 + 3*n3 + 4*n4 + 5*n5}{5 * nt/100}$$

Where : n1-n5 are the number of plants in each category and nt the total number of plants assessed

In the first season disease levels were assessed across all varieties at early grain fill to establish if there was any differential in varietal susceptibility to the disease. Additionally at Rosemaund assessments were made at GS 31 and GS 59 on two varieties to monitor progression of the disease epidemic. In 1994-5 and 1995-6 the same assessment was made but in addition more frequent (approx. fortnightly) samples were taken on one variety to give a more precise picture of disease progress, which could be linked to crop growth.

2.4.2. Crop growth

Crop samples were taken at specified critical crop development stages, and analysed according to standard protocols (see Vol. I, 1.6). In 1993-4 these were taken at GS 31, GS 59, GS 61+75°Cd, GS 87 and grab samples pre-harvest, and assessed for crop biomass, those at GS 31 and GS 59 also being used to determine crop GAI. In 1994-5 the samples were taken at the same developmental stages at Boxworth but without any GAI assessments, and an additional sample at Rosemaund at GS 39+650^{0}Cd days to obtain a measure of canopy senescence, along with GAI being assessed at all the earlier samples. In 1995-6 the crop sampling at Boxworth was not carried out due to the lack of response in either crop growth or yield due to the rotational positions and the almost complete absence of the disease. The sampling procedure at Rosemaund was intensified in order to more fully understand the effects of take-all on crop growth and the economy of tillering of the varieties. To achieve this an additional sample was added at GS 33 and sampling for the first three dates carried out according to tiller hierarchy. This involved the measurement of biomass and GAI on the main stem, tiller 1, tiller 2, tiller 3, and remaining tillers separately.

2.5. Establishing a suitable testbed for varietal suitability

As described in the introduction, the level of yield loss due to take-all depends on suitable environmental conditions. Firstly, warm and moist conditions are needed for significant levels of the disease to develop, and then dry weather for the loss of root function to interfere with crop growth. In order to test for varietal suitability to a non-first wheat position, both of the above conditions must be met to some extent and result in yield loss in the non-first wheats. Of the six site/seasons included within this Sub-Project, in only 3 were the above conditions met, leading to a yield loss of over 0.25 t/ha in second or third wheats compared to the first wheats. The sites on which the second or third wheat position resulted in this level of yield loss were Boxworth 93-4 and Rosemaund in 94-5 and 95-6, and the report concentrates on these.

3. RESULTS

3.1. Take-all

3.1.1. Effect of site and season

In the event Boxworth, chosen as the low take-all risk site, did consistently show lower take-all levels (Table 3.2.a) than Rosemaund (Table 3.1). At Boxworth the final take-all index on second or third wheats exceeded 10% only in 1993-4 (12%). At these low levels no difference was discernible in final disease incidence on first and second wheats. The reason for the difference in take-all experienced at the two sites does not appear to be explained by differences in climatic conditions. The temperature and rainfall pattern during early spring at Boxworth in 1994 (Fig. 3.1) was more conducive to disease development than at Rosemaund in either 1994-5 or 1995-6 (Figs 3.2.b & 3.3.b). The apparently consistent difference between the sites must therefore be due to some aspect of the soil either physical, chemical or due to microflora.

Although disease levels were higher at Rosemaund (maximum levels 26% in 1994-5 & 31% in 1995-6), none of the years could be classed as a high take-all season. The absence of severe take-all resulting in large yield reductions was brought about by differing patterns of disease. In the 1994-5 season the disease was present over winter at a level that could potentially develop into seriously damaging levels (Figure 3.2.a.). However, lack of rain in spring retarded disease development until significant rain fell in mid-to-late May (Fig. 3.2.b) allowing the disease to reach low-moderate final levels. Over wintering disease levels in 1995-6 (Fig. 3.3.a) were similar to those in 1994-5. A trickle irrigation system was installed in order to avoid the problems of the previous year. However, unseasonably cold conditions prevailed for much of the spring and early summer hampering the development of the disease (Fig. 3.3.b), which again failed to develop significantly until early May, resulting in low-moderate final disease levels.

3.1.2. Effect of rotational position

At Rosemaund in 1994-5 and 1995-6 non-first wheat crops had significantly more disease than first wheat crops (Table 3.1). In 1994-5 although the difference in index was small, 10.2 vs. 16.7, it was significant. A much greater contrast was between the first and third wheats in 1995-6, 9.9 vs. 23.0, respectively. At Boxworth there was no significant effect of rotational position on take-all level in any season.

3.1.3. Effect of variety

In order to identify any varietal influence on take-all resistance at both sites and in each season, all treatment combinations were assessed for take-all severity (Tables 3.1 & 3.2). This was done at or soon after ear emergence, when the disease levels were likely to be close to maximum and the plants could still be relatively easily assessed. In no site in any season was there a significant effect of variety on the level of take-all infection. This supports the original hypothesis that differences in the performance of varieties when grown as non-first wheats must be due to differences in tolerance to the disease.

Table 3.1. Take-all Indices during grain filling, ADAS Rosemaund

	1993-4		1994-5		1995-6			93-4 to 95-6 mean	
	First	Second	First	Second	First	Second	Third	First	Second
Brigadier	32.3	31.7	8.7	16.7	10.3	20.7	23.0	17.1	23.0
Cadenza	31.0	29.3	9.3	18.0	8.7	15.3	22.3	16.3	20.9
Lynx	33.3	27.3	12.0	16.3	12.0	20.3	21.3	19.1	21.3
Rialto	26.3	33.3	10.7	15.3	11.3	18.0	21.7	16.1	22.2
Riband	34.3	29.0	9.0	18.7	10.3	19.0	20.3	17.9	22.2
Soissons	35.0	30.0	17.3	14.7	12.7	18.7	26.0	21.7	21.1
Spark	19.7	29.7	7.7	12.3	5.7	23.0	30.7	11.0	21.7
Zentos	36.7	32.0	7.0	21.3	8.3	18.3	18.3	17.3	23.9
Mean	31.1	30.3	10.2	16.7	9.9	19.2	23.0	17.1	22.0

	1993-4	1994-5	1995-6	93-4 to 95-6 mean
Year SED	-	-	-	3.925
P value				0.008
Df	-	-	-	6
Type SED	9.44	0.765	2.560	3.375
P value	NS	0.014	0.016	NS
Year x Type SED	-	-	-	5.700
P value				NS
Df	2	2	4	6
Variety SED	4.51	2.067	2.710	1.995
P value	NS	NS	NS	NS
Year x Variety SED	-	-	-	5.085
P value				NS
Type x Variety SED	11.16	2.839	5.083	4.284
P value	NS	0.020	NS	NS
Year x Type x Variety SED	-	-	-	7.306
P value				NS
Df	28	28	42	84

Table 3.2. Take-all Indices during grain filling, ADAS Boxworth

	1993-4		1994-5		1995-6			93-4 to 95-6 mean	
	First	Second	First	Second	First	Second	Third	First	Second
Brigadier	16.00	12.00	7.33	9.33	2.33	4.33	3.67	8.56	8.56
Cadenza	15.67	9.67	10.33	12.33	2.67	5.00	5.33	8.44	10.11
Lynx	14.67	14.00	7.67	11.33	2.33	3.00	3.33	8.89	8.78
Rialto	16.67	13.33	10.33	4.67	2.67	5.33	1.67	8.44	9.22
Riband	12.00	10.33	5.33	6.67	2.33	3.00	6.67	6.67	6.56
Soissons	14.00	13.00	7.67	7.00	2.33	2.00	2.33	7.78	7.56
Spark	11.67	14.00	8.00	10.00	2.67	3.67	4.00	7.89	8.78
Zentos	12.33	10.67	7.00	9.00	3.00	2.67	5.00	7.44	7.44
Mean	14.13	12.13	7.96	8.79	2.54	3.62	4.00	8.01	8.38
Year SED	-		-		-			1.480	
P value								0.002	
Df	-		-		-			6	
Type SED	2.672		1.884		0.689			1.034	
P value	NS		NS		NS			NS	
Year x Type SED	-		-		-			1.948	
P value								NS	
Df	2		2		4			6	
Variety SED	2.063		2.808		0.816			1.201	
P value	NS		NS		NS			NS	
Year x Variety SED	-		-		-			2.444	
P value								NS	
Type x Variety SED	3.819		4.165		1.492			1.895	
P value	NS		NS		NS			NS	
Year x Type x Variety SED	-		-		-			3.371	
P value								NS	
Df	28		28		42			84	

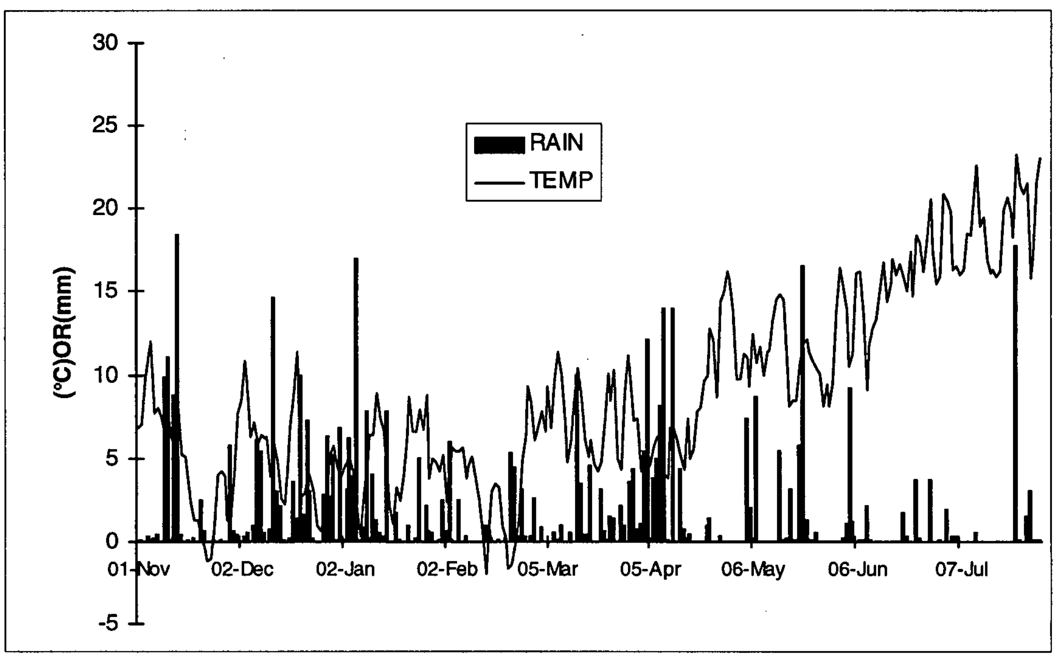

Figure 3.1. ADAS Boxworth, 1993-4, rainfall (mm) and average daily temperature for the growing season.

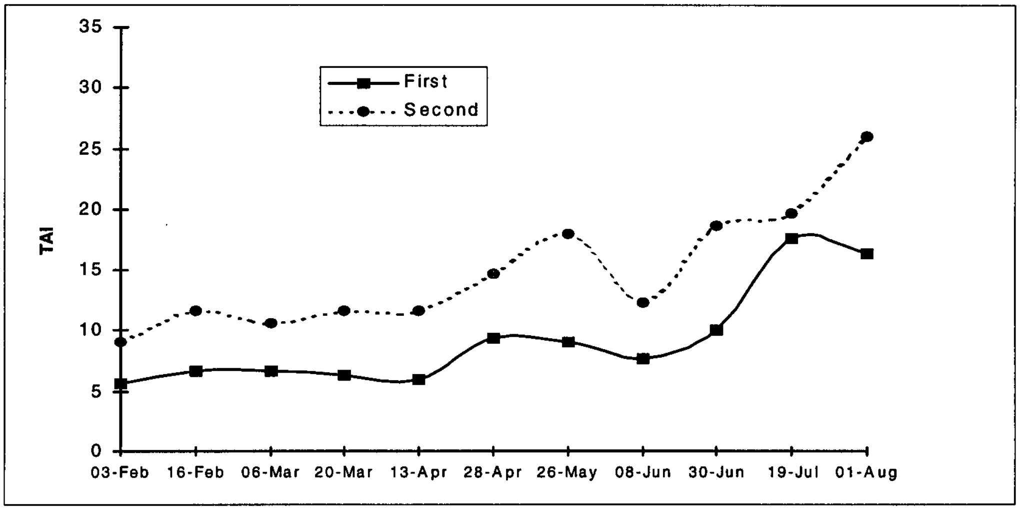

Figure 3.2.a.

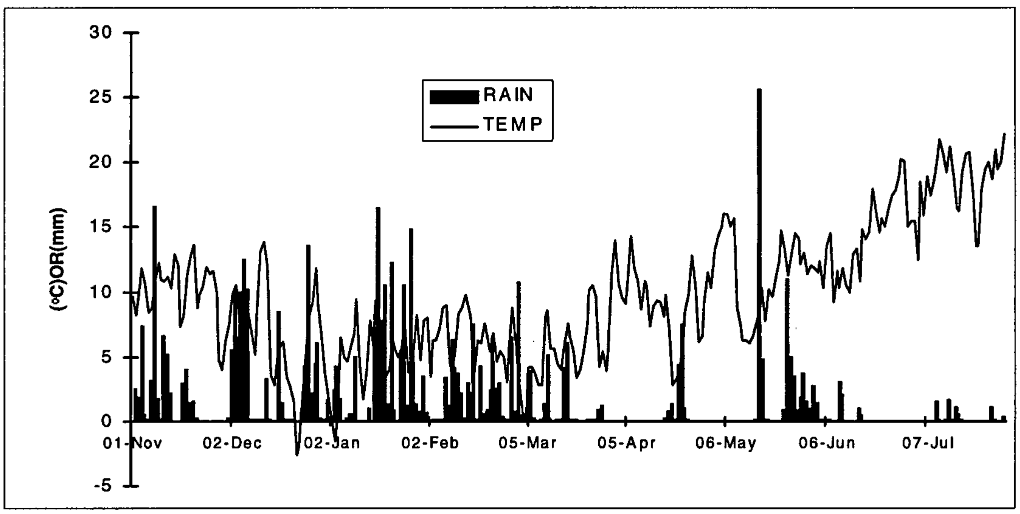

Figure 3.2.b.

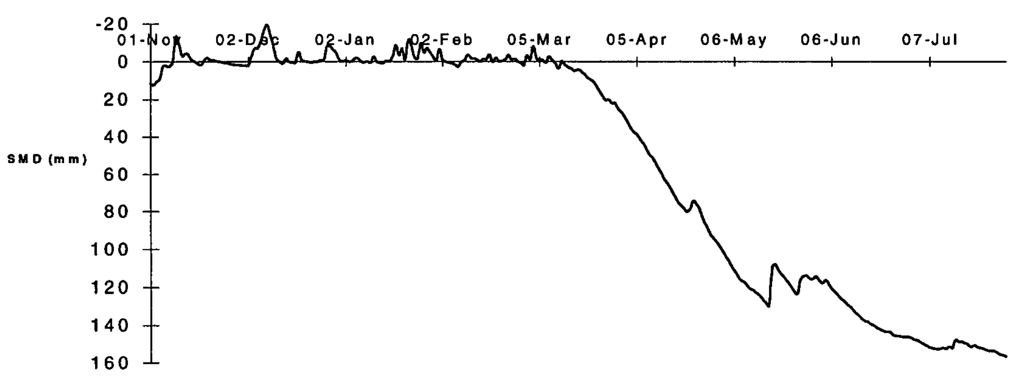

Figure 3.2.c.

Figure 3.2. ADAS Rosemaund, 1994-5, Take-all progression expressed as an index on first and second wheats (a), and rainfall (mm) and average daily temperature for the growing season (b) and SMD (c).

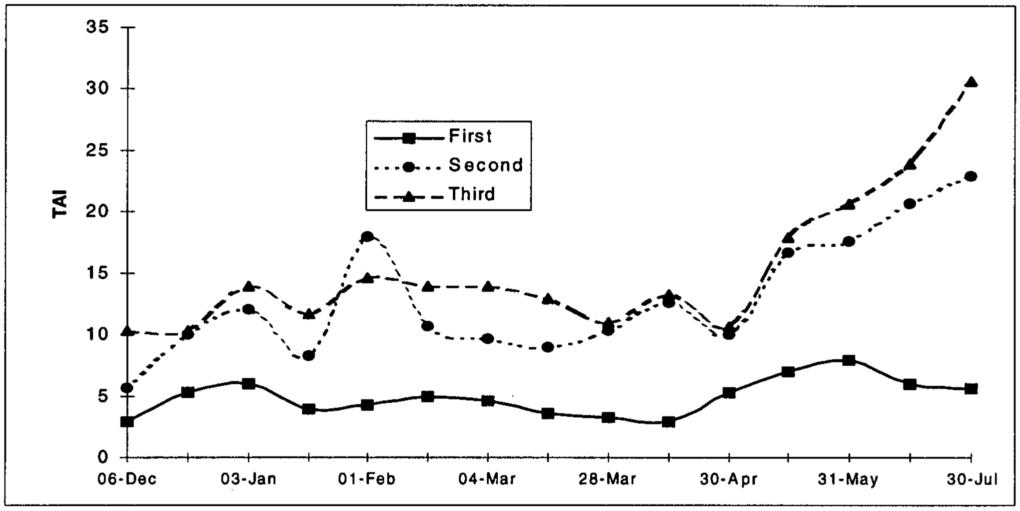

Figure 3.3.a.

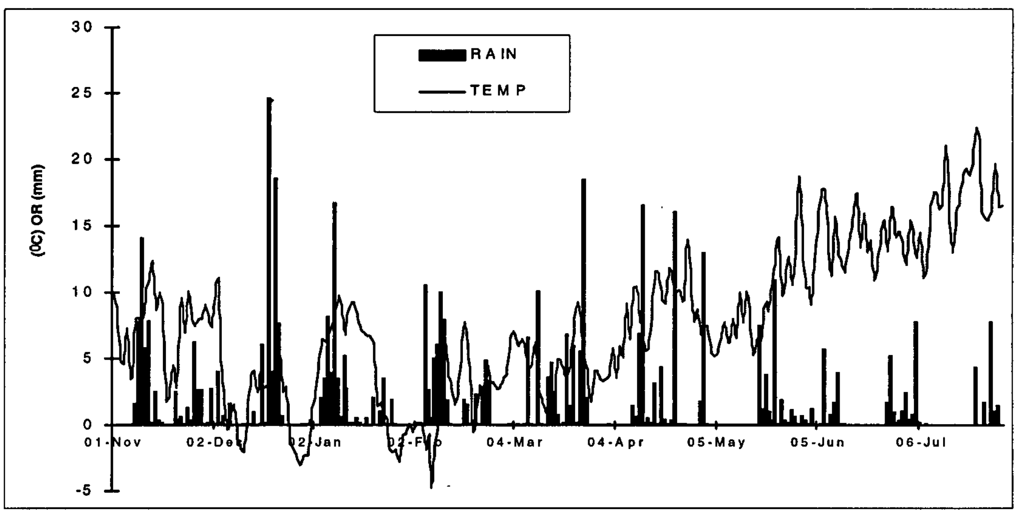

Figure 3.3.b.

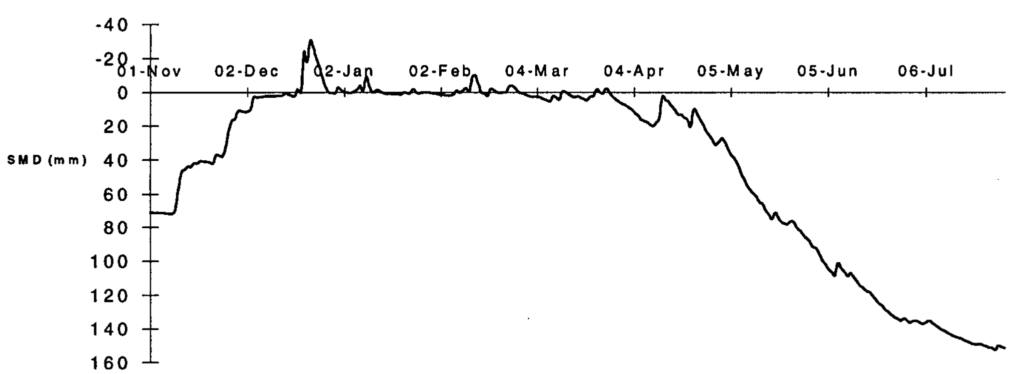

Figure 3.3.c.

Figure 3.3. ADAS Rosemaund, 1995-6, Take-all progression expressed as an index on first, second and third wheats (a), and rainfall (mm) and average daily temperature for he growing season (b) and SMD (c).

3.2. Yield

3.2.1. Effect of site, season and rotational position

Mean yields were close to the average for each site with the exception of Rosemaund in 95-6, where the yields were above average but not at record levels (Table 3.3a). High yields were general in the country in 95-6 due to relatively cool, bright growing conditions.

At three of the six site-seasons (Rosemaund 93-4, and Boxworth 94-5 and 95-6) yield reduction due to a non-first wheat position was small, 0.2 t/ha or less. For Boxworth 93-4 and Rosemaund 94-5 and 95-6 the yield loss due to a non-first wheat position was 0.3 t/ha, 0.5 t/ha and 0.85 t/ha and it is here that suitability of varieties is explored. The lack of statistical significance of the effect of rotational position in these latter 3 site-seasons probably conceals a real effect. There was a lack of precision at the main plot level in the split-split plot design. This design was, however, necessary to provide large enough areas of different rotational positions to minimize the risk of spread of take-all inoculum from one to the other.

A full set of yield data from the two sites and three seasons, including the results from the experimental take-all control chemical is presented in Appendix table 3.

3.2.2. Effect of variety

3.2.2.1. Boxworth 1993-4

Average yield loss of second compared to first wheats was relatively small at 0.3 t/ha. As first wheats, the varieties performed broadly in line with what would be expected from their rankings on the NIAB Recommended List, that is with the exception of Cadenza. This was the highest yielding variety, with Brigadier also producing high yield at 9.7 t/ha; Rialto and Lynx were the next best yielders closely followed by Riband and Soissons. Spark and Zentos were the poorest performers yielding only 8.4 and 7.8 t/ha respectively.

Despite the small overall yield loss of the second wheats there were indications that the varieties were responding differently to the second wheat position. Brigadier, Cadenza and Rialto yielded as well as Soissons with only 0.04 t/ha between them. Lynx and Riband were intermediate in their performance, and Spark and Zentos the poorest performers as second wheats, yielding 1.5 t/ha less than the best varieties. Soissons yielded slightly better as a second wheat whilst at the other end of the range Spark lost 0.67 t/ha as a second wheat. For the other six varieties, yield loss as a second wheat ranged from 0.17 to 0.47 t/ha. In terms of yield lost, Rialto, Riband and Lynx were at the lower end of the scale, whilst Brigadier, Cadenza and Zentos lost relatively more. Varietal performance as second wheats was largely in line with the expectation according to indicative traits. The relatively small yield loss of Riband appeared to be due more to its poor performance as a first wheat than a particularly good performance as a second wheat.

3.2.2.2. Rosemaund 1994-5

In this season with the earliest and most sustained drought (Fig. 3.2.c) all the varieties yielded less as first wheats than in either 1993-4 or 1995-6. Varietal ranking order of the first wheats was slightly at odds with the expectation from the Recommended List. Rialto performed better than expected, producing the equal top yield with Brigadier (8.65 t/ha) which was closely followed by Lynx (8.62 t/ha). Soissons and Spark were the next highest yielding varieties, producing over 8.0 t/ha, whilst Riband and Cadenza performed particularly poorly yielding on a par with Zentos at less than 8.0 t/ha. Average yield loss in second wheats was again relatively small at 0.5 t/ha. Rialto maintained its position as the highest yielding variety as a second wheat and Lynx its place as second highest yielding, 8.4 and 8.0 t/ha, respectively. Riband and Spark performed respectably yielding 7.7 t/ha, Brigadier dropped well down the ranking compared to its first wheat performance producing only 7.6 t/ha. Soissons, Cadenza and Zentos were the poorest yielding second wheats producing 7.5, 7.3 and 7.2 t/ha respectively. As at Boxworth the previous year the relatively small overall yield loss of second wheats masked a significant range between the varieties, Riband and Rialto lost the least yield (0.2 and 0.25 t/ha, respectively) and Brigadier the most 1.06 t/ha. The low yield loss displayed by Riband again appeared to be due more to a poor performance as a first wheat than a particularly good performance as a second wheat. Yield loss among the remainder of the varieties ranged from 0.4 t/ha for Cadenza to 0.65 t/ha for Lynx.

3.2.2.3. Rosemaund 1995-6

Without exception the first wheats yielded higher than in 94-5, although yields were only slightly above average. The yield ranking of the first wheats was not what would be expected from their performance in the Recommended List trials. Rialto was clearly the highest yielding variety (10.8 t/ha), Soissons and Lynx were the nearest in yield to Rialto but still produced almost 1 t/ha less. Brigadier and Cadenza were close to the yield of Soissons and Lynx at 9.5 and 9.7 t/ha respectively followed by Riband at 9.2 t/ha. Spark and Zentos produced the lowest yield at 9.0 and 8.7 t/ha, respectively, about 2 t/ha less than Rialto. Yield loss in the second wheats was smaller than in either of the other two seasons. However, the greater disease pressure in the third wheats resulted in an average yield loss of 0.85 t/ha. This comparison of first vs. third wheats represents the most rigorous testbed for identifying differential varietal suitabilities to the non-first wheat position. Ranking of the varieties in terms of absolute third wheat yields were very similar to those for second wheats in the previous year. Rialto was clearly the highest yielding followed by Lynx and Soissons (Rialto producing 0.62 t/ha more than Soissons at 9.0 t/ha). Brigadier and Cadenza were the next highest yielding with Spark and Riband ranking sixth and seventh. As in the previous site-seasons Zentos was the poorest yielding non-first wheat. Yield loss due to the third wheat position ranged from 0.65 to 1.11 t/ha for Lynx and Rialto, respectively. More so than in the previous years the level of yield loss in the non-first wheat position appeared to owe more to abnormal performance as first wheats rather than notable unexpected non-first wheat performance.

3.2.2.4. Varietal performance averaged across site-seasons

Drought conditions affected the performance particularly of the first wheats in 1994-5 and 1995-6. The lower yield in 94-5 appeared to be due to the sustained drought which started at about GS 31 and was effectively maintained until harvest (Fig. 3.2.c). In 95-6 although there was a drought it was later developing occuring predominately post anthesis. As in the drought experiments at Gleadthorpe (Part 1), late drought discriminated between the varieties, those with high stem reserves and to a lesser extent early development tending to pull away from others (e.g. Rialto, Lynx and Soissons performing well as third wheats at Rosemaund 95-6 and Rialto and Haven under drought at Gleadthorpe 93-4). This is demonstrated by the yield interval between Rialto and Riband in Rosemaund 95-6 being much greater than in Rosemaund 94-5, a similar although not as large effect occured with Soissons and Riband. For first wheat performance overall the ranking of the varieties was more like that expected under drought than from the NIAB Recommended List. Rialto was clearly the highest yielding variety, followed by Brigadier and Lynx, then Cadenza yielding just over 9 t/ha. Soissons, Riband, Spark and Zentos were progressively poorer performers down to only just over 8 t/ha. (cf. Part 1, where Rialto was shown to be the most drought resistant of the six varieties examined). When non-first wheat performance is considered, the varietal ranking is very much in line with what would be predicted from their physiological characteristics. Rialto was overall the highest yielding non-first wheat, being absolute highest by at least 0.4 t/ha at Rosemaund and within 0.04 t/ha of the highest at Boxworth. Lynx ranked second again performing consistently at Rosemaund but not exceptionally at Boxworth. Soissons, Brigadier, Cadenza and Riband performed similarly yielding between 8.3 and 8.6 t/ha. Spark and Zentos consistently performed poorly as non-first wheats averaging only 7.9 and 7.5 t/ha respectively. These rankings are different to those that would be expected from their performance in the NIAB RL trials. However, overall differences in response to rotational position in the three particular site-seasons examined, were not large amongst varieties (Table 3.3b). The mean yield loss for varieties varied in the range 0.42 to 0.72 t/ha. In absence of drought, it is probbale but not certain that differences amongst varieties would have been greater. Thus, a note of caution should be sounded. It seems likely that varietal types such as Rialto will perform significantly better as second or subsequent wheats and the converse for other types, e.g. exemplified by Spark. For many intermediate varieties, however, yield loss as a non-first wheat seemed to be inconistent with respect to individual site-seasons, and, when averaged across site-seasons, broadly similar.

Table 3.3.a Crop yield (t/ha @ 85% dm)

	Boxworth 1993-4		Rosemaund 1994-5		Rosemaund 1995-6			Cross site mean	
	First	**Second**	**First**	**Second**	**First**	**Second**	**Third**	**First**	**Second**
Brigadier	9.66	9.23	8.65	7.59	9.52	9.34	8.81	9.28	8.72
Cadenza	9.68	9.21	7.70	7.30	9.67	9.64	8.76	9.02	8.72
Lynx	9.30	9.03	8.62	7.97	9.83	10.02	9.18	9.25	9.01
Rialto	9.39	9.19	8.65	8.40	10.83	10.22	9.62	9.62	9.27
Riband	9.03	8.86	7.90	7.70	9.20	8.99	8.32	8.71	8.52
Soissons	9.01	9.21	8.01	7.46	9.92	9.65	9.00	8.98	8.77
Spark	8.38	7.71	8.24	7.70	9.02	8.78	8.36	8.54	8.06
Zentos	7.84	7.45	7.64	7.22	8.67	9.14	7.96	8.05	7.94
Mean	9.04	8.74	8.17	7.67	9.58	9.47	8.75	8.93	8.63
Site SED	-		-			-		0.490	
df	-		-					6	
Type SED	0.354		0.154			0.932		0.350	
Site x Type SED	-		-			-		0.650	
df	2		2			4		6	
Variety SED	0.1902		0.190			0.169		0.121	
Site x Variety SED	-		-			-		0.527	
Type x Variety SED	0.435		0.294			0.971		0.384	
Site x Type x Variety SED	-		-			-		0.707	
df	28		28			42		84	

Table 3.3.b Mean crop yield (t/ha @ 85% dm) as i) first wheats, ii) non-first wheats (2nd Boxworth 93-4, 2nd Rosemaund 94-5 and 3rd Rosemaund 95-6)

	Mean first	*Mean non-first*	*Yield loss*
Brigadier	*9.28 (1)*	*8.54 (2)*	*0.74*
Cadenza	*9.02 (2)*	*8.42 (2)*	*0.60*
Lynx	*9.25 (1)*	*8.73 (1)*	*0.52*
Rialto	*9.62 (1)*	*9.07 (1)*	*0.55*
Riband	*8.71 (3)*	*8.29 (3)*	*0.42*
Soissons	*8.98 (2)*	*8.56 (2)*	*0.42*
Spark	*8.55 (3)*	*7.92 (3)*	*0.63*
Zentos	*8.05 (3)*	*7.54 (3)*	*0.51*

3.3. Rate of Development

At Rosemaund, Soissons was the earliest developing variety at all growth stages in all seasons. Cadenza although similar to Soissons in the date at which GS 31 was reached was later to GS 39 and GS 61. Spark (a British wheat with spring wheat parentage) and Zentos (a German wheat) were invariably the latest developing varieties. Spark and Zentos respectively being; 14 - 23 and 17 - 33 days later to GS 31, 11 - 13 and 9 - 16 days later to GS 39, and 8 - 15 and 9 - 16 days later to GS 61 than Soissons (Table 3.4). The large range in the difference between the varieties particularly in the date of GS 31 being due to the relative importance of vernalisation and daylength response in determining crop development between the varieties.

Table 3.4. Dates of critical developmental stages, ADAS Boxworth (Bw) 1994 and ADAS Rosemaund (Rm) 1995 & 1996

		GS 31	GS 39	GS 61	GAI 0
Brigadier	Bw 1994	28 April	-	17 June	27 July
	Rm 1995	11 April	23 May	12-June	-
	Rm 1996	15-April	03-June	19-June	10-August
Cadenza	Bw 1994	30 April	-	16 June	26 July
	Rm 1995	22 March	15 May	11-June	-
	Rm 1996	13-April	26-May	15-June	01-August
Lynx	Bw 1994	30 April	-	18 June	27 July
	Rm 1995	11 April	22 May	14-June	-
	Rm 1996	17-April	31-May	21-June	12-August
Rialto	Bw 1994	25 April	-	16 June	27 July
	Rm 1995	4 April	18 May	12-June	-
	Rm 1996	09-April	30-May	16-June	01-August
Riband	Bw 1994	30 April	-	15 June	27 July
	Rm 1995	11 April	22 May	11-June	-
	Rm 1996	22-April	01-June	17-June	07-August
Soissons	Bw 1994	25 April	-	07 June	25 July
	Rm 1995	22 March	9 May	03-June	-
	Rm 1996	12-April	23-May	14-June	08-August
Spark	Bw 1994	05 May	-	19 June	01 August
	Rm 1995	14 April	22 May	18-June	-
	Rm 1996	26-April	03-June	22-June	05-August
Zentos	Bw 1994	04 May	-	20 June	01 August
	Rm 1995	24 April	25 May	19-June	-
	Rm 1996	29-April	01-June	23-June	12-August
Mean	Bw 1994	29-April	-	16 -June	28-July
	Rm 1995	07-April	19-May	12-June	
	Rm 1996	17-April	30-May	18-June	07-August

Developmental dates for the varieties at Boxworth is more limited, that which is available is in general agreement with that from Rosemaund. Soissons was always the earliest variety to any given growth stage and Spark and Zentos invariably the latest. There were some differences between the sites however, most notably that Cadenza at Boxworth tended to be relatively later to GS 31 than at Rosemaund.

3.4. Harvest components of yield and grain quality characteristics

Table 3.5. Harvest components of yield and grain quality characteristics, ADAS Rosemaund 1994-5

	HI	Ear no./m^2	Grains /ear	Grain weight mg	Specific weight kg/hl	Protein % @ 14% m.c.
First						
Brigadier	55.87	468	44	43.70	76.27	10.13
Cadenza	51.55	454	36	48.48	79.97	10.46
Lynx	58.73	414	42	43.91	75.53	10.33
Rialto	55.07	426	43	44.35	79.97	10.21
Riband	54.81	373	39	46.48	76.40	10.18
Soissons	52.36	572	26	46.72	84.00	10.65
Spark	50.64	502	35	39.03	81.43	10.34
Zentos	51.35	395	40	45.97	82.80	10.74
Mean	53.72	456	38	44.83	79.55	10.38
Second						
Brigadier	53.21	411	44	43.00	74.90	10.38
Cadenza	48.72	388	44	46.61	77.50	10.90
Lynx	50.65	449	41	43.25	75.10	11.16
Rialto	51.13	463	41	43.57	79.73	10.70
Riband	55.46	388	35	45.50	76.30	10.49
Soissons	52.54	705	26	42.97	84.40	11.13
Spark	50.10	609	34	36.40	82.07	10.88
Zentos	49.16	428	36	44.77	82.03	10.93
Mean	51.37	480	38	43.26	79.00	10.82
Position. SED	0.952	8.570	1.983	2.558	0.815	0.519
P value	NS	0.068	NS	NS	NS	NS
df	2	2	2	2	2	2
Variety SED	1.254	25.010	2.950	1.096	0.880	0.191
P value	<0.001	<0.001	<0.001	<0.001	<0.001	0.019
Position. x						
Variety SED	1.913	34.180	4.378	2.940	1.421	0.577
P value	0.103	0.007	NS	NS	NS	NS
df	24	24	24	28	28	28

Table 3.6. Harvest components of yield and grain quality characteristics, ADAS Rosemaund 1995-6

	HI	Ear no./m^2	Grains /ear	Grain weight mg	Specific weight kg/hl	Protein % @ 14% m.c.
First						
Brigadier	56.08	620	36	42.90	75.33	10.31
Cadenza	52.03	552	39	42.57	77.37	11.26
Lynx	54.85	641	35	44.30	75.37	11.67
Rialto	52.87	504	44	44.43	77.10	11.37
Riband	54.57	634	35	42.71	74.13	10.78
Soissons	52.50	659	30	40.41	78.33	11.34
Spark	51.01	893	31	33.57	78.93	11.62
Zentos	46.08	547	28	45.38	81.23	11.63
Mean	52.50	622	35	42.03	77.23	11.25
Second						
Brigadier	57.16	645	38	41.71	74.90	10.33
Cadenza	53.26	609	37	42.68	77.17	11.14
Lynx	54.97	582	39	43.71	75.13	11.14
Rialto	53.80	592	39	44.09	76.87	11.19
Riband	55.90	564	43	41.71	74.17	10.96
Soissons	55.56	772	29	41.22	78.70	11.39
Spark	52.83	750	33	33.12	78.70	11.59
Zentos	47.46	569	30	45.48	81.10	11.42
Mean	53.87	635	36	41.71	77.09	11.15
Third						
Brigadier	57.64	610	40	41.86	74.90	10.46
Cadenza	50.72	542	39	41.27	77.20	11.14
Lynx	55.86	554	37	40.44	72.87	11.57
Rialto	54.57	552	43	42.79	75.83	11.24
Riband	57.65	496	38	40.64	74.20	11.06
Soissons	55.48	652	33	39.98	78.40	11.39
Spark	51.63	775	33	30.91	77.77	12.03
Zentos	45.53	531	36	42.17	79.87	12.03
Mean	53.64	588	37	40.01	76.38	11.36
Position. SED	1.588	24.900	1.971	2.038	0.839	0.362
P value	NS	NS	NS	NS	NS	NS
df	4	4	4	4	4	4
Variety SED	0.991	35.600	1.881	0.654	0.379	0.127
P value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Position. x						
Variety SED	2.258	62.820	3.629	2.297	1.040	0.416
P value	NS	NS	NS	NS	NS	NS
df	42	38	38	42	42	42

Table 3.7. Harvest components of yield and grain quality characteristics, ADAS Boxworth 1993-4

HI	Ear no./m^2	Grains /ear	Grain weight mg	Specific weight kg/hl	Protein % @ 14% m.c.
First					
Brigadier	46.60	675	39	38.05	76.35
Cadenza	47.83	608	41	39.98	77.57
Lynx	42.50	692	30	44.61	76.26
Rialto	46.23	535	44	40.32	78.42
Riband	45.84	523	47	39.23	75.22
Soissons	42.40	708	31	41.89	83.56
Spark	38.57	901	34	28.65	75.98
Zentos	44.34	601	35	38.50	78.84
Mean	44.13	657	37	38.90	77.78
Second					
Brigadier	44.01	616	39	39.73	75.06
Cadenza	48.08	622	35	42.40	76.67
Lynx	40.88	703	30	43.29	75.30
Rialto	42.71	555	40	42.70	77.95
Riband	40.80	589	37	41.65	74.79
Soissons	46.69	618	34	44.53	83.71
Spark	37.38	815	32	30.40	74.41
Zentos	38.12	583	34	38.28	78.82
Mean	42.33	638	35	40.37	77.09
Position. SED	5.050	74.400	6.189	3.156	0.735
P value	NS	NS	NS	NS	NS
df	2	2	2	2	2
Variety SED	2.890	42.400	2.946	0.920	0.443
P value	0.149	<0.001	0.002	<0.001	<0.001
Position. x Variety					
SED	6.334	93.200	7.314	3.383	0.941
P value	NS	NS	NS	NS	NS
df	27	27	27	28	28

The effect of an attack of take-all on the yield components and grain quality of a crop would be expected to be different depending on the timing of the attack relative to the developmental stage of the crop. A very early attack may be expected to reduce ear number, grain number per ear and grain size, in combination with reduced N uptake. This may have no effect or a positive or negative effect on grain protein depending on the degree of restriction on each process. A late attack of the disease would be likely to affect only grain weight adversely. Assuming no effect on N uptake, this would be expected to increase grain protein concentration through a dilution of N in less starch deposition. No one mode of action of the disease on yield components was observed in these experiments but a combination of the above two effects and degrees of each noted in different sites and years (Tables 3.5, 3.6 & 3.7). Grain size in second or subsequent wheats tended to be lower than in first wheats. Specific weights tended to follow the same pattern as grain size, which is to be expected as shrivelling of grain tends to reduces weight to volume ratio. There was a tendency for reductions in ear number to be compensated for to some extent by increases in grain number per ear particularly at Rosemaund in 1995-6.

3.5. Growth

3.5.1. Green area index

Maximum canopy size as measured at GS 61+75°C days in 1994-5 was smaller than would normally be expected in a conventionally grown wheat crop, reaching a green area index (GAI) of only 4.5. In contrast in 1995-6 canopy sizes were above those that would be expected peaking at a GAI of 7.7 at GS 39. The occurrence of the largest canopy size at GS 39 rather than at GS 61+75°Cd, as would be expected, appeared to be due to large green area per leaf in the lower canopy associated with relatively bright and cool growing conditions during canopy formation. By anthesis these leaves had senesced and were not compensated for by the increase in GAI afforded by the newly emerged ear.

GAI was unaffected by rotational position in 1995-6. In 1994-5, however, there was an indication that the second wheat crops had larger canopies than the first wheat crops (GS 31 $p = 0.068$, GS 39 $p = 0.103$, GS 61+75°C days $p= 0.131$). Assessment of soil mineral N in the autumn of planting showed first wheats to have 53 kg N/ha available compared to 67 kg N/ha for the second wheats. This difference was small and it was thought its effects would not be detectable in the following spring and summer. This difference was, however, reflected in crop N uptake at GS 31, the first wheats containing only 38 kg N/ha, 9.5 kg N/ha less than the second wheats. These levels of N uptake were low enough that canopy expansion is likely to have been affected by the difference in N supply. The persistence of the effect on canopy size does not appear to be due to these early effects limiting canopy potential; similar and significant shoot death occurred in both rotational positions between GS 31 and GS 39. It may well have been due to some other undetected effect such as greater mineralisation of N during the spring and summer following the first wheat than the oat break crop.

Canopy size was consistently affected by variety, particularly during canopy production. Variety effect on maximum GAI (as measured at GS 61+75°C days) was only approaching significance in 1994-5 ($p = 0.134$). In 1995-6 the effect of variety on GS 61+75°Cd canopy size was highly significant; in this season however the canopy had already started to senesce by this stage. GAI during senescence measured at GS 39+650°C days was affected by variety in 1995-6 and approached significance in 1994-5 ($p = 0.091$). On no occasion was there a significant interaction between rotational position and variety on GAI. Overall, maximum GAI varied between varieties less in 1994-5 in the range 4.2 to 4.7 than in 1995-6 in the range 7.4 to 9.9. In 1995-6 Rialto was amongst the varieties with lowest GAI in both seasons consistent with its low varietal ranking for maximum canopy size in the Moisture Availbility sub-project (Part 2, Section 3).

Table 3.8. ADAS Rosemaund statistics for total crop GAI.

Growth stage	31		39		61+ 75 ^{0}Cdays		39+650 ^{0}Cdays	
Year	1995	1996	1995	1996	1995	1996	1995	1996
Type SED	0.122	0.085	0.129	0.776	0.175	0.720	0.380	0.786
Df	2	4	2	4	2	4	2	4
Variety SED	0.155	0.208	0.261	0.521	0.330	0.489	0.305	0.282
Type x Variety SED	0.239	0.348	0.369	1.146	0.470	1.070	0.509	0.910
Df	24	42	23	42	22	42	24	42

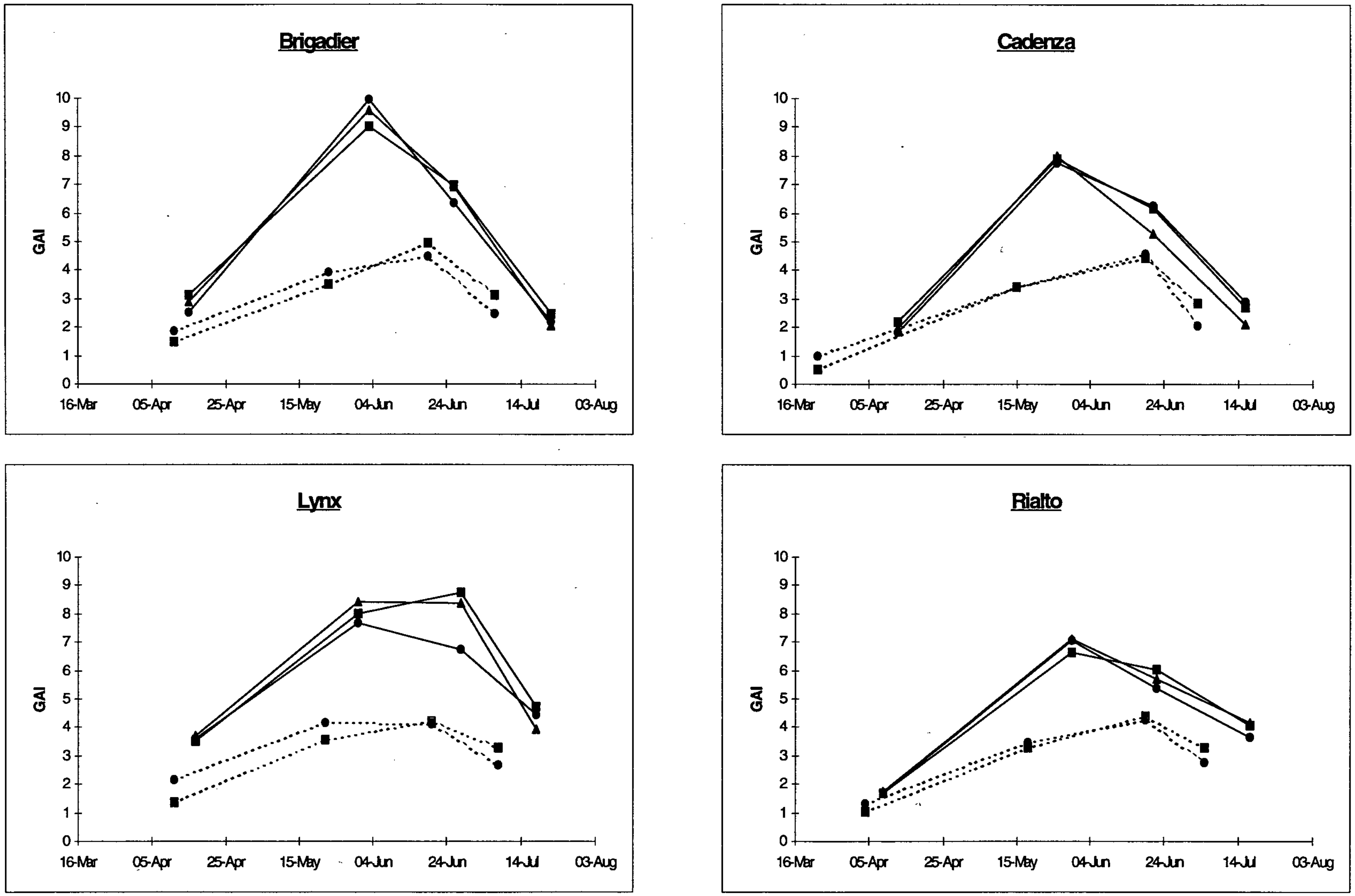

Figure 3.4. ADAS Rosemaund crop green area index for 1995 (......) and 1996 (—) for first (•), second (●) and third (▲) wheat crops

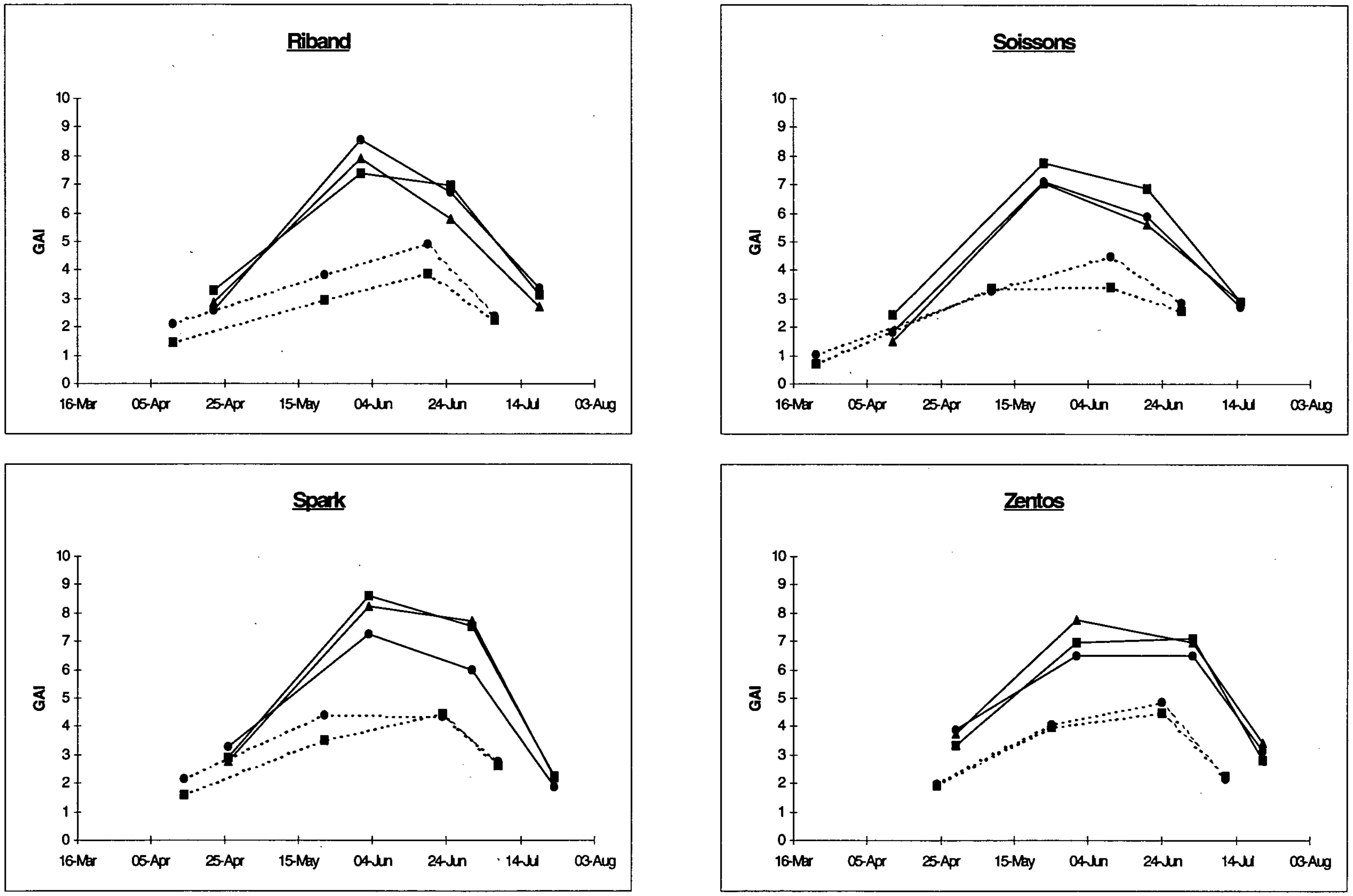

Figure 3.4 cont. ADAS Rosemaund crop green area index for 1995 (......) and 1996 (—) for first (•), second (●) and third (▲) wheat crops

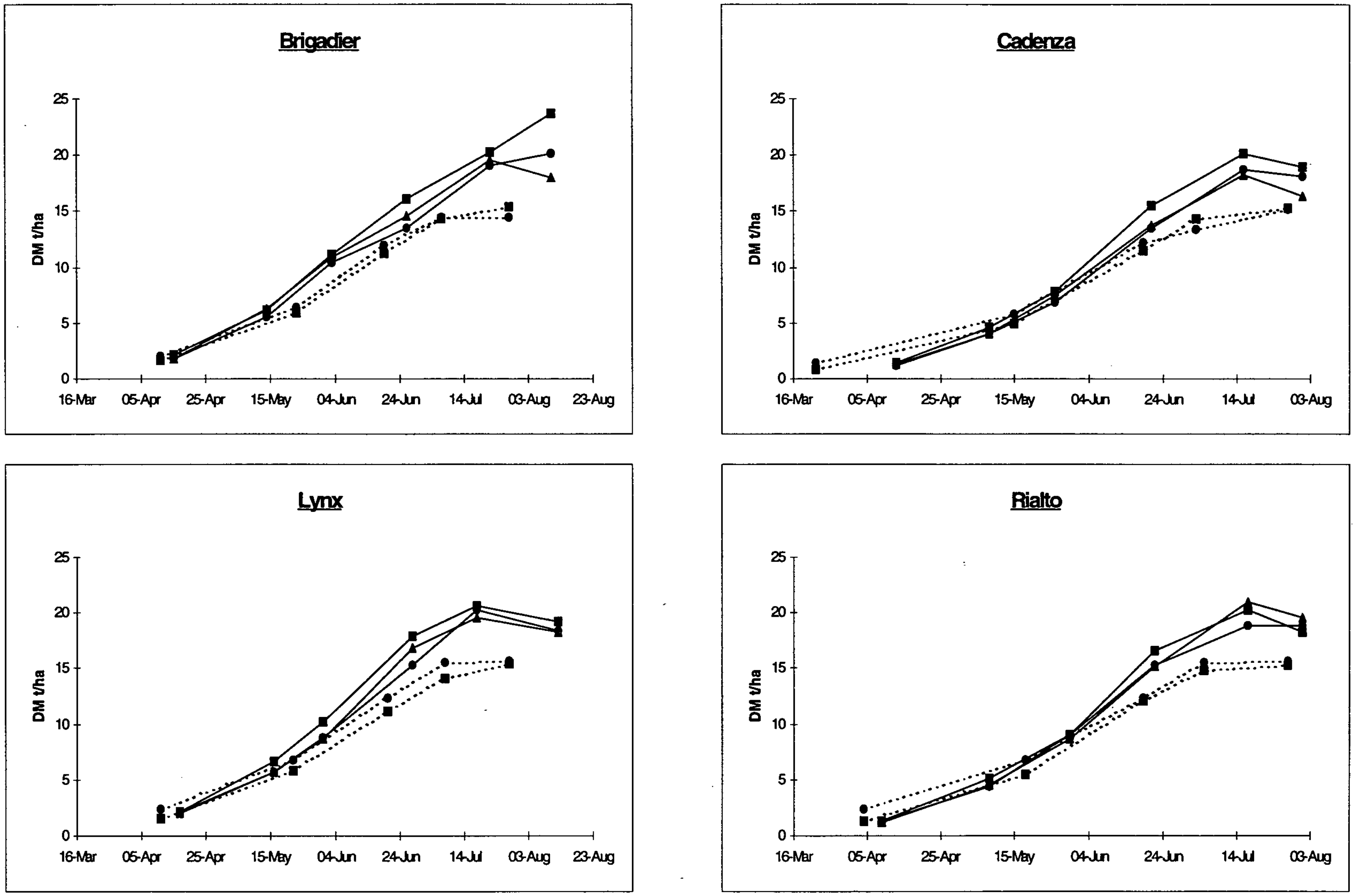

Figure 3.5. ADAS Rosemaund crop biomass (t dm/ha) for 1994 (- - -), 1995 (......) and 1996 (—) for first (•), second (●) and third (▲) wheat crops

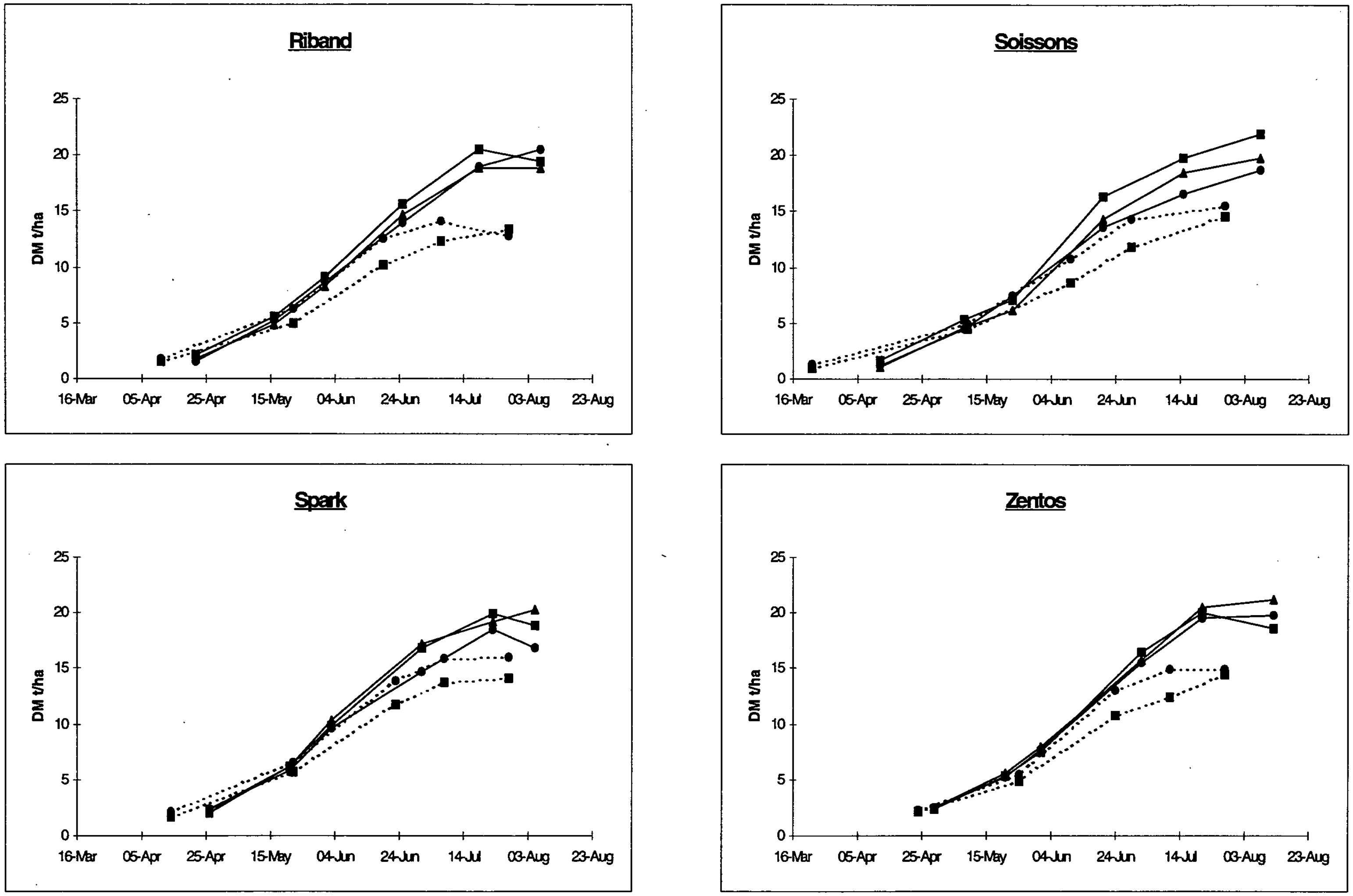

Figure 3.5 cont. ADAS Rosemaund crop biomass (t dm/ha) for 1995 (......) and 1996 (—) for first (•), second (●) and third (▲) wheat crops

3.5.2. Crop dry mass

Effects of rotational position on crop dry mass were generally small and inconsistent at GS 31. This was accounted for by the combination of relatively late disease epidemics and balancing the N in the preceding crops.

Table 3.9. ADAS Rosemaund statistics for total above-ground crop dry mass

Growth stage	31		33	39		61+75^{0}C days		39+650^{0}Cdays		Zero GAI	
Year	1995	1996	1996	1995	1996	1995	1996	1995	1996	1995	1996
Type SED	0.229	0.083	0.138	0.108	0.521	0.103	0.504	0.444	0.551	0.910	1.060
P value	NS	0.112	0.032	0.026	NS	0.005	0.039	0.098	0.147	NS	NS
df	2	4	4	2	4	2	4	2	4	2	4
Variety SED	0.143	0.160	0.316	0.273	0.416	0.580	0.577	0.707	0.627	0.749	0.901
P value	<0.001	<0.001	<0.001	<0.001	<0.001	0.001	<0.001	0.031	0.072	0.052	0.002
Type x Variety SED	0.297	0.272	0.530	0.377	0.853	0.774	1.062	1.035	1.155	1.345	1.803
P value	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

In 1994-5 there was a tendency for greater dry mass for second wheats between GS 39 and GS 39+650^{0}Cd (Fig. 3.5 & Table 3.9). This result is the reverse of what may be expected but is likely to be due to increased mineralisation of the wheat residues compared to the oat residues as postulated in the GAI section.

In 1995-6 there was also a significant effect of rotational position on crop dry mass, an effect which was most noticeable at anthesis (Fig. 3.5 & Table 3.9). The first wheats produced greater dry mass than either the second or third wheat crops, reflecting the lower severity of take-all in first wheat plots. The rapid divergence of the take-all epidemics began in late April and is consistent with effects on crop growth at anthesis around the end of June.

In all site-seasons up to GS 61+75^{0}Cd, variety had a highly significant effect on total crop dry mass (Table 3.9). This effect was largely explained by differences in development rate between the varieties (Table 3.4), those which developed later having longer in which to intercept light and grow up to the growth stage specified for sampling. At the later sampling times taken at mid-senescence and zero GAI, the differences between the varieties became less significant. However, the varietal differences were still significant ($P< 0.05$) or highly significant ($P< 0.01$) when analysed across years. At these later stages the developmental differences between varieties were reduced (in terms of calendar days). Soissons, however, was still 8 days earlier to anthesis than the next fastest developing varieties and produced significantly less dry mass. Rialto and Zentos were the varieties which most noticeably broke the trend for crop dry mass to be related to development, being one of the earliest and the latest, and producing the highest and one of the lowest biomasses respectively. It is not immediately apparent that this is due to large differences in canopy size relative to other varieties although Rialto did tend to show a slower rate of canopy senescence during grain filling; an additional explanation for these observations may be that these varieties exhibit above and below average radiation conversion efficiencies. This effect for greater biomass for Rialto was also observed in the Mositure Availability Sub-Project. For example, overall in 1993-4 and 1994-5 at ADAS Gleadthorpe, under irrigated conditions at GS 61, Rialto had lowest GAI at 4.2. Its crop dry mass at GS 61, however, was greatest at 12.2 t/ha (see Part 1, this volume).

Table 3.10. GS 87 Total above-ground crop dry mass t/ha (100% DM)

Rotational position and variety	1993-4	1994-5	1995-6
First	**Bw**	**Rm**	**Rm**
Brigadier	18.51	15.91	18.88
Cadenza	18.10	14.93	20.00
Lynx	18.84	14.76	19.79
Rialto	18.54	14.63	20.04
Riband	17.75	13.12	18.91
Soissons	18.23	14.67	15.88
Spark	19.18	14.36	20.66
Zentos	19.76	14.38	16.81
Mean	18.61	14.59	18.87
Second			
Brigadier	16.65	14.33	19.61
Cadenza	18.51	15.18	19.62
Lynx	17.20	15.61	19.04
Rialto	17.07	16.82	21.31
Riband	15.71	12.83	19.53
Soissons	18.11	15.52	19.15
Spark	18.90	16.01	18.02
Zentos	18.99	14.95	17.08
Mean	17.64	15.16	19.17
Third			
Brigadier	-	-	19.96
Cadenza	-	-	18.20
Lynx	-	-	17.67
Rialto	-	-	21.47
Riband	-	-	15.62
Soissons	-	-	17.02
Spark	-	-	18.01
Zentos	-	-	16.53
Mean	-	-	18.06
Type SED	0.398	0.910	1.060
P value	NS	NS	NS
df	2	2	4
Variety SED	0.829	0.749	0.901
P value	NS	0.052	0.002
Type x Variety SED	1.166	1.345	1.803
P value	NS	NS	NS
df	28	24	39

There was no evidence that the varieties responded differently to rotational position. It must again be borne in mind however that the expression of varietal traits as non-first wheats in comparison to first may have been masked to an extent by drought conditions.

Observation of maximum total dry mass production as measured at zero GAI shows that in both 1993-4 and 1994-5, Boxworth produced larger crops than Rosemaund, first wheats being 2.4 and 3.8 t/ha heavier, respectively. This greater crop growth was not reflected in significantly greater grain yield at Boxworth, first wheats yielding 0.6 and 0.07 t/ha more than at Rosemaund in 1993-4 and 1994-5, respectively. The inefficiency of conversion of extra crop growth into grain yield and the masking of varietal differences in terms of biomass production may indicate the curtailing of late season growth at Boxworth by some site factor. This may be due to greater drought stress on its soils having a slightly lower available water capacity than the silty soils at Rosemaund. In neither season at Boxworth was there any significant effect of variety on maximum dry mass production, whilst at Rosemaund variety had a significant effect in and across all seasons. The effect of greater maximum biomass for Rialto compared to other varieties detected in the Moisture Availability Sub-Project was clearly evident in the experiments at Rosemaund. Similarly, the effect for the shorter lifecycle variety Soissons to have lower maximum dry mass (see Part 1, this volume) was also detected at Rosemaund 1995-6 but not in the previous season in 1994-5.

3.5.3. Nitrogen offtake

3.5.3.1. GS 31 nitrogen uptake

There was a large effect of season on GS 31 nitrogen uptake by the two crops at Rosemaund in 1994-5 and 1995-6 (Table 3.11). The levels of soil mineral nitrogen (SMN) preceding each of the crops were not significantly different enough to account for the differences between the seasons (section 2.2.3). Winter temperatures were higher for the 1994-5 crop than the 1995-6 crop (Appendix table 1), indicating that N uptake was unlikely to have been restricted by poor crop growth. This is supported by the measures of GS 31 crop dry mass (section 3.4.2). The most likely cause of the large difference between the seasons would appear to be water supply in the spring, restricting the acquisition of applied nitrogen. The 1994-5 and 1995-6 crops received their first application of nitrogen on 23 March and 20 March, respectively. In 1994-5 this was followed by a period of 4 weeks with no significant rain (Fig. 3.2.b). This resulted in a predicted SMD of almost 80 mm by the time significant sustained rainfall occurred (Figure 3.2.b). In 1995-6 in the week following the early application of nitrogen there was more than 30 mm of rain, and no significant sustained SMD developed until mid-April in this year.

There was an effect of rotational position on early N uptake in both 1994-5 and 1995-6 (Table 3.11). The effect was, however, different in the two seasons; in 1994-5 the second wheats had taken up 48 kg N/ha compared to 38 kg N/ha for first wheats. This appears to have been due to what was thought to have been an insignificant difference of 15 kg N/ha in SMN measured in the previous autumn. However, as stated above, the particularly dry conditions in the spring of this year may have resulted in a much greater reliance of the crop on residual rather than applied N pre GS 31, than would normally be expected. In 1995-6, however, the first wheats had taken up 10 and 8 kg N/ha more than the second and third wheats respectively, a small but significant amount. The first wheats did have higher SMN reserves in the previous autumn than either of the other two crops (section 2.2.3). This was, however, countered by the application of 40 kg N/ha applied to the second and third wheats as ammonium nitrate pre-ploughing of the experimental area. This should have resulted in a slightly higher nitrogen supply on the second and third wheats (93 and 85 kg N/ha) compared to the first wheat (78 kg N/ha). The poorer recovery of N by the second and third wheats, despite this slightly higher supply may indicate some loss of root function early in the growth of the crop. This would be supported by the higher levels of take-all observed early in the life of this crop.

Table 3.11. Total crop nitrogen uptake (kg/ha) at GS 31, ADAS Rosemaund 1994-5 & 1995-6

	1994-5		1995-6		
	First	**Second**	**First**	**Second**	**Third**
Brigadier	42.12	51.39	99.1	83.2	84.4
Cadenza	20.50	32.84	78.8	62.0	67.6
Lynx	42.67	63.66	98.8	91.8	89.3
Rialto	39.02	44.64	77.0	76.3	76.8
Riband	42.18	52.96	97.9	74.7	84.3
Soissons	23.27	31.43	89.6	67.7	64.4
Spark	45.05	58.05	92.1	99.5	99.9
Zentos	50.58	46.33	103.2	103.1	105.3
Mean	38.17	47.66	92.1	82.3	84.0
Position SED	2.32		2.30		
P value	0.055		0.027		
df	2		4		
Variety SED	3.96		5.34		
P value	<0.001		<0.001		
Position x Variety	5.73		8.95		
SED	NS		NS		
P value					
df	24		42		

Variety had a highly significant effect on nitrogen uptake in both site-seasons. Nitrogen uptake varied from 27 kg N/ha for Soissons and Cadenza to 53 kg N/ha for Lynx in 1994-5, and 48 kg N/ha for Cadenza to 76 kg N/ha for Zentos in 1995-6. The varietal effect was almost completely accounted for by rate of development, the varieties attaining GS 31 the earliest (and therefore sampled earliest) having the lowest N uptake and the latest developing varieties the highest N uptake. Meaned across the 2 seasons date of GS 31 accounted for 87 % of the variation in N uptake. In neither season was there any significant interaction between variety and rotational position.

3.5.3.2. Harvest nitrogen uptake

There was no significant effect of rotational position on N offtake at Boxworth in 1993-4 or Rosemaund in 1994-5 (Table 3.12). There was however an indication at Rosemaund in 1995-6 that the effect measured at GS 13 was still present. Although the effect was not significant at harvest the difference between the rotational positions had increased. Total N recovered by the crop was reduced from 234 kg N/ha in the first wheat, to 226 kg N/ha in the second and 211 kg N/ha in the third wheat.

Varietal differences in total N uptake were significant at Rosemaund in 1995-6 and nearly significant in 1994-5 (Table 3.12). There was a tendency for the varieties which performed well as second wheats (Rialto and Lynx) to exhibit greater N recovery than those varieties which performed poorly, Spark consistently having the poorest N recovery despite its potential as a bread making variety. The ranking of the varieties at harvest had changed completely from those observed at GS 31. The earlier developing varieties (Soissons, Cadenza and Rialto) tending to acquire the largest amounts of nitrogen, and the later developing varieties tending to recover less N. This effect was particularly noticeable in the third wheat at Rosemaund in 1995-6, the only exception being Lynx which whilst relatively late developing consistently recovered one of the highest levels of nitrogen.

Table 3.12. Total crop N offtake at harvest (kg/ha)

	1994	1995	1996
First	**Bw**	**Rm**	**Rm**
Brigadier	264.16	186.84	213.32
Cadenza	267.85	175.62	235.91
Lynx	282.22	190.45	247.47
Rialto	263.67	188.15	255.83
Riband	261.06	177.00	221.01
Soissons	258.69	184.27	243.82
Spark	277.79	179.66	226.96
Zentos	228.87	176.00	224.73
Mean	262.83	182.25	233.63
Second			
Brigadier	269.47	177.67	209.01
Cadenza	218.91	173.01	230.82
Lynx	300.29	194.17	241.59
Rialto	266.77	191.07	242.06
Riband	289.23	176.17	210.94
Soissons	248.94	176.23	232.05
Spark	237.62	180.52	208.98
Zentos	239.80	170.25	230.48
Mean	258.88	179.88	225.74
Third			
Brigadier	-	-	192.93
Cadenza	-	-	213.47
Lynx	-	-	223.25
Rialto	-	-	226.34
Riband	-	-	193.62
Soissons	-	-	216.15
Spark	-	-	209.00
Zentos	-	-	211.66
Mean	-	-	210.80
Type SED	16.81	4.72	16.33
P value	NS	NS	NS
Df	2	2	4
Variety SED	21.91	6.67	4.99
P value	NS	0.079	<0.001
Type x Variety SED	33.51	10.00	18.22
P value	NS	NS	NS
Df	27	24	42

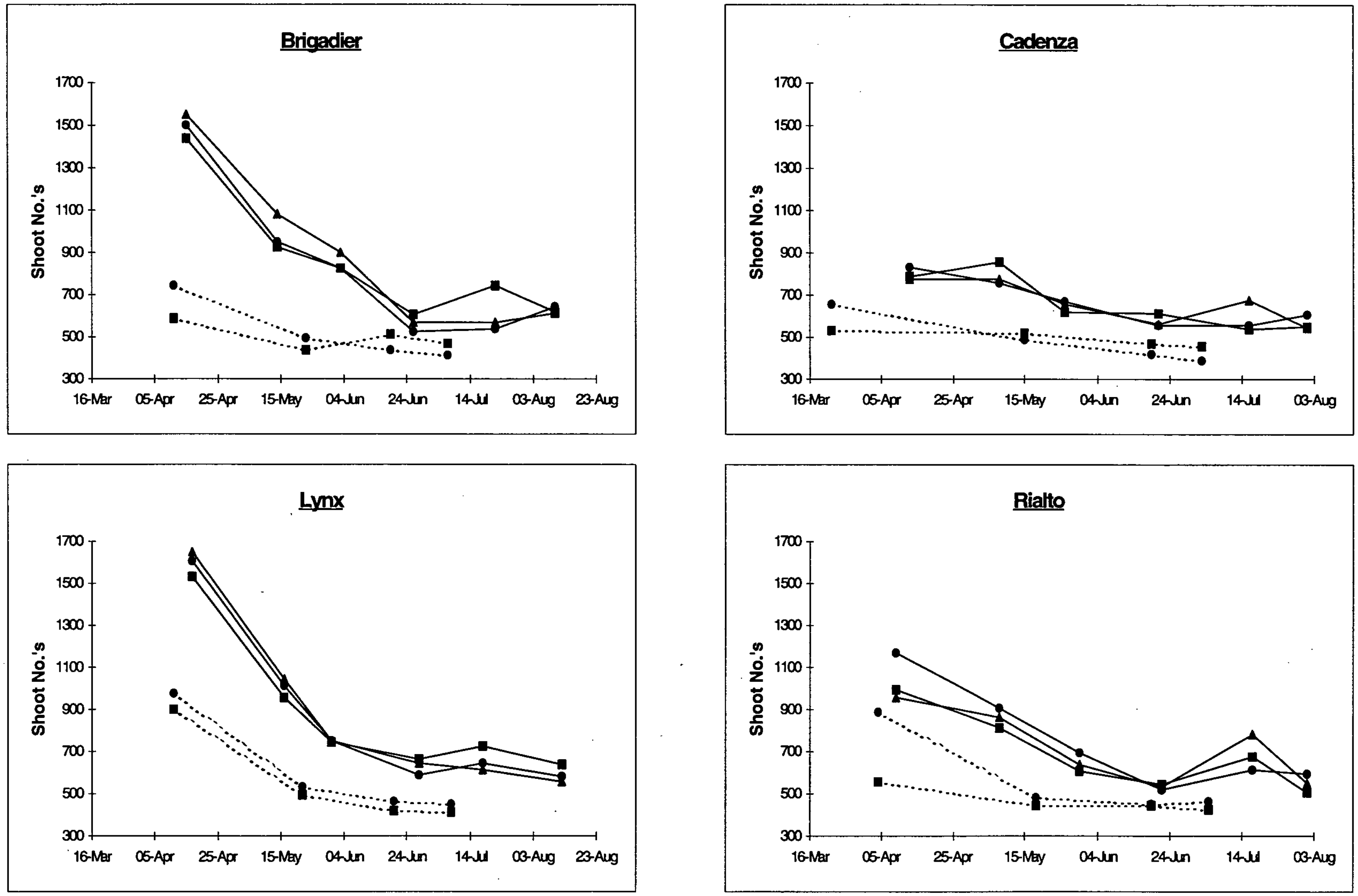

Figure 3.6. ADAS Rosemaund, shoot number per m^2 for 1995 (......) and 1996 (—) for first (•), second (●) and third (▲) wheat crops

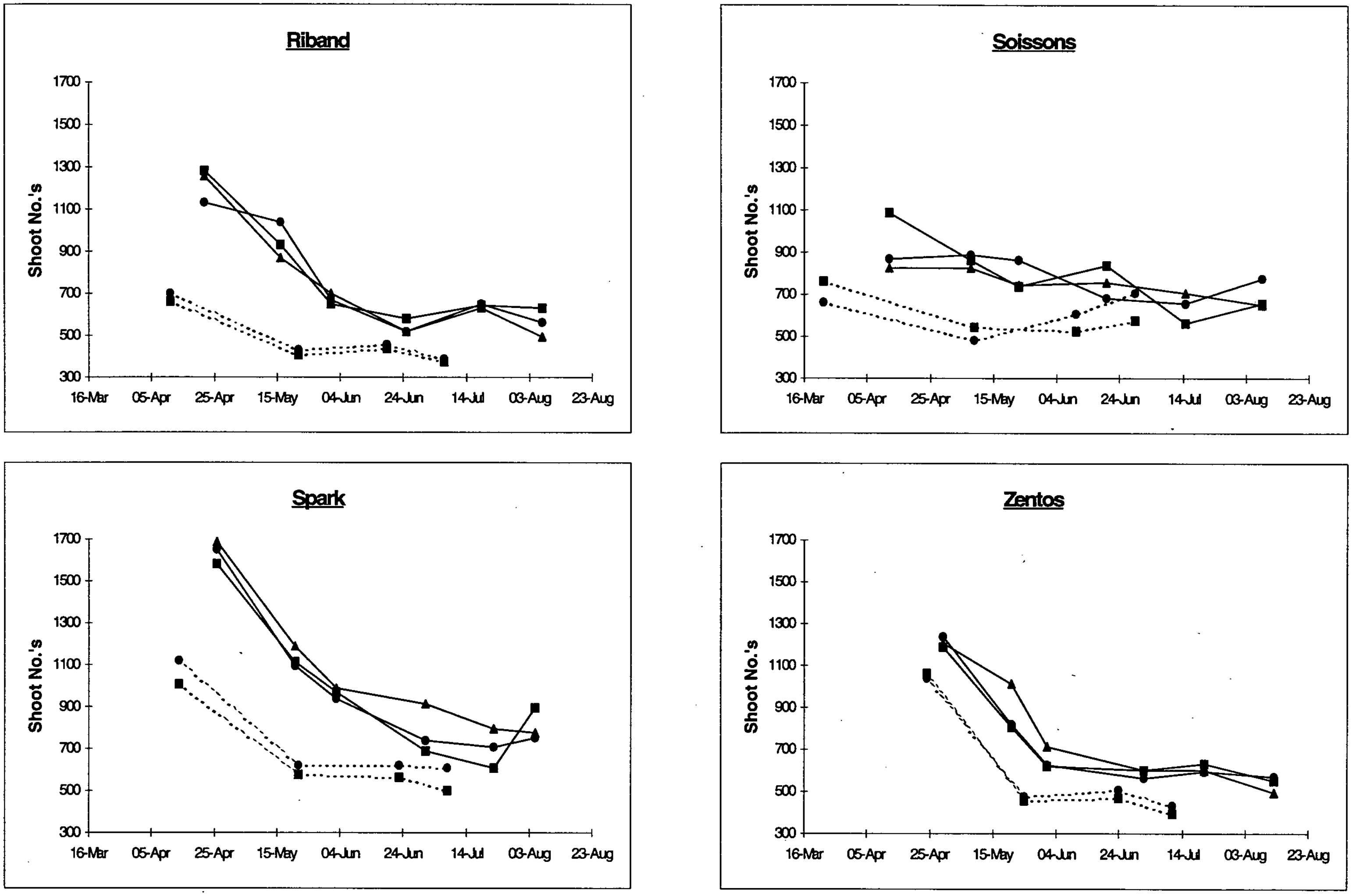

Figure 3.6 cont. ADAS Rosemaund, shoot number per m^2 for 1995 (......) and 1996 (—) for first (•), second (●) and third (▲) wheat crops

3.5.4. Tillering

3.5.4.1. Effect of season

There was a significant effect of season on shoot number at all stages of crop development assessed (Table 3.13). This would appear to be due to the efficiency of use of applied N, particularly the early application being restricted in 1994-5 through lack of moisture (section 3.4.3.1). This is supported by the much smaller magnitude of the effect on Cadenza and Soissons. They, due to their earlier date of GS 31, were more reliant on residual N for tiller production than the other varieties in which GS 31 occurred significantly after the application of the early nitrogen.

Table 3.13. ADAS Rosemaund, analysis of variance of shoot number per m^2

Growth stage	31		33	39		61+ 75 ^{0}Cdays		39+650 ^{0}Cdays		Zero GAI
Year	1995	1996	1996	1995	1996	1995	1996	1995	1996	1996
Position SED	65.30	66.30	34.20	13.50	47.6	15.06	39.53	8.54	18.08	24.80
P	NS	NS	NS	NS	NS	NS	NS	0.068	0.133	NS
Df	2	4	4	2	4	2	4	2	4	4
Variety SED	97.40	104.80	65.80	31.86	53.2	32.81	36.93	24.99	35.39	35.58
P	<0.001	<0.001	<0.001	<0.001	<0.001	0.001	<0.001	<0.001	<0.001	<0.001
Variety * Position SED	144.40	182.30	111.90	44.26	98.5	45.94	71.71	34.15	60.12	62.75
P	NS	NS	NS	NS	NS	NS	NS	0.007	NS	NS
Df	24	42	42	24	42	23	42	24	42	38

3.5.4.2. Effect of rotational position

There was generally no effect of rotational position on shoot number, although rotational position differences as measured mid-senescence in 1994-5 were apparently approaching significance; there was also a significant rotational position/variety interaction (Table 3.13). This apparent interaction with some varieties producing more shoots as first wheats and others more as second wheats was unrelated to other parameters measured. This in combination with the fact that final shoot number is often determined by GS 39 and always by anthesis, and no hint of an effect was detected at either of these assessments, indicated that this is likely not to be a real effect.

3.5.4.3. Effect of variety

Variety had a highly significant effect on shoot number in all samples in all seasons (Table 3.13). There was a relationship apparent between maximum shoot number produced and the date of GS 31 of the variety, this was particularly noticeable in 1995-6. The later developing wheats, Brigadier, Lynx, Riband, Spark and Zentos, displaying significantly higher maximum shoot numbers than the more rapidly developing varieties, Cadenza, Soissons and Rialto (Fig. 3.6). Such an effect amongst varieties was also detected in the parallel Variety Typing Trials exercise (see Vol. V, Part 1) and Additional Character Assessments in NIAB RL trials 1995-6 (see Vol. V, Part 2). Among the varieties displaying high maximum shoot numbers there were apparent differences in the phasing of tiller death. Lynx, Riband and Zentos lost the majority of their excess tillers by the sample taken at GS 39, whilst Brigadier and Spark were still loosing significant numbers of shoots until the sample taken at GS 61 + 75^0C days. Differences between varieties in final shoot number were not as large as those displayed for maximum shoot number but significant differences still existed. The relationship between developmental rate and shoot number was lost by the final samples. Soissons which initially had low shoot numbers maintained high numbers, of a similar order of magnitude to Spark, which initially had the highest number of shoots. Cadenza which had initially low numbers of shoots maintained an intermediate number of a similar order to Brigadier, Lynx and Zentos which initially had high numbers. Rialto and Riband, which were both intermediate in terms of maximum shoot number, maintained the fewest shoots to harvest (Fig. 3.6).

In order to assess the likely importance of these shoots which are produced but are not going to contribute to yield, at Rosemaund in 1995-6 the crops were sampled according to shoot hierarchies. For the first three samples (GS 31, GS 33 and GS 39) the biomass of each shoot group was measured. Thus at each of the first three samples, the biomass which was contained in dead shoots or shoots destined to die could be assessed (Fig. 3.7).

The proportion of the total dry matter contained in shoots which are dead or destined to die showed a large range between varieties. Brigadier which was the least efficient contained 33% and 22% of its dry matter in non-yield producing shoots at GS 31 and GS 39, respectively. At GS 39 this was equivalent to 2.3 t/ha dm. Soissons by virtue of its initially low numbers of shoots and high shoot survival had the most efficient tillering pattern containing 7% and 9% in non-yield producing shoots at GS 31 and GS 39 respectively. Lynx and Riband which initially had relatively large proportions of their dry matter in non-yield producing shoots with 32% and 29% at GS 31 respectively, apparently aborted these shoots early and contained only 12% and 14% respectively in non-yield producing shoots by GS 39. Rialto and Spark were a contrast, the former loosing relatively few shoots (500/m^2) and the latter one of the most inefficient in terms of shoot numbers loosing 900/m^2. In dry matter terms, the situation was reversed with Rialto containing 1.75 t/ha dm in non-yield producing shoots and Spark 1.4 t/ha dm at GS 39. This indicates that whilst maximum and final shoot numbers may act as a guide to economy in crop growth, the relative size of shoots and the distribution of shoot size in different shoot hierarchies must be taken into account to get a true picture.

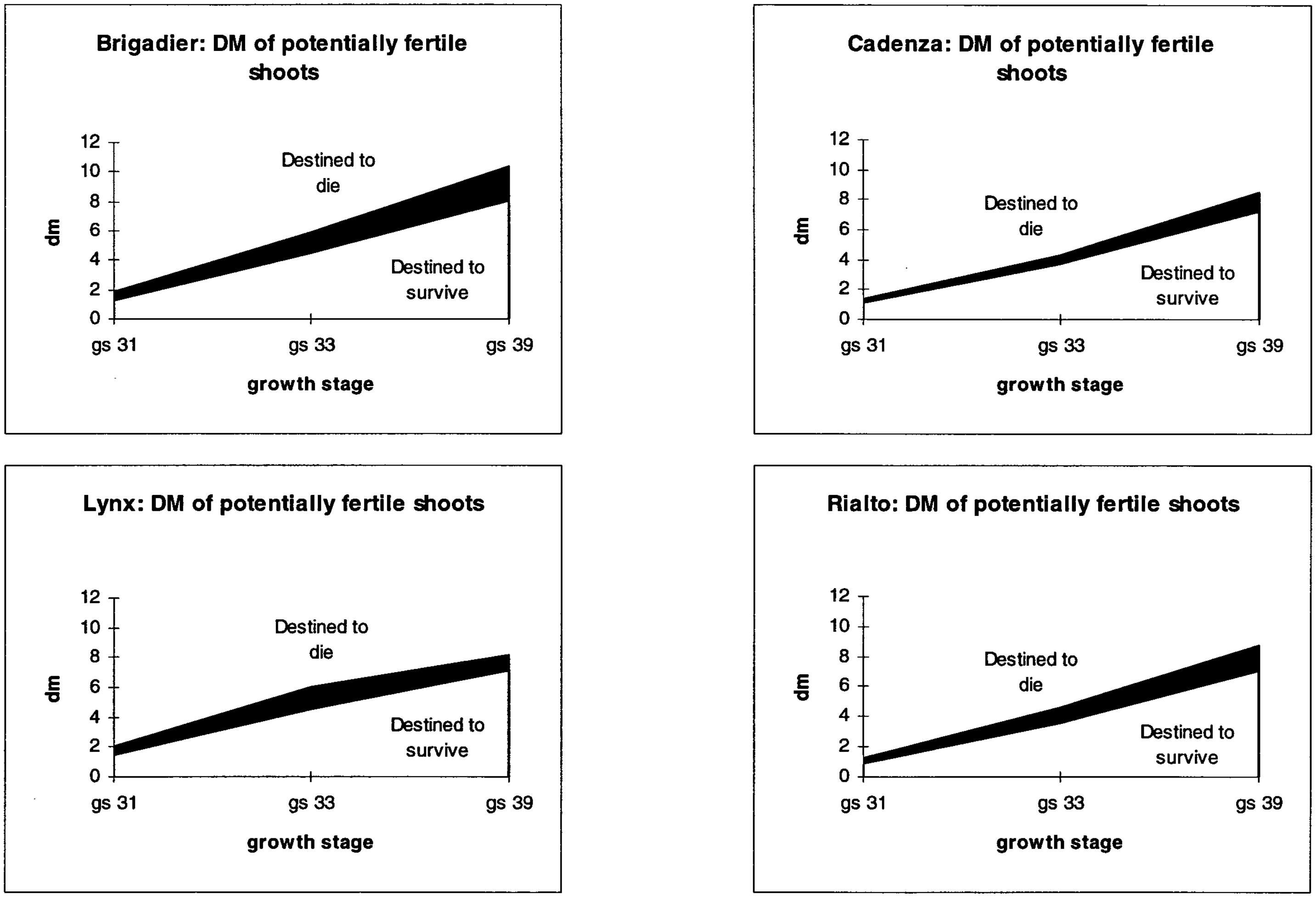

Fig. 3.7. ADAS Rosemaund, 1995-6, economy of tillering.
Total crop biomass and proportion contained in shoots destined to die (mean of first, second and third wheats).

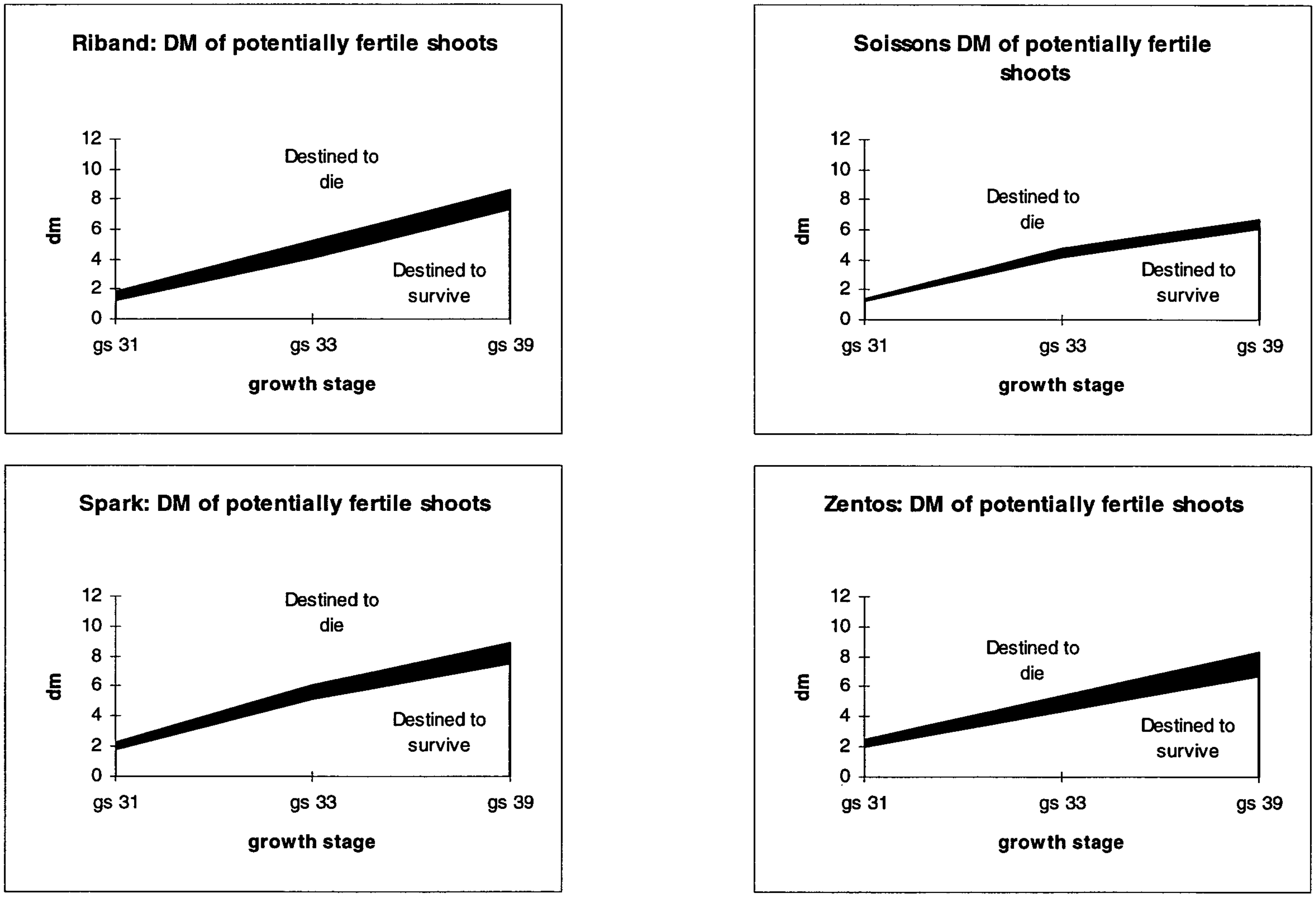

Fig. 3.7. cont. ADAS Rosemaund, 1995-6, economy of tillering.
Total crop biomass and proportion contained in shoots destined to die (mean of first, second and third wheats).

Table 3.14. Soluble stem carbohydrate measured at GS 61 + 75°Cdays at ADAS Rosemaund (Rm) and ADAS Boxworth (Bw), (t dm/ha)

	1993-4	1994-5	1995-6
First	**Bw**	**Rm**	**Rm**
Brigadier	3.00	2.21	3.55
Cadenza	3.27	2.37	2.70
Lynx	3.39	2.50	4.00
Rialto	3.69	2.66	3.64
Riband	2.66	1.98	2.54
Soissons	3.06	1.92	3.40
Spark	1.93	2.26	2.87
Zentos	1.77	2.02	2.88
Mean	2.84	2.24	3.20
Second			
Brigadier	3.08	2.75	2.94
Cadenza	3.19	2.95	2.45
Lynx	3.05	2.93	3.57
Rialto	3.56	2.88	3.68
Riband	2.62	2.63	2.35
Soissons	3.01	2.42	3.01
Spark	1.88	2.53	2.58
Zentos	1.43	2.91	3.00
Mean	2.73	2.75	2.95
Third			
Brigadier	-	-	3.14
Cadenza	-	-	2.22
Lynx	-	-	3.74
Rialto	-	-	3.55
Riband	-	-	2.54
Soissons	-	-	2.98
Spark	-	-	2.87
Zentos	-	-	2.52
Mean	-	-	2.94
Type SED	0.15	0.13	0.074
P value	NS	0.061	0.044
Df	2	2	4
Variety SED	0.20	0.19	0.165
P value	<0.001	0.055	<0.001
Type x Variety SED	0.30	0.29	0.277
P value	NS	NS	NS
Df	28	28	42

3.5.5. Stem water soluble carbohydrate reserves

The level of water soluble carbohydrate reserves stored in the stems was measured at GS 61+75^{0}C days. From previous work this is the time when the reserves are at or close to maximal. The results are expressed as tonnes of stem soluble carbohydrate dry matter per hectare (Table 3.14).

There was no consistent effect of rotational position on stem carbohydrate reserves in the three site-seasons. There was no effect at Boxworth 1993-4. At Rosemaund 1994-5 the difference was close to significance (Table 3.14), second wheats containing on average 0.5 t/ha more than the first wheats. The absolute amount of stem soluble carbohydrate is a product of the total stem dry mass and the concentration of water soluble carbohydrate (WSC) in stems. As has been stated earlier, the crop dry mass was higher in the second wheats than first wheats at this growth stage (Table 3.9). It is this apparent effect associated with increased reliance on SMN reserves due to inefficient recovery of applied N on crop growth which resulted in more stem reserves in the second wheats. The reverse trend was recorded at Rosemaund in 1995-6 with second and third wheats containing 0.25 t/ha less than the first wheats. This was again due to differences in crop dry mass (Table 3.9) rather than differences in the concentration of soluble carbohydrate in the stems. In this case, however, differences in crop growth appeared to be due to the effect of take-all on nitrogen acquisition. This was an expected effect of the disease, rather than a coincidental effect of environmental conditions on efficiency of recovery of applied N.

In all site-seasons there was a significant effect of variety on soluble carbohydrate reserves (Table 3.14). There was also a significant effect of variety across seasons within a site (Table 3.14) which is indicative of this being a heritable varietal characteristic. There was, however, a significant season/variety interaction pointing to the fact that the ranking of the varieties changed soemwhat between seasons. This might be expected due to the absolute amount of stem reserves being due not only to the genetic ability of a variety to store stem reserves, but also the rate and duration of photosynthesis between the specific developmental stages. Changes in environmental conditions whilst structural stem carbohydrates and soluble carbohydrates are being deposited would be expected to alter the absolute amount of soluble carbohydrates stored. Relatively short term differences in radiation and temperature, affecting the rate of photosynthesis and the duration between critical developmental stages respectively, would therefore be expected to interact with varietal potential for amassing reserves given that significant changes in the timing of the developmental stages exist between the varieties tested. It is also noticeable that the varieties with the most extreme rates of development, Soissons (early) and Zentos (late), were those which changed most in their ranking between sites and years. Soissons ranked third at Boxworth in 1993-4 and Rosemaund 1995-6, but ranked eighth at Rosemaund in 1994-5. Similarly, Zentos which was ranked eighth at Boxworth in 1993-4, accumulated more reserves than Soissons, Riband and Spark and was on a par with Brigadier at Rosemaund in 1994-5. Not only did the order of some of the varieties change between sites and years but also the absolute range of soluble carbohydrate stored by the different varieties changed between sites and seasons. At Rosemaund in 1994-5 there was a relatively small range of 0.6 t/ha : the range was greater in the other site-seasons; 1.34 t/ha for Rosemaund 1995-6 and 2.02 t/ha for Boxworth 1993-4.

Despite the interaction between variety and season in the amounts of stem soluble carbohydrate the varietal rankings at the extremes of the range were fairly consistent. Either Lynx or Rialto were consistently first in the range in terms of the amounts stored whilst, Spark was consistently at or close to the bottom of the range.

4. DISCUSSION

The original hypothesis stated that although varietal resistance to take-all is apparently absent from all past and current wheat varieties, there is empirical evidence to suggest that varietal tolerance of take-all infection may exist. The evidence for differing tolerances of the disease was based on the change in grain yield ranking of varieties in NIAB and ADAS variety trials when sited in first and non-first wheat crops.

4.1. Evidence for varietal resistance to take-all

The original hypothesis that varietal resistance to take-all was absent was based on the weight of evidence in publications (e.g. Hollins *et al.*, 1986) to that effect. Although there have been infrequent reports suggesting that resistance may exist, such differences have never been consistently expressed over a run of site-seasons. In each site-season as well as the seasonal disease progress being monitored (Figs. 3.2.b & 3.3.b), at about ear emergence (when the disease should be at a reasonable level but the roots can still be reliably assessed), all treatment combinations were assessed for take-all. The results, expressed as an index accounting for both incidence and severity, consistently showed no effect of variety on the take-all level (Tables 3.1 & 3.2). Given the number of individual assessments which have gone into the cross-season analysis of these results, and the apparent absence of a variety effect, it can be confidently stated that varietal resistance to the disease was not a factor in the results of this work.

4.2. Evidence for varietal suitability to rotational position

The expectation of this project was that when varieties were grown as first and subsequent wheats randomised within a single experiment, and all other variables limited, there would be a significant interaction between variety and rotational position. This interaction could not be detected. There are a number of possible explanations for the lack of significant rotational position/variety interactions, namely:

i) None of the seasons in which the experiment was conducted was a particularly severe take-all season, the disease development being limited by either cool or very dry (or both) conditions in the spring and early summer. The effect of the disease on yield was therefore not as large as expected.

ii) Take-all is an inherently variable disease which occurs in patches within the crop rather than as a uniformly distributed effect. This by its very nature causes significant variation within such experiments and differences must be large before they can be detected statistically.

In the majority of site-season combinations the growing conditions were characterised by drought occurring at some point during growth, and the varieties did not perform in first wheats as expected according to their NIAB RL rankings. The comparison of first and second wheats was therefore equivalent to a comparison between i) drought-affected and ii) drought-affected plus take-all-infected crops. Comparison of the traits predicted to confer suitability to drought and non-first wheat crops shows that they are similar : i.e. economy of tillering, flowering date and ability to amass stem soluble carbohydrate. Therefore, for varieties predicted to tolerate take-all root loss, when their non-first wheat yield was compared to their first wheat performance (as affected by drought), the vartietial rankings for these types appear similar. This is not because they are not good second wheats, but rather they are performing above their expected level as first wheats under drought also. The effect of environment on first wheat yield can be seen by comparing the ranking of six of the varieties common to these experiments and the NIAB Recommended List (1996). The first wheat yields at Rosemaund and Boxworth are expressed as a percentage of the yield of Riband (100%) for ease of comparison.

Table 4.1 Rankings for six varieties as first wheats on NIAB RL 1996 and in experiments at Boxworth 1993-4, Rosemaund 1994-5 and Rosemaund 1995-6

Variety	NIAB RL 1996	Boxworth 1993-4	Rosemaund 1994-5	Rosemaund 1995-6
Brigadier	104	107	109	103
Rialto	100	104	109	118
Riband	100	100	100	100
Cadenza	97	107	97	105
Soissons	93	100	101	108
Spark	94	93	104	98

Those varieties (e.g. Rialto and Soissons) which could be expected to perform relatively better in drought conditions (see Moisture Availability Sub-Project, Part 1, this volume) yielded well above their predicted level as first wheats in experiments at Rosemaund and Boxworth (Table 4.1). For example, in the experiments at ADAS Gleadthorpe 1993-4 to 1995-6 (see Part 1, this volume), Rialto and Soissons's yield under drought as a percentage of Riband was 107% and 96%, respectively. This is compared with their expected NIAB RL percentage yields of 100% and 94%, respectively (NIAB, 1996). If first wheat yield was affected by drought in rotational position experiments then expression of yield in the second wheats must be due to a combination of both drought plus some additional effect of the take-all disease. The varieties grown as second wheats are likely to separate more than when one or the other stress is present but the comparison with first wheat performance will be masked to some extent by a common response to drought. It is not entirely surprising therefore that significant interactions of rotational position and variety were not found.

Even given the nature of the data set outlined above, there appears to be good evidence, particularly in comparison with the expected performance of the varieties from the NIAB Recommended List as first wheats, that varieties differed in their susceptibility to yield loss caused by take-all. For certain varieties there was a clear tendency for deviations from NIAB rankings; for example, the better than expected performance of Rialto and the converse for Spark.

4.3. Evidence for varietal characteristics indicating suitability

4.3.1. Rate of development

There were consistent and relatively large differences in the developmental rates of the varieties tested. The range was significantly increased by the inclusion of varieties bred in other countries, Soissons (France) and Zentos (Germany). The average range in date of GS 31 at Rosemaund within the British-bred wheats was 13 days (Cadenza - 10 April to Spark - 23 April). This range was increased by the inclusion of Soissons (7 April) and Zentos (28 April) to 21 days. The range in date for start of anthesis (GS 61) for British-bred varieties was shorter (6 days), the extremes again being Cadenza and Spark, 14 June and 20 June, respectively. As with the earlier growth stages, the range was increased through inclusion of Soissons (9 June) and Zentos (21 June) to 12 days.

Overall date of flowering did not relate well to non-first wheat performance. This was due mainly to the extreme early date of flowering of Soissons, which did not result in a particularly high yield. A variety such as this from a very different genetic background compared to the bulk of the varieties will differ in a large number of characteristics as well as its very different developmental pattern. It may, for example, due to its very early development, suffer adverse affects due to radiation frosts post-ear emergence, which would negate the possible benefits of early grain filling. If Soissons is removed from the data set there is a slight trend for later date of flowering to relate to lower yield. This trend exists for both first and non-first wheat crops. However, the rate of decline in yield due to delayed flowering in non-first wheat crops is greater than in first wheat crops. As well as the generally less favourable environmental conditions for grain filling experienced with delayed flowering which are outlined in the Length of Growing Season Sub-Project (See Part 4, Section 4), in a non-first wheat situation there will be additional pressure on grain filling due to water shortage caused by root loss. This effect may have been, in part, responsible for the relatively poorer performance of the late flowering Spark as a second wheat. There are, however, some dangers in drawing conclusions about effects of individual traits from a restricted sub-set of varieties. The trend for lower yield with later flowering in this experiment could have been because the two late developing varieties selected, Spark and Zentos, happened to be of low yield potential. In other circumstances, for example, the late developing varieties chosen could have been of higher yield potential, e.g. Haven or Consort. More generally, the lack of a clear-cut correlation between earlier flowering and better tolerance of late-season stress corroborates findings in the drought work (see Part 1). In that Sub-Project, early flowering did not increase water uptake during grain filling greatly under drought, even though water uptake to anthesis was much less; this was because total seasonal water uptake was greater for the slower developing varieties. With take-all, the loss of water uptake capacity occurs more suddenly than with drought. It could be that late-season stress avoidance is relatively more important for tolerance of take-all than it is for resistance to drought. The fact that the rate of decline in yield due to delayed flowering currently reported was greater in non-first wheats than in first wheats might suggest this. Thus, there still may be grounds for including date of flowering in the group of desirable traits describing tolerance of take-all root loss. Evidence from current experiments, however, would suggest that it should be included at a lower order of priority than first envisaged in our original hypotheses.

4.3.2. Economy of tillering

There was an inconsistent relationship between economy of tillering (as measured by the dry mass contained in dead tillers and those destined to die at GS 39) and the performance of a variety as a non-first wheat. This inconsistency was, however, due to a large extent to the high dry mass contained in dead and destined-to-die shoots as measured in Rialto, which performed best as a second wheat. For most other varieties there was a broad correspondence with the original hypothesis, in that those varieties losing least dry matter in aborted shoots performed relatively better than their overall NIAB RL rankings as third wheats in Rosemaund 1995-6. For example, Soissons, with least dry matter in aborted shoots, performed relatively better as a third wheat than its NIAB RL ranking. Conversely, Brigadier which contained the greatest proportion of its dry mass in aborted shoots, was intermediate among the varieties in its performance as a third wheat and thus lower than its NIAB top ranking for yield (NIAB, 1996). It must be borne in mind that this analysis was carried out only at Rosemaund in 1995-6. However, given the background variability between the varieties there is a strong basis for postulating that loss of dry mass in shoots that die may be detrimental in a crop grown in a high take-all situation.

It should be noted that at Rosemaund in 1995-6 there was a poor relationship between numbers of shoots lost and the dry matter contained within them. This was exemplified by Rialto, which had one of the lowest levels of shoot loss, but also one of the highest proportion of its dry mass contained in non-yield contributing shoots. Thus, assessment of economy of tillering solely on the basis of maximum and final shoot numbers may not be as useful as that incorporating some assessment of the size of individual shoots lost.

4.3.3. Stem carbohydrate reserves

Of the varietal characteristics recorded the amount of soluble carbohydrate reserves in the stem at GS61+75°Cd (about 5 days after the start of anthesis) had the greatest and most consistent effect on non-first wheat performance. This trait was also the candidate trait best correlated with yield performance under drought (see Part 1).

The response, in terms of yield increase to increasing soluble stem reserves, was higher than expected. In the third wheat at Rosemaund in 1995-6 for every 1 t/ha increase in soluble stem reserves there was a 0.75 t/ha increase in third wheat yield. If an average is taken across the second wheats in the three site-seasons, then for every 1 t/ha increase in stem reserves there was about a 1 t/ha increase in second wheat yield. These results indicate an efficiency of use of stored reserves somewhat greater than the reported literature of about 70% (Schnyder, 1993), when an allowance is made for a loss of carbohydrate through respiration and a cost to the plant due to transport. There is, however, evidence from other work that a proportion of the structural carbohydrate in the stem may be remobilised and used to fill the grain (Austin *et al.*, 1977). Compensation for inefficiencies in the use of soluble stem reserves by remobilisation of structural carbohydrate may be giving the impression that soluble reserves can be used with 100% efficiency. Whatever the route by which stem carbohydrates buffer grain filling against poor finishing conditions, the evidence from this work suggests that some indication of a variety's buffering abilities can be gained by measuring stem storage of soluble carbohydrates. It should be noted that there was also a good correlation between varietal differences in stem reserves and yield performance in first wheats, and this relationship was also detected in the first wheats comprising the parallel Variety Typing

Trials exercise (see Vol. V). However, even if reserves are used to maximize yield in more optimal conditions, it can be concluded that the proportional contribution of reserves in non-first wheats (where yields are generally at lower overall levels) will be greater than in first wheats and thus stem reserves should influence yield performance relatively more in these late-seasons stress environments.

The value of this trait, as a means of judging a variety's potential to perform well in a take-all prone situation, is the stability of the ranking of the varieties for their soluble carbohydrate reserves. The ranking of varieties remains broadly the same across sites and seasons, except where significant changes in growing conditions influence the period of rapid soluble carbohydrate deposition differentially in different varieties. This was only noted to occur to any extent where a variety was particularly early or late in its development (e.g. Soissons and Zentos), but appeared to be of relatively little importance in relation to the majority of varieties which vary in their development by only a few days. For the three common varieties to the Rotational Position and Drought Sub-Projects (Rialto, Riband and Soissons), there was a good correlation in their rankings for stem reserves between data sets. In the experiments at ADAS Gleadthorpe, overall Rialto at 3.0 t/ha had more reserves than Soissons at 2.5 t/ha and Riband at 2.4 t/ha. In the three site-seasons currently reported, the corresponding amounts were Rialto (3.4 t/ha), Soissons (2.8 t/ha) and Riband (2.5 t/ha). Also in both Sub-Projects, there was the same tendency for those varieties with lowest amounts of reserves to perform relatively worse under stress conditions. Thus, M. Hunstman's poor drought resistance in the experiments at Gleadthorpe and Spark's poor relative performance of as a non-first wheat in current experiments were, in a way, comparable. The conclusion drawn is that the ability to accumulate soluble stem carbohydrate is an important component of the varietal type best suited to maintaining yield under late-season stress conditions due to either take-all root loss or drought.

4.3.4. Combinations of characteristics

Given that each of the varieties under test has a different genetic background, they will differ for expression of a whole range of characteristics. Even from a visual inspection of the varieties it can be seen that this is the case; the inclusion of varieties bred in other countries serves only to increase the range. To expect single characteristics to explain varietal responses to different rotational positions may therefore be considered unreasonable. In selecting a variety for a take-all prone site the agronomist should be searching for the variety with a combination of desirable characteristics. It may be that the traits under investigation in this work are not totally independent of each other. For example, it would be easy to imagine that if a variety was slow developing (late date of GS 31), the period from GS 39 to GS 69 may be truncated, and it may have a tendency to amass smaller amounts of soluble stem sugars. To establish the effects of individual traits more explicitly would require work over a greater number of seasons and varieties, or the examination of isogenic lines for genes controlling the various traits across a range of rotational position treatments. In the absence of this work, the evidence from the current work is that characteristics identified in this study can be used to improve the choice of variety for high take-all risk situations.

In order to improve varietal choice for high take-all risk situations a relatively simple analysis of the combination of traits within the varieties such as that in Table 4.2 can be made. However, in making such a choice the more traditional varietal characteristics must not be forgotten. In the above analysis Soissons would appear to be the variety of choice for a high take-all risk situation. However, high take-all risk will occur in the same situations as high eyespot risk, and Soissons has the poorest resistance to eyespot of any variety currently on the NIAB RL.

Table 4.2 Mean values for varietal traits averaged across all rotational positions at Boxworth 1994, and Rosemaund 1995 and 1996, except Economy of tillering from Rosemaund 1996 only. And ranking of varieties; 1 = suited to non-first wheat position, 8 = ill-suited to non-first wheat position.

	Rate of development (date of GS 61)		Economy of tillering (dm of tillers destined to die as a percentage of total (GS 39)		Soluble Carbohydrate reserves (maximum at GS 61 + 75^{0}C days)		Overall score
	Ranking	date	Ranking	%	Ranking	dm(t/ha)	
Brigadier	5	16-June	8	22.0	3	2.95	16
Cadenza	2	14-June	4	14.6	5	2.74	11
Lynx	6	17-June	2	12.5	2	3.31	10
Rialto	2	14-June	7	19.9	1	3.38	10
Riband	2	14-June	3	14.2	6	2.47	11
Soissons	1	08-June	1	8.7	4	2.83	6
Spark	7	19-June	5	15.5	7	2.42	19
Zentos	8	20-June	6	18.9	8	2.36	22

The varietal traits discussed above are most probably not of equal importance. In this work, soluble carbohydrate reserves have had the largest influence on variety performance. It is, however, difficult to assign relative importance to the other characteristics. If this type of work were carried out over a wider range of conditions, then there would be sufficient robustness to the data to attempt a more quantitative assessment of the traits. In the absence of such information, however, it still appears that a more straightforward assessment of varietal traits, such as is attempted in Table 4.2 above, can be used to improve variety selection for a non-first wheat position.

Averaged across the three site-seasons, the non-first yield loss for the eight varieties varied between 0.42 and 0.74 t/ha. In Rosemaund 1995-6, the average yield loss was greatest at 0.83 t/ha compared to only 0.30 t/ha at Boxworth 1993-4. Experimental error in any trial series of this nature means that in the middle of the range of varietal responses it may be difficult to distinguish the small differences with statistical confidence. At the extremes of the range, however, it appears there is scope for identifying suitabilities. For example, in current experiments, extremes were exemplified by Soissons (take-all tolerant) and Spark (take-all intolerant). The results reported here do seem to show a correspondence between these more extreme responses and varietal types. Against this the varietal responses to rotational position in the current data were observed to be relatively small and in the cases of some varieties were inconsistent from site-season to site-season. Thus, the poor non-first wheat performance of Spark was less evident in Rosemaund 1994-5 than it was at the other two site-seasons. This inconsistency of the rotational position/variety interaction is also apparent in the NIAB RL where varietal performance has been ranked separately for both first and second wheats. For example, Rialto's second wheat performance (% mean of control varieties) has varied from 103 (1995), to 100 (1996) and to 96 (1997). This inconsistency may be due to unaccounted for second order interactions between season and rotational position/variety. Such second order interactions may also have been responsible for some of the inconsistency observed in present experiments. Currently, it could therefore only be stated with confidence that the indicative traits outlined above are sufficient to predict particular exceptional resistances or susceptibilites to take-all root loss rather than a systematic ranking all varieties entered into RL trials for relative performance as non-first wheats.

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Appendix 1 Weather Data

ROSEMAUND 1993-4

MONTH	MEAN AIR TEMP (^{0}C)	TOTAL RAINFALL (mm)	AV. SOLAR RAD. $MJ/M^2/day$
SEPTEMBER	11.7	80	9.7
OCTOBER	9.3	97	6.5
NOVEMBER	4.5	63	2.5
DECEMBER	5.5	92	2.1
JANUARY	5.4	59	2.9
FEBRUARY	3.0	80	4.0
MARCH	8.0	34	8.9
APRIL	8.2	34	14.4
MAY	11.5	61	19.3
JUNE	14.2	17	19.4
JULY	17.8	32	19.1
AUGUST	15.8	45	14.4

1994-5

MONTH	MEAN AIR TEMP (^{0}C)	TOTAL RAINFALL (mm)	AV. SOLAR RAD. $MJ/M^2/DAY$
SEPTEMBER	12.5	120	9.2
OCTOBER	9.5	68	6.5
NOVEMBER	10.0	58	2.4
DECEMBER	6.4	99	1.7
JANUARY	4.9	116	2.2
FEBRUARY	6.4	61	4.3
MARCH	5.5	15	10.3
APRIL	9.0	15	16.0
MAY	11.3	59	13.5
JUNE	14.0	12	20.7
JULY	18.3	6	17.9
AUGUST	19.1	18	18.2

1995-6

MONTH	MEAN AIR TEMP (^{0}C)	TOTAL RAINFALL (mm)	AV. SOLAR RAD. $MJ/M^2/DAY$
SEPTEMBER	13.3	81	10.6
OCTOBER	12.5	49	6.2
NOVEMBER	7.3	57	3.2
DECEMBER	1.9	72	1.6
JANUARY	4.2	57	1.6
FEBRUARY	2.2	62	5.6
MARCH	4.5	69	6.8
APRIL	8.5	53	12.5
MAY	9.1	43	12.3
JUNE	13.8	22	17.0
JULY	16.7	52	9.8
AUGUST	16.4	15	9.5

BOXWORTH 1993-4

MONTH	AV. MAX TEMP (^{o}C)	TOTAL RAINFALL (mm)	AV. SUNSHINE HOURS/DAY
SEPTEMBER	16.26	94	3.2
OCTOBER	11.85	84	3.6
NOVEMBER	7.55	60	2.0
DECEMBER	8.06	79	1.2
JANUARY	7.98	71	2.3
FEBRUARY	6.31	28	2.7
MARCH	11.51	42	4.1
APRIL	12.39	73	6.0
MAY	15.11	52	4.9
JUNE	20.27	24	8.5
JULY	24.78	26	8.2
AUGUST	21.49	62	6.3

1994/95

MONTH	AV. MAX TEMP (^{o}C)	TOTAL RAINFALL (mm)	AV. SOLAR RAD. MJ/M^{2}/DAY	AV. SUNSHINE HOURS/DAY
SEPTEMBER	16.67	78		3.8
OCTOBER	13.73	68		3.9
NOVEMBER	12.19	31		1.4
DECEMBER	9.33	39		2.6
JANUARY	7.50	78	2.1	
FEBRUARY	9.40	53	3.8	
MARCH	9.89	45	9.4	
APRIL	13.87	11	13.3	
MAY	18.05	23	15.6	
JUNE	19.41	20	17.5	
JULY	26.78	18	17.3	
AUGUST	26.59	8	17.7	

1995/96

MONTH	AV. MAX TEMP (^{o}C)	TOTAL RAINFALL (mm)	AV. SOLAR RAD. MJ/M^{2}/day
SEPTEMBER	18.06	92.6	8.1
OCTOBER	17.58	19.6	3.1
NOVEMBER	10.54	54.6	5.7
DECEMBER	3.60	59.4	5.3
JANUARY	5.11	43.8	1.5
FEBRUARY	5.33	53.6	3.8
MARCH	7.23	18.2	5.5
APRIL	13.57	11.6	11.0
MAY	13.94	18.6	11.8
JUNE	21.82	27.8	14.0
JULY	24.25	40.0	16.5
AUGUST	23.02	54.2	12.5

Appendix 2 Site Details

_ADAS Rosemaund 1993-4

Field Name:	Bottom Holbach South	
Drainage:	Good	
Soil type:	Silty clay loam (Bromyard series)	
1993/4		
Soil analysis:	pH 7.0 P 6 K 4 Mg 3	
Previous cropping:	1993 Winter Wheat/Winter oats 1992 Peas 1991 Winter Oats 1990 Winter Wheat	
Seed rate:	350 seeds/m^2	
Sowing date:	25 Oct 1993	
Cultivations:	Ploughed Power Harrow x 1 Crumbler x 1	20 Oct 1993 22 Oct 1993 22 Oct 1993
Herbicides:	Tribunil 2.25 kg/ha Cheetah 2.0 l/ha	7 Nov 1993 6 May 1994
Insecticides:	Aphox 0.28 kg/ha	30 Jun 1994
Fertiliser:	P 50 kg/ha K 75 kg/ha N 32 kg/ha N 119 kg/ha	2 Sept 1993 2 Sept 1993 30 Mar 1994 4 May 1994
P.G.R.'s:	Chlormequat 70% 1.65 l/ha	22 Apr 1994
Fungicides:	Tern 750 0.75 l/ha Sportak 45 0.9 l/ha Folicur 1.0 l/ha Silvacur 1.0 l/ha	29 Apr 1994 29 Apr 1994 28 May 1994 23 Jun 1994
Harvest:	13 August 1994	

ADAS Rosemaund *1994-5*

Soil analysis:	pH 7.1 P 6 K 4 Mg 3	
Seed rate:	350 seeds/m²	
Sowing date:	7 Oct 1994	
Cultivations:	Ploughed Power Harrow x 1 Crumbler x 1	6 Oct 1994 7 Oct 1994 7 Oct 1994
Herbicides:	Javelin Gold 5.0 l/ha	24 Nov 1994
Insecticides:	Phantom 0.1 kg/ha	28 Jun 1995
Molluscicide:	Draza 5.5 kg/ha	10 Oct 1994
Fertiliser:	P 44 kg/ha K 99 kg/ha N 40 kg/ha N 135 kg/ha	17 Sept 1994 17 Sept 1994 23 Mar 1995 4 May 1995
P.G.R.'s:	Cycocel 5C 2.5 l/ha	4 Apr 1995
Fungicides:	Tern 750 0.75 l/ha Sportak 45 0.9 l/ha Folicur 1.0 l/ha Silvacur 1.0 l/ha	4 Apr 1995 4 Apr 1995 26 May 1995 16 Jun 1995
Harvest:	9 August 1995	

ADAS Rosemaund *1995-6*

Soil analysis:	pH 7.0 P 5 K 3 Mg 3	
Seed rate:	350 seeds/m²	
Sowing date:	11 Oct 1995	
Cultivations:	Ploughed	10 Oct 1995
	Power Harrow x 1	11 Oct 1995
	Crumbler x 1	11 Oct 1995
Herbicides:	Javelin Gold 2.0 l/ha	1 Mar 1996
	IPU 500 1.0 l/ha	1 Mar 1996
Insecticides:	Cyperkill 0.25 l/ha	1 Mar 1996
Molluscicide:	Draza 5.5 kg/ha	19 Oct 1995
Fertiliser:	P 18 kg/ha	7 Oct 1995
	K 41 kg/ha	7 Oct 1995
	N 40 kg/ha (second and third wheats only)	9 Oct 1995
	N 50 kg/ha	20 Mar 1996
	N 128 kg/ha	25 Apr 1996
	N 51 kg/ha	17 May 1996
P.G.R.'s:	Cycocel 5C 2.5 l/ha	22 Apr 1996
Fungicides:	Tern 750 0.75 l/ha	22 Apr 1996
	Sportak 45 0.9 l/ha	22 Apr 1996
	Folicur 1.0 l/ha	13 Jun 1996
	Tern 750 0.33 l/ha	13 Jun 1996
Harvest:	31 August 1996	

ADAS Boxworth 1993-4

Field Name:	Rough Ground	
Drainage:	Good	
Soil type:	Clay (Hanslope series)	

1993/4

Soil analysis:	pH	7.8	
	P	3	
	K	2	
	Mg	3	
Previous cropping:	1993	Winter wheat/Winter oats	
	1992	Linseed	
	1991	Winter wheat	
	1990	Winter wheat	
Seed rate:	350 seeds/m²		
Sowing date:	23 Oct 1993		
Cultivations:	Ploughed		14 Sept 1993
	Dynadrive		15 Sept 1993
	Spring tines		25 Sept 1993
	Spring tines		19 Oct 1993
Herbicides:	Arelon 2.9 l/ha		9 Mar 1994
	Panther 1.0 l/ha		9 Mar 1994
	Starane 0.75 l/ha		20 May 1994
	Ally 15 g/ha		20 May 1994
Insecticides:	Dursban 1.0 l/ha		13 Jun 1994
Fertiliser:	N 46 kg/ha		10 Mar 1994
	N 119 kg/ha		21 April 1994
P.G.R.'s:	Stand-up 1.6 l/ha		22 Apr 1994
Fungicides:	Sportak 45 0.9 l/ha		20 Apr 1994
	Folicur 1.0 l/ha		23 May 1994
	Silvacur 1.0 l/ha		13 Jun 1994
Harvest:	3 August 1994		

ADAS Boxworth 1994-5

Sowing date:	29 Sept 1994	
Cultivations:	Ploughed	19 Sept 1994
	Maschio	27 Sept 1994
	Harrow	29 Sept 1994
Herbicides:	Arelon 3.7 l/ha	7 Nov 1994
	Panther 1.0 l/ha	7 Nov 1994
	Cheetah 2.5l/ha	21 Apr 1995
	Starane 0.75 l/ha	21 Apr 1995
	Ally 20 g/ha	21 Apr 1995
Insecticides:	Aphox 140g/ha	30 Jun 1995
Fertiliser:	TSP467 kg/ha	2 Dec 1994
	N 40 kg/ha	10 Mar 1995
	N 75 kg/ha	5 April 1995
	N 66 kg/ha	29 April 1995
Fungicides:	Radar 0.5 l/ha	2 May 1995
	Bombadier 1.0 l/ha	2 May 1995
	Folicur 1.0 l/ha	16 Jun 1995
	Silvacur 1.0 l/ha	30 Jun 1995
Harvest:	5/6 Aug 1995	

ADAS Boxworth 1995-6

Sowing date:	28 Sept 1995	
Cultivations:	Dynadrive	22 Aug 1995
	Ploughed	30 Aug 1995
	Dynadrive	1 Sept 1995
	Maschio	26 Sept 1995
	Harrow	28 Sept 1995
Herbicides:	CMPP 2.0 l/ha	30 Oct 1995
	Panther 1.0 l/ha	22 Nov 1995
	Hawk 0.25 + 2.3 l/ha	22 Nov 1995
	Hurler 0.75 l/ha	25 Apr 1996
	Ally 15 g/ha	25 Apr 1996
Insecticides:	Cypermethrin 0.25l/ha	8 Nov 1995
Fertiliser:	N 40 kg/ha	14 Mar 1996
	N 81 kg/ha	9 April 1996
	N 75 kg/ha	29 April 1996
P.G.R.'s:	Cycocel 1.75 l/ha	5 Apr 1996
Fungicides:	Sportak 0.9 l/ha	5 Apr 1996
	Opus 0.5 l/ha	6 Jun 1996
	Bravo 1.0 l/ha	6 Jun 1996
	Folicur 0.25 l/ha	25 Jun 1996
	Mistral 0.5 l/ha	25 Jun 1996
Harvest:	8 Aug 1996	

Appendix 3 Full Yield data Data

Yield - Rosemaund

	1994		1995		1996	
First	**- Mon**	**+Mon**	**- Mon**	**+Mon**	**- Mon**	**+Mon**
Brigadier	8.53	10.17	8.65	9.32	9.52	9.83
Cadenza	7.30	9.04	7.70	8.26	9.67	9.47
Lynx	8.93	10.06	8.62	9.18	9.83	10.15
Rialto	9.32	10.21	8.65	8.90	10.83	10.04
Riband	8.08	9.73	7.90	8.32	9.20	8.67
Soissons	8.88	10.11	8.01	8.90	9.92	9.64
Spark	8.57	9.25	8.24	7.85	9.02	8.56
Zentos	7.93	8.66	7.64	8.01	8.67	8.38
Mean	8.44	9.65	8.17	8.59	9.58	9.34
Second						
Brigadier	9.37	10.47	7.59	9.25	9.34	9.67
Cadenza	8.75	9.13	7.30	8.15	9.64	10.07
Lynx	9.11	9.51	7.97	9.10	10.02	10.13
Rialto	9.33	9.32	8.40	9.08	10.22	9.58
Riband	9.42	8.97	7.70	8.56	8.99	9.11
Soissons	8.57	9.28	7.46	8.65	9.65	10.32
Spark	7.78	8.11	7.70	8.70	8.78	8.63
Zentos	7.95	7.95	7.22	8.19	9.14	9.15
Mean	8.79	9.09	7.67	8.71	9.47	9.58
Third						
Brigadier	-	-	-	-	8.81	10.16
Cadenza	-	-	-	-	8.76	9.54
Lynx	-	-	-	-	9.18	9.70
Rialto	-	-	-	-	9.62	10.15
Riband	-	-	-	-	8.32	9.12
Soissons	-	-	-	-	9.00	9.72
Spark	-	-	-	-	8.36	8.92
Zentos	-	-	-	-	7.96	8.63
Mean	-	-	-	-	8.75	9.49
Posn. SED		1.045		0.154		0.547
df		2		2		4
Seed Trt SED		0.299		0.402		0.328
Posn. x Seed Trt SED		1.087		0.430		0.678
df		4		4		6
Variety SED		0.234		0.190		0.143
Posn. x Variety SED		1.090		0.294		0.594
Seed Trt x Variety SED		0.431		0.474		0.379
Posn. x Seed Trt x						

Yield - **Rosemaund - Cross Year Analysis**

	94-96 mean	
First	**- Mon**	**+Mon**
Brigadier	8.90	9.78
Cadenza	8.22	8.93
Lynx	9.13	9.80
Rialto	9.60	9.72
Riband	8.40	8.91
Soissons	8.94	9.55
Spark	8.61	8.55
Zentos	8.08	8.35
Mean	8.73	9.20
Second		
Brigadier	8.77	9.80
Cadenza	8.56	9.12
Lynx	9.03	9.58
Rialto	9.32	9.33
Riband	8.71	8.88
Soissons	8.56	9.42
Spark	8.08	8.48
Zentos	8.10	8.43
Mean	8.64	9.13
Year SED	0.240	
df	6	
Type SED	0.387	
Year x Type SED	0.532	
df	6	
Seed Trt SED	0.211	
Year x Seed Trt SED	0.353	
Type x Seed Trt SED	0.441	
Year x Type x Seed Trt SED	0.645	
df	12	
Variety SED	0.118	
Year x Variety SED	0.306	
Type x Variety SED	0.417	
Seed Trt x Variety SED	0.262	
Year x Type x Variety SED	0.596	
Year x Seed Trt x Variety SED	0.444	
Type x Seed Trt x Variety SED	0.493	
df	182	

Yield - Boxworth

	1994		1995		1996	
First	**- Mon**	**+Mon**	**- Mon**	**+Mon**	**- Mon**	**+Mon**
Brigadier	9.66	9.58	8.92	8.67	9.24	9.44
Cadenza	9.68	8.82	8.36	8.11	8.81	8.82
Lynx	9.30	9.42	8.30	8.03	9.63	9.73
Rialto	9.39	9.24	8.43	8.85	9.36	9.89
Riband	9.03	8.74	8.05	8.09	9.01	9.30
Soissons	9.01	9.29	8.69	8.61	9.06	9.31
Spark	8.38	8.74	7.87	8.00	8.18	8.23
Zentos	7.84	8.02	7.32	7.49	8.36	8.44
Mean	9.04	8.98	8.24	8.23	8.96	9.15
Second						
Brigadier	9.23	9.11	8.76	8.95	8.99	9.13
Cadenza	9.21	8.58	8.42	8.40	8.61	8.53
Lynx	9.03	8.85	8.01	8.31	9.54	9.49
Rialto	9.19	8.88	8.93	8.66	9.06	9.52
Riband	8.86	8.74	8.28	8.31	8.95	9.02
Soissons	9.21	9.04	8.59	8.74	8.98	8.91
Spark	7.71	7.49	8.07	7.92	8.02	8.39
Zentos	7.45	7.38	7.44	7.30	8.05	8.33
Mean	8.74	8.51	8.31	8.32	8.78	8.92
Third						
Brigadier	-	-	-	-	9.25	9.49
Cadenza	-	-	-	-	8.65	8.71
Lynx	-	-	-	-	9.50	9.60
Rialto	-	-	-	-	9.42	9.56
Riband	-	-	-	-	9.05	8.79
Soissons	-	-	-	-	8.99	9.09
Spark	-	-	-	-	7.98	8.28
Zentos	-	-	-	-	8.25	8.51
Mean	-	-	-	-	8.89	9.00
Posn. SED		0.353		0.100		0.653
df		2		2		4
Seed Trt SED		0.162		0.114		0.042
Posn. x Seed Trt SED		0.388		0.152		0.083
df		4		4		6
Variety SED		0.141		0.115		0.074
Posn. x Variety SED		0.399		0.183		0.136
Seed Trt x Variety SED		0.247		0.190		0.106
Posn. x Seed Trt x						
df		56		56		84

Yield - Boxworth - **Cross Year Analysis**

	94-96 mean	
First	**- Mon**	**+Mon**
Brigadier	9.27	9.23
Cadenza	8.95	8.58
Lynx	9.08	9.06
Rialto	9.06	9.33
Riband	8.69	8.71
Soissons	8.92	9.07
Spark	8.32	8.15
Zentos	7.84	7.98
Mean	8.75	8.79
Second		
Brigadier	9.27	9.23
Cadenza	8.74	8.50
Lynx	8.86	8.88
Rialto	9.06	9.02
Riband	8.70	8.70
Soissons	8.93	8.89
Spark	8.15	9.27
Zentos	7.65	7.67
Mean	8.61	8.58
Year SED	0.216	
df	6	
Type SED	0.127	
Year x Type SED	0.266	
df	6	
Seed Trt SED	0.069	
Year x Seed Trt SED	0.232	
Type x Seed Trt SED	0.144	
Year x Type x Seed Trt SED	0.292	
df	12	
Variety SED	0.069	
Year x Variety SED	0.244	
Type x Variety SED	0.156	
Seed Trt x Variety SED	0.115	
Year x Type x Variety SED	0.310	
Year x Seed Trt x Variety SED	0.281	
Type x Seed Trt x Variety SED	0.194	
df	182	