COMPONENTS OF GRAIN YIELD IN WHEAT

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FRONTISPIECE

A general view of the 1975-6 experiment on the Lincoln College Henley Research Farm showing plot size and layout.

CERTIFICATE

I hereby certify that the work embodied in this thesis was carried out by the candidate under my immediate supervision and that he planned, executed and described the research contained in the published papers which are now submitted.

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R.H.M. LANGER
(Supervisor)

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FOREWORD

This thesis is presented in the form of a series of papers some of which have already been published. It is prefaced by a review of research on the agronomy and physiology of wheat yield in New Zealand, and concluded with a general discussion. Other relevant papers in which the author was a contributor may be found in the Appendix.

CHAPTER 1

REVIEW OF LITERATURE

Comprehensive reviews on the physiology and development of wheat have recently been published by Evans and Wardlaw (1976) and Rawson and Bremner (1976), while Lazenby and Matheson (1975) gave a detailed description of wheat growing in Australia. This review emphasises New Zealand work on wheat, particularly those aspects relevant to the present study.

1.1 YIELD COMPONENTS

To understand the causes of variation in final grain yield, its components must be studied along with the growth of the crop. In wheat (*Triticum aestivum* L.) the yield components are the number of spikes per unit area, the number of grains per spike and the weight per grain. From a physiological viewpoint the number of grains per spike is the result of the number of spikelets and the number of grains produced in each spikelet, often referred to as grain set, each of these components being determined at a different stage in crop development.

Although studies on yield components can be criticised on the basis that they tend to be compensatory (Adams & Grafius 1971), such an analysis does define with more certainty the yield limiting processes in crop growth. In wheat the yield components are determined in overlapping sequence, and although there is considerable scope for compensation, the amount of scope for such compensation decreases with ontogeny (Rawson & Bremner 1976).

The first quantitative study on flower initiation and the development of yield components of New Zealand wheats was undertaken by Langer (1965) and Langer and Khatri (1965). Broadly speaking, these studies showed that for autumn-sown wheat at Lincoln the double-ridge stage was reached in early-mid September with ear emergence taking place between late October and early November depending on cultivar. Thus the number of spikelets per spike was determined by late September and the number of grains per spikelet over the following six weeks, with most of the grain filling occurring in December and early January. Langer and Khatri (1965) also found that rapid stem elongation began in late September, presumably the time when maximum tiller numbers were present (Rawson, 1971; Jewiss 1972), but that a proportion of these tillers died during October, the survivors constituting the bulk of the final spike population.

The timing of these different growth stages is critical in determining the effects of both environmental factors and agronomic treatments on yield components. For this reason the stage of crop development was regularly monitored in the experiments reported in this thesis.

1.2 CULTIVARS

In 1973 the three most commonly grown wheat cultivars in New Zealand were Aotea, Hilgendorf and Arawa, these cultivars occuping 44, 23 and 12% respectively of the area (1972-3 Farming Statistics). Two major changes have occurred since that time (Wheat Research Institute Bulletin 5/76). Firstly, the semi-dwarf Karamu, which was released for commercial production in the 1972-3 season now constitutes 29% of the total wheat area and secondly, Kopara accounts for 28% of the area. In 1976 Aotea was still the most popular cultivar in New Zealand occupying 32% of the area but the amount of Hilgendorf and Arawa had dropped to 6 and 3% respectively.

Coles and Wrigley (1976) recently published the derivation of the common New Zealand cultivars. Descriptions of Hilgendorf (Frankel & Hullett 1948), Arawa (Copp 1956; Copp & Lobb 1956), Aotea (Copp 1958), Kopara (Copp 1972; Copp & Cawley 1973), and Karamu (McEwan *et al.* 1972) have been published together with information on some of the less commonly used cultivars (McEwan 1959). These descriptions indicate that Karamu is a true spring wheat, but the standard New Zealand cultivars are intermediate in growth period and cannot be described as either true winter or spring wheats. Karamu and the other cultivars may be sown in either autumn or spring, although for spring sowing Karamu generally gives the highest yields in all districts except South Otago and Southland where Kopara, Aotea and Takahe are the recommended cultivars (Smith 1974; McEwan 1975).

The basis for the superiority in yield of spring sown Karamu over standard New Zealand cultivars has been attributed in part to its resistance to lodging on fertile soils and to its tillering capacity (McEwan & Vizer 1970). However Clements *et al.* (1974) found that the tillering pattern of Karamu was no different to that of Gamenya and Triple Dirk and that the 16% higher grain yield of the semi-dwarf was due to a higher grain yield per spike. From their data it is not possible to assess whether this greater yield per spike was due to more spikelets or more grains per spikelet, but overseas studies would suggest that both components may be involved where the crop is spring sown (Syme 1970; Fisher 1973).

Douglas *et al.* (1971) found that Kopara gave higher grain yields than Aotea when autumn sown in Marlborough, Canterbury and South Canterbury although the physiological basis for this superiority was not discussed. As Kopara, Aotea and Karamu constitute most of the New Zealand wheat crop, these cultivars were included in several of the experiments described in the present study in order to examine the development of their yield components as affected by several agronomic treatments.

1.3 EFFECTS OF NITROGEN

The optimum growth of wheat, as of any cereal, depends on adequate mineral nutrition of the plant, especially that of nitrogen (hereafter designated N), often the most limiting nutrient and one which may influence all the yield components, as is now reviewed.

Number of Spikes

The number of tillers that survive to form spikes at maturity can be increased either by greater production of tillers initially or by a higher percentage survival (Thorne 1966). N generally stimulates tiller production when applied before the time of rapid stem elongation (Langer 1959; Bremner 1969) and may also result in increased tiller survival (Watson *et al.* 1958; Thorne 1962; Barley & Naidu 1964).

Number of Spikelets

The development of the wheat shoot apex has been described by several workers (Bonnett 1936; Barnard 1955; Williams 1966; Fisher 1973). The beginning of the reproductive stage is indicated by the appearance of a double-ridge in the lower-central part of the apex, the upper member of which develops into a spikelet primordium and ultimately a spikelet. Development then proceeds basipetally and acropetally towards the elongating apex until it is halted by the appearance of the terminal spikelet. This is referred to as the double-ridge stage. Nitrogen supply up to and including the double-ridge stage has a big effect on the number of spikelets produced by influencing both the number of primordia present at the double-ridge stage and also the number that are produced subsequently before the formation of the terminal spikelet (Single 1964; Rawson 1970; Lucas 1972; Langer & Liew 1973).

Number of Grains Per Spikelet

The number of florets per spikelet varies between 7 and 9 and appears to be little influenced by nitrogen supply (Langer & Hanif 1973). However, the number of florets that produce grain is markedly influenced by N supply through its effect on leaf growth and hence presumably the supply of assimilate (Rawson & Ruwali 1972a, 1972b; Langer & Hanif 1973) and also because N is a major component of physiologically active tissue and may become limiting in the terminal florets within a spikelet (Bremner 1972).

Weight Per Grain

The effects of N on grain size appear to be variable depending mainly on time of application. Application of N at seeding may decrease grain size (Watson 1936; Barley & Naidu 1964) presumably due to competition among the increased number of grains for assimilates and N. Increases in individual grain weight from late application of N have been reported by Holmes and Tahir (1956) and Bremner (1969).

Effect of N on Leaf Growth

Reference has been made previously (section 1.3) to the effect of N on tillering. Application of N increases the number of leaves mainly through its effect on the number of tillers. Syme (1972) showed that increasing the N supply increased the rate of leaf emergence as well as the total leaf number on the main stem of wheat while Langer (1972) showed that N may also modify the succession of leaf sizes on a tiller. Finally nitrogen may slow down the rate of leaf senescence particularly when applied late (Thorne 1962). The net result of the three effects described above is that nitrogen generally increases leaf area index (abbreviated to LAI) and several studies have investigated the relationship between leaf area and yield as reviewed by Thorne (1973).

The effect of N in increasing vegetative growth may ultimately lead to increases in grain N content, due to redistribution of N from these vegetative organs during grain filling (Williams 1955; Langer & Liew 1973).

Effect of N on Grain Yield

The combined effects of N on the individual yield components are ultimately reflected in grain yield. Reviews on the use of N fertilisers on wheat in New Zealand (Walker 1969; Wright 1969; Douglas 1970; Ludecke 1972, 1974) indicate that responses to N fertiliser are variable and that it is difficult to predict responses from previous cropping histories without reference to a soil test for plant available N. Ward (1971) reviewed research on the NO_3-N soil test of the Great Plains area of the United States, and Ludecke (1974) using a similar soil test, obtained a relationship between grain yield response and NO_3-N level in the top 60 cm of soil in August. As NO_3-N is readily leached from the soil by rainfall when the soil is at field capacity, it is not surprising that more recent predictions of the response to N fertiliser have been based on the amount and intensity of rainfall during the cool season (C. Feytor pers. comm.).

Where nitrogen has given increases in grain yield the component most affected seems to be spike number (McLeod 1973). In other cases N has increased spike number without causing an increase in grain yield due to a reduction in the number of grains per ear and grain weight (Drewitt & Rickard 1973). On unirrigated, low moisture retentive soils, the lack of grain yield response to N and sometimes even yield depressions (Stephen 1973) have been explained on the basis of increased moisture stress associated with increased vegetative growth (section 1.3), and accelerated use of soil water (Ludecke 1974). Although this situation probably develops in some instances the use of irrigation and nitrogen combined does not always give increases in grain yield (Drewitt & Rickard *loc cit*). In an endeavour to explain some of these unexpected responses to N, a research contract between Lincoln College and the Department of Scientific and Industrial Research was set up in 1970. One of the main aims of this contract was to investigate the effects and interactions of nitrogen and irrigation on wheat yield. The results of some of these experiments are reported later in this thesis following a review of the effects of water stress.

1.4 EFFECTS OF WATER STRESS ON WHEAT YIELD

It has long been recognised that soil moisture deficits during spring are the main limiting factor of wheat yields in Canterbury and the cause of much of the variation in yield between seasons (Frankel 1935; Walker 1956). Like nitrogen, the supply of water has a major influence on the development of the yield components (Salter & Goode 1967; Fischer 1973).

Number of Spikes

Tillering in autumn wheat in Canterbury occurs mainly in August and September (Langer & Khatri 1965), a time when it is highly unlikely that there is water stress. However, tiller survival which is determined over the following 2 months is very sensitive to water stress even when it occurs after ear emergence (Barley & Naidu 1974). In spring sown crops this stress is accentuated as the crop has less time to develop an extensive root system and is developing under higher levels of solar radiation than autumn wheat (Drewitt & Rickard 1971).

Number of Spikelets

On an individual spike, spikelet number is determined by the end of September, and like tiller number, is unlikely to be affected by water stress under field conditions. However, due to its effect on tiller survival, water stress may alter the mean spikelet number in a spike population by causing the smaller late formed tillers with fewer spikelets to die first (Bremner 1969). The net effect of a water stress would thus be to increase the mean number of spikelets per ear.

Number of Grains Per Spikelet

Fischer (1973) showed in a pot experiment that grain yield was most sensitive to plant water stress at a stage about 10 days before ear emergence, the number of grains per spikelet being the sensitive component, results similar to those found by Langer and Ampong (1970). Similarly, in field grown wheat in Canterbury, Wright (1972) found that only a few hours of severe stress 4 or 5 days before ear emergence caused death of some upper spikelets.

Weight Per Grain

There is evidence that prolonged stress throughout grain filling almost invariably reduces grain weight (Salter & Goode 1967) presumably by influencing the amount of assimilate reaching the grain (Fisher & Kohn 1966; Fischer 1973; section 4.5).

Effects of Water Stress of Leaf Growth

Leaf area is affected by water stress through its effects on both cell division and cell enlargement, particularly the latter (Hsiao 1973). Reduced cell size results in reduction in leaf area and thus effective photosynthetic surface (Denmead & Shaw 1960; Fischer & Kohn 1966). In their review Fisher and Hagan (1965) concluded that this effect of water stress in reducing leaf area was more important than any temporary effect on photosynthesis. It was also stressed that besides preventing complete development of leaf area, water stress also results in an earlier senescence of leaves, the magnitude of this effect depending on the severity of stress (Fischer 1973).

Effects on Yield

Prior to 1972 research into the effects of irrigation on wheat in New Zealand was confined to soils of low moisture retention and low levels of plant available soil water on the Canterbury Plains. Under these circumstances, yield responses to irrigation of winter sown wheat have ranged from 800 to 1800 kg/ha or increases of 23 to 149% (Drewitt 1974a, 1974b). One irrigation applied at the 'boot' stage was sufficient to achieve this level of response in five out of six seasons. The additional response to heavier irrigation rates averaged 260 kg/ha or 7%. With spring sown wheat on soils of low moisture retention such as those of the Lismore series, yields generally increase with increasing irrigation frequency up to three applications (Drewitt & Rickard 1971).

On a more moisture retentive Templeton silt loam Wilson (1974) found that responses from irrigation of winter sown wheat were small, but that spring sown wheat gave large positive responses, presumably because it was developing later under higher rates of evaporation and with a more shallow root system.

The yield increases attributable to irrigation on soils of low moisture retention at Winchmore have been due mainly to increases in spike number, and to a lesser extent the number of grains per spike. Irrigation increased the mean grain weight of Arawa and Kopara substantially, but had less of an effect in Aotea (Drewitt & Rickard 1973). In contrast, on a moisture retentive soil type Wilson (1974) found that irrigation gave only a slight increase in grain size but had similar effects on spike number as those which occurred at Winchmore.

Finally, water supply during the growing season is the major factor influencing the sowing rate of wheat (Rawson & Bremner 1977), an aspect which formed part of the present study and which is now reviewed.

1.5 EFFECTS OF SOWING RATE

Commercial sowing rates of wheat vary considerably from less than 40 kg/ha in Australia (Syme 1970) up to 180 kg/ha in England (Thorne & Blacklock 1971). Assuming a grain weight of 45 mg and 90% field establishment these sowing rates would give populations of 80 and 360 plants/m^2 respectively.

In South Canterbury McLeod (1960) found that maximum yields of winter wheat were produced by sowing at around 100 kg/ha although sowing rates up to 200 kg/ha did not significantly reduce yield. For spring wheat at Palmerston North Clements *et al.* (1974) found that sowing rates of at least 150 kg/ha were required.

From work with other crops in this environment (J.G.H. White pers. com.) there is evidence to show that the benefits of irrigation are not fully exploited until greater than normal plant populations are established. At the other extreme there is evidence to show that excessive sowing rates can reduce yields mainly by causing a decrease in the number of grains per spikelet (Willey & Holliday 1971). For these reasons the effect of varying sowing rate was one of the agronomic treatments imposed on the experiments described in this thesis.

The aim of the experiments reported in this thesis was to examine the effects of cultivar, nitrogen, irrigation and sowing rate, as they influence grain yield in wheat. In the first field experiment, which was carried out during the 1971-2 growing season, irrigated Kopara wheat gave a 30% reduction in grain yield when high rates of N fertiliser were applied (Dougherty & Langer 1974). This yield depression did not appear to be caused by the treatments inducing water stress or lodging and Dougherty and Langer (*loc cit*) suggested that grain set may have been restricted by the level of carbohydrate available for floret development during the critical pre-anthesis period.

In the next season a low fertility site, which had grown three successive cereal crops, was chosen in an endeavour to obtain a positive response to N fertiliser. The semi-dwarf cultivar Karamu had just been released to commercial growers and this was included in the experiment along with the two standard New Zealand cultivars Aotea and Arawa (Dougherty *et al.* 1974).

At the same time there was considerable interest in the wheat-white clover rotation (Ryde 1965). Thus a second experiment was laid down in 1972 to examine aspects of the wheat-white clover association. This experiment was grown on a very fertile soil, as a concurrent objective to those described previously was to determine the yield components of high-yielding wheat crops. Details of the white clover establishment have been published (Scott 1974) while aspects of the wheat component of the experiment are presented in Chapter 2.

CHAPTER 2

WHEAT YIELD AS AFFECTED BY SOWING RATE, IRRIGATION, AND TIME OF WHITE CLOVER INTRODUCTION*

2.1 INTRODUCTION

On moisture-retentive soils in Canterbury, winter wheat is conventionally sown at 100-130 kg/ha, a sowing rate which has evolved through farmer experience and limited research work (McLeod 1960). Increasing areas of wheat are being irrigated on soils of low moisture retention belonging to the Lismore and Eyre series (Drewitt 1967). Australian work indicates that higher sowing rates are required to exploit the benefits of irrigation (Syme 1970), but little information is available for New Zealand conditions.

In Canterbury moisture-retentive soils are also used for intensive small seed production, especially white clover, which is commonly oversown with the wheat in May or in spring at a sowing rate of 2-4 kg/ha (Ryde 1965). Little agronomic research has been conducted on the cereal-white clover association in seed-producing areas, although red clover (Dougherty 1972) and lucerne (Janson & Knight 1973) establishment under cereals has been studied. Research on undersowing overseas stresses the need for lower than normal cereal sowing rates and sowing the legume at the same time as the cereal if satisfactory legume establishment is to be obtained (Santhirasegaram & Black 1965). Spring overdrilling of cereals

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* W.R. Scott, C.T. Dougherty, R.H.M. Langer and G. Meijer
N.Z. Journal of Experimental Agriculture 1: 369-76 (1973).

appears to cause some superficial damage to the crop, but the effects on grain yield are unknown.

An experiment was designed to provide information on the effects of sowing rate of wheat, time of white clover introduction, and irrigation on the wheat-white clover association. This paper presents data obtained from the wheat component of the experiment.

2.2 MATERIALS AND METHODS

Trial Site

The experimental area was on the Lincoln College Research Farm on a Wakanui silt loam soil. Vining peas that occupied the site the previous year were sown after permanent pasture.

Experimental Design

A 3 x 3 x 3 factorial design with twofold replication was used. Each plot measured 30 x 3 m. The three levels of wheat sowing rate, time of white clover introduction, and irrigation were as follows:

Sowing rate of wheat	S_0:	50 kg/ha
	S_1:	100 kg/ha
	S_2:	150 kg/ha
Time of white clover introduction	T_0:	26.6.72 with wheat
	T_1:	Overdrilled 5.9.72
	T_2:	Overdrilled 8.10.72
Irrigation treatments	W_0:	Not irrigated
	W_1:	Irrigated to 2 weeks after anthesis
	W_2:	Irrigated to harvest

Wheat (*Triticum aestivum* L. cv. Aotea) was sown in 15 cm rows by a combine drill together with superphosphate at 250 kg/ha on 26 June 1972. 'Grassland Huia' white clover (*Trifolium repens* L.) planted at the same time as the wheat was broadcast behind the coulters and lightly harrowed. For later times of planting the clover was direct-drilled in 15 cm rows in the same direction as the wheat rows. The sowing rate of clover was 3 kg/ha for all times of sowing. In irrigated plots soil water was restored to field capacity through a microtube trickle system whenever soil water was depleted to -0.5 bars according to tensiometers permanently installed in representative plots at depths of 30 cm.

Measurements

On 6 September 1972 plant numbers were counted by sampling six 0.2 m^2 quadrats per plot. At monthly intervals one 0.1 m^2 quadrat was cut from each plot. Living tillers were counted and then partitioned into a "leaf" and "stem" fraction. The "leaf" fraction consisted of all green laminae removed at the junction with the leaf sheath. The "stem" fraction consisted of all the remaining material. Leaf area was determined with a planimeter. After oven drying at 75^{o}C the separate fractions were weighed.

Just before the final harvest ten 0.1 m^2 quadrats per plot were cut to ground level for determination of straw yield and components of grain yield. Combine-harvester yields were determined by direct heading one 30 x 1.60 m strip down the centre of each plot. After machine dressing the grain was weighed and the yields were corrected to a moisture content of 14%. From late October through to harvest, soil water content was monitored by taking three 0-20 cm soil samples per plot at approximately weekly intervals. Water content was calculated on a dry-weight basis after drying to a constant weight at 105°C.

2.3 RESULTS

During October 74.2 mm of rainfall was recorded, well above the monthly average of 42.8 mm, and it was not until 27 October that irrigation became necessary. Irrigation was the only treatment that significantly affected soil-water levels, and the main effects of irrigation on soil-water levels, together with rainfall and irrigation water applied, are presented in Figure 2.1. Rainfall during November, December, and January was well below average, and this was reflected in low levels of soil water in the non-irrigated plots. The wilting point for the 0-20 cm layer of this particular soil is 11.3% of dry weight, and field capacity is 28.8%. Approximately 4.9 cm of water is available to plants in this soil layer between field capacity and wilting point.

In the non-irrigated plots (W_0) soil-water levels dropped to near wilting point in November and, after some recovery in December, dropped to wilting point again in early December, remaining near this level until harvest. Plots irrigated to 2 weeks after anthesis (W_1) had high levels of soil moisture up until late December, but were near wilting point for most of January. The W_2 treatment had high soil-water levels right through the growing season and only dropped to 20% moisture at harvest time.

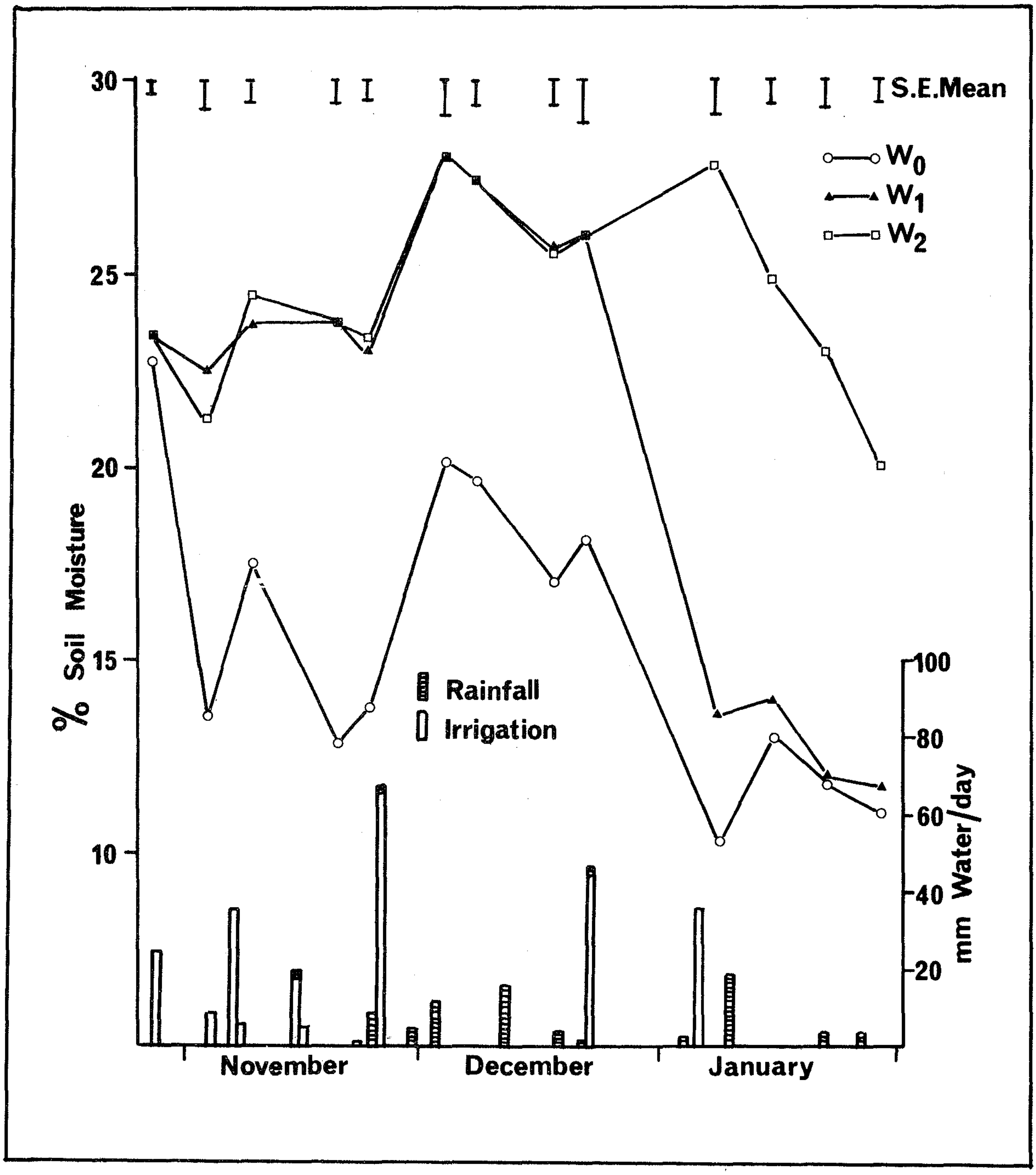

Figure 2.1 - Water inputs from rainfall and irrigation, and effects of irrigation on soil water content.

Grain Yields

The main effects of the treatments on grain yield are shown in Table 2.1, as there were no significant interactions.

Table 2.1 - Effect of sowing rate, time of white clover introduction, and irrigation on combine grain yield and hand-harvested grain yield.

Treatment		Grain Yield (kg/ha)	
		Combine	Hand-harvested
Sowing rate	S_0	5089	6191
	S_1	5889	6651
	S_2	5549	6369
Time of clover introduction	T_0	5492	6148
	T_1	5515	6514
	T_2	5520	6550
Irrigation	W_0	5173	6064
	W_1	5556	6534
	W_2	5797	6613
LSD 5%		269	327

Hand-harvested yields were consistently higher than those determined by the combine harvester, but showed similar trends. Combine grain yields were high, the highest treatment yielding double the national average of the 1970-71 growing season (N.Z. Year Book 1972). For the purposes of examining the effects of treatments on components of yield, only data derived from the hand-harvested quadrats will be considered. For more practical purposes the combine yields should suffice.

A conventional sowing rate of 100 kg/ha gave the highest yield. At the lower rate of 50 kg/ha, grain yields were reduced by 450 kg/ha, but when the sowing rate was increased to 150 kg/ha there was a smaller depression in grain yield. Wheat which was overdrilled with white clover in spring produced significantly more grain than when the white clover was established with the wheat in June. Irrigation gave large and significant increases in grain yield. When the crop was irrigated up to 2 weeks after anthesis, grain yields were increased by approximately 500 kg/ha over the non-irrigated treatments. Continuing the irrigation to near harvest gave a further small increase which failed to reach significance.

Plant and Tiller Numbers

As there was no significant interaction of treatments on plant, tiller, or ear numbers, the main effects are presented in Table 2.2.

In Table 2.2 the results of the October overdrilling and irrigation effects have not been included in the August and early October samplings, as these treatments had not been applied at the times of sampling. The plant population in August was almost linearly related to sowing rate, and differences in plant population caused by sowing rate were highly significant. Tiller numbers followed a similar trend over the growing season, so that at harvest ear numbers were also positively related to sowing rate, although not linearly.

Up until late November, time of sowing white clover had no effect on tiller numbers, but by harvest, wheat which had been overdrilled in October (T_2) produced significantly more ears. The increase in ear numbers produced by the September (T_1) overdrilling

Table 2.2 - Effects of wheat sowing rate, time of white clover introduction, and irrigation on plant, tiller, and ear numbers per m^2.

Treatment		No. Plants	No. tillers			No. Ears at Harvest
		6 Sept	3 Oct	25 Oct	28 Nov	
Sowing rate	S_0	111	980	960	649	585
	S_1	196	1096	1027	724	678
	S_2	276	1271	1136	810	771
Time of clover introduction	T_0	192	1131	1039	722	653
	T_1	197	1106	1044	754	683
	T_2			1039	707	697
Irrigation	W_0			1059	693	625
	W_1			1038	753	701
	W_2			1026	737	708
LSD 5%		16	146	127	86	30

just failed to reach significance at the 5% level. Similarly, irrigation had no effect on tiller numbers in the initial stages, but by harvest this treatment resulted in the production of more ears. When irrigation was extended to near harvest it did not add to the ear population.

Ear and Grain Size

Main effects of treatments on grain yield per ear and components responsible for this yield are presented in Table 2.3. With every increase in sowing rate above 50 kg/ha there was a corresponding decline of about one spikelet per ear. Overdrilling in September (T_1) gave a highly significant increase, but irrigation had no significant effect on the mean number of spikelets per ear.

Differences in single-grain weight caused by the three treatments were small but significant. The standard sowing rate (S_1) produced the heaviest grain, and sowing rates above or below this level tended to depress single-grain weight. Although wheat over-drilled in September (T_1) produced significantly more spikelets per ear than the other two times of sowing, grain weight per ear was not significantly different, as the T_1 treatment had a significantly lower weight per grain. The two irrigated treatments also significantly reduced mean weight per grain.

The significant S x T x W interactions in grain weight per ear and number of grains per ear were caused mainly by highly significant treatment interactions on the number of grains per spikelet (Table 2.4). At all sowing rates, overdrilling had no effect on number of grains per spikelet where irrigation was continued to harvest. In the absence of irrigation the October

Table 2.3 - Effect of sowing rate, time of white clover introduction, and irrigation on yield components of the ear.

Treatment		No. spikelets/ ear	No. grains/ spikelet	No. grains/ ear	Wt/grain (mg)	Grain wt/ear (mg)
Sowing rate	S_0	17.7	1.38	24.5	43.6	1069
	S_1	16.7	1.33	22.2	44.3	983
	S_2	15.7	1.20	18.8	43.9	826
Time of clover introduction	T_0	16.5	1.31	21.7	44.1	958
	T_1	17.1	1.29	22.2	43.6	969
	T_2	16.5	1.30	21.6	44.1	952
Irrigation	W_0	16.8	1.30	22.0	44.9	989
	W_1	16.6	1.30	21.7	43.4	944
	W_2	16.7	1.30	21.8	43.4	945
LSD 5%		0.3	0.04	0.6	0.5	32
Significant Interactions		None	S x T x W**	S x T x W*	None	S x T x W*

Table 2.4 - Effects of sowing rate, time of white clover introduction, and irrigation on mean number of grains per spikelet.

Sowing Rate	Irrigation	Time of Clover Introduction T_0	T_1	T_2
S_0	W_0	1.49	1.42	1.35
S_0	W_1	1.41	1.30	1.39
S_0	W_2	1.33	1.32	1.37
S_1	W_0	1.26	1.36	1.32
S_1	W_2	1.38	1.27	1.28
S_1	W_2	1.40	1.37	1.29
S_2	W_0	1.13	1.12	1.25
S_2	W_1	1.15	1.28	1.24
S_2	W_2	1.21	1.14	1.23

LSD 5% between treatment means 0.12

overdrilling significantly reduced the number of grains per spikelet at the low sowing rate, had no effect at the medium sowing rate, and gave a significant increase at the high sowing rate. The September overdrilling significantly increased the number of grains per spikelet only at the high sowing rate and when water was applied to 2 weeks after anthesis. Increases in sowing rate generally reduced the number of grains per spikelet. Because of this 3-factor interaction, the largest ears were produced by non-irrigated wheat sown at the low sowing rate without spring overdrilling.

Plant Height and Harvest Index

There were no significant interactions of treatments on plant height or harvest index (Table 2.5).

Plant height was not affected by sowing rate or time of white clover introduction, but both irrigated treatments significantly increased plant height by about 10 cm. Conversely, irrigation significantly reduced the harvest index, as did alterations in sowing rate above or below 100 kg/ha.

Leaf Area Index

The main effects of the treatments on leaf area index (LAI) and leaf/stem ratio are presented in Table 2.6, as there were no significant interactions.

Treatment means not included in Table 2.6 indicate that those treatments had not been imposed at the time of sampling. In early October LAI increased with increasing sowing rate, but as the season progressed differences tended to decrease, so that by late November sowing rate had no significant effect of LAI. Time of white clover

Table 2.5 - Main effects of sowing rate, time of white clover introduction, and irrigation on plant height and harvest index.

Treatment		Plant Height (cm)	Harvest Index† (%)
Sowing rate	S_0	92.3	35.0
	S_1	91.6	36.4
	S_2	92.5	35.2
Time of clover introduction	T_0	92.0	35.7
	T_1	92.9	35.6
	T_2	91.6	35.3
Irrigation	W_0	85.2	36.8
	W_1	95.3	34.8
	W_2	96.0	34.9
LSD 5%		2.0	1.2

† The proportion of grain in the total above-ground weight (Donald 1962).

introduction had no significant effect on LAI. Conversely, both irrigated treatments produced large and significant increases in LAI in late November, and also significantly increased the leaf/stem ratio. As the season progressed the leaf/stem ratio declined markedly.

Table 2.6 - Main effects of sowing rate, time of white clover introduction, and irrigation on LAI and leaf/stem ratio.

Treatment		3 October		25 October		28 October	
		LAI	Leaf/stem	LAI	Leaf/stem	LAI	Leaf/stem
Sowing rate	S_0	1.28	1.66	3.58	0.84	3.05	0.15
	S_1	1.70	1.60	4.36	0.72	3.16	0.14
	S_2	2.31	1.58	4.84	0.62	2.91	0.15
Time of clover introduction	T_0	1.85	1.66	4.27	0.67	2.90	0.15
	T_1	1.72	1.61	4.23	0.79	3.14	0.15
	T_2			4.28	0.72	3.08	0.14
Irrigation	W_0					2.42	0.13
	W_1					3.55	0.15
	W_2					3.15	0.16
LSD 5%		0.30	0.10	0.60	0.06	0.57	0.01

2.4 DISCUSSION

Sowing rates of wheat above or below 100 kg/ha resulted in lower yields. The low rate of 50 kg/ha reduced yield mainly because of lower tiller numbers (Table 2.2). It can be calculated that at this sowing rate plants formed more ears, but this compensatory tillering was still insufficient to offset the lower initial plant numbers. At all sowing rates tiller numbers reached a maximum in early October, but about 40% of them failed to produce an ear. Tiller mortality appeared to be largely unaffected by sowing rate, but was somewhat higher than the 25% tiller mortality in the Aotea wheat crop analysed by Langer (1964). At the 50 kg/ha sowing rate tillers had larger ears with significantly more spikelets and grains per ear, but the grains were smaller (Table 2.3). The increase in grain yield per ear did not compensate for the reduction in ear numbers.

The depression in grain yield caused by the high sowing rate (150 kg/ha) had a different basis. Lower yield was primarily due to a drastic reduction in grain weight per ear. Ears from this treatment had significantly fewer spikelets and fewer grains per spikelet, and these two factors resulted in a low grain number per ear (Table 2.3). The size of grain was unaffected. Floret development was occurring during October and early November. During this period crops sown at 150 kg/ha had a higher LAI but lower leaf/stem ratio than those sown at lower rates (Table 2.6). The effects of sowing rate on crop growth rate (CGR) and net assimilation rate (NAR) during this period are shown in Table 2.7. During October the CGR of the high-density crop was significantly greater than that of the low-density crop. This difference appeared to be due to a greater LAI

Table 2.7 - Effects of sowing rate on crop growth rate and net assimilation rate ($gm/m^2/wk$).

Sowing* Rate	Crop Growth Rate		Net Assimilation Rate	
	3 Oct-25 Oct	25 Oct-28 Nov	3 Oct-25 Oct	25 Oct-28 Nov
S_0	81.8	152.6	33.9	46.5
S_1	99.0	129.3	31.7	34.8
S_2	105.2	114.3	29.4	29.5
LSD 5%	19.6	29.8	5.7	8.3

giving superior light interception, as differences in NAR between sowing rates were smaller. During November the situation was reversed and, although all crops were subjected to increasing levels of solar radiation, the CGR and NAR of the crop sown at 150 kg/ha were significantly lower than those of the crop sown at 50 kg/ha. This suggests that the high-density crop was relatively deficient in assimilate over this period. This growth analysis does not take into account any dry weight which may have been produced by the leaf sheaths, as the LAI measured was based on lamina area alone. However, the data do indicate that the LAI of the high sowing rate treatment was supra-optimal during November, and that early ear development under these conditions was probably limited by the supply of assimilate, a suggestion also made by Willey and Holliday (1971) in England. Using the data of Puckridge and Donald (1969), they suggested that low levels of carbohydrate restricted early ear development in high-density crops which were above the optimum leaf area index. In the present experiment the high mean density of ears

(770 per m^2) did not compensate for the lower grain yield per ear. More work is obviously required on the carbohydrate status of wheat plants during ear development, preferably in conjunction with detailed studies on concurrent morphological development, as many agronomic treatments tend to alter the rate of development.

The standard sowing rate of 100 kg/ha resulted in the highest yield because of its moderate density of medium-sized ears. McLeod (1960) showed that maximum yields of winter wheat in South Canterbury were produced by a sowing at around 100 kg/ha, although sowing rates up to 200 kg/ha did not significantly reduce yield. However, this sowing rate may not be optimal under all situations, as allowance must be made for cultivar differences in tillering capacity, time of sowing, soil fertility, and moisture responses, as well as the large differences in seed quality and size that exist both within and between cultivars. This difference in seed size between cultivars was graphically demonstrated in one of our recent trials where Hilgendorf and Aotea wheat were sown at 200 kg/ha and 150 kg/ha respectively to give the same density of viable seeds. Results of the present experiment also imply that plant density should be considered in cultivar evaluation trials if promising new lines are to produce at their genetic potential.

The increase in grain yield produced by both spring over-drilling treatments appeared to be due mainly to an increase in tiller survival very late in the season (Table 2.2). However, the cause of this increased survival remains obscure. Even more obscure is the reason why the September overdrilling gave a highly significant increase in the number of spikelets per ear (Table 2.3). This treatment took place while the plants were still vegetative, but whether it may have caused an increase in the number of primordia accumulating on the stem apex or by improving the soil environment remains unknown. It used to be common farm practice in wheat-growing districts of New Zealand to harrow and roll autumn-sown wheat in September in an attempt to control weeds (Holford 1927; Hilgendorf 1938), but in recent years the practice has declined. Overdrilling in this trial may have had an effect similar to harrowing, but the yield response did not appear to be due to weed control, as weed growth was negligible in all plots.

Yield increases attributable to irrigation were near 500 kg/ha (12%) and, although substantial, were not as spectacular as those at Winchmore where, on lower-yielding crops, increases of up to 150% have been recorded (Drewitt & Rickard 1970). In our experiment soil-water levels in October, during the water-stress-sensitive and yield-determining phases of early reproductive development (Langer & Ampong 1970), were relatively high (Fig. 2.1). However, in the non-irrigated plots soil water fell to low levels in November, corresponding with ear emergence, and it was probably at this stage that irrigation played its role by increasing tiller survival (Table 2.2). Irrigation did not stimulate tillering but only permitted the survival of tillers already formed, since in late October tiller numbers were identical for all irrigation treatments and tillering had ceased. By late November tiller numbers dropped slightly in the non-irrigated plots, and by harvest significantly fewer ears were present.

Irrigation through to harvest gave a small increase in the combine yields over that of the irrigation treatment which ceased soon after anthesis. At Winchmore, irrigation during the grain-filling stages produces only marginally more grain. The possible deleterious effects of late irrigation on baking score have yet to be evaluated (Drewitt 1967). Although irrigation raised grain yields, it also produced more straw and increased crop height by about 10 cm (Table 2.5). Grain yield was obviously less responsive to irrigation than vegetative yield, and this was reflected in the harvest index (Table 2.5). This effect also occurs in other wheat cultivars grown in this locality.

Although the combine yields were lower than those measured by hand-harvesting, similar trends were apparent, and some practical conclusions can be drawn. When sowing rates of wheat much below 100 kg/ha are used with the objective of aiding establishment of undersown white clover, wheat yields on high-fertility, moisture-retentive soils may be reduced. However, as far as grain yields are concerned the time of legume introduction into the cereal can be delayed until early October with no deleterious effects. In dry years irrigation may be beneficial to wheat yields, but there is no evidence to suggest that higher than normal plant populations of Aotea wheat are required to exploit the benefits of irrigation.

2.5 SUMMARY

On a fertile, moisture-retentive Wakanui silt loam Aotea wheat sown at 100 kg/ha yielded 6650 kg/ha, considerably more than when sown at 50 or 150 kg/ha. Lower yields of wheat planted at the 50 kg/ha rate were caused largely by low ear numbers, and the 150 kg/ha sowing rate resulted in the formation of many small ears. Ear size is discussed in relation to physiological factors, including carbohydrate supply during early ear development.

Wheat overdrilled with white clover in September or October outyielded wheat and clover sown together in June. Irrigation up to 2 weeks after anthesis increased grain yield, and continuing irrigation through to harvest gave a further small response. Yield responses to irrigation were largely attributable to tiller survival.

2.6 POSTSCRIPT

The 1972-3 experiment with Aotea indicated that at spike populations greater than $700/m^2$ the number of grains per spikelet could decline to such an extent that grain yield was reduced. It was postulated that this reduction was due to low levels of carbohydrate in the young developing ear (section 2.4), an assumption based on the fact that the NAR of these crops was low (Table 2.7).

A limitation of this experiment was that it involved only one cultivar, Aotea, and thus one of the aims of the 1973-4 experiment was to investigate the factors affecting grain set in a number of cultivars. It also seemed that preference should be given to a high fertility site where the spike population and yields would be high, so as to examine the apparent negative relationship between spike population and number of grains per spikelet.

The 1972-3 experiment reported by Dougherty *et al.* (1974) showed that N and irrigation could cause major differences in leaf development between crops with possible effects on grain set (Dougherty & Langer 1974). It was therefore decided to include N and irrigation as treatments designed to modify grain set and to analyse the effects of these treatments on other yield components.

Observations on the previous crops also indicated that agronomic treatments such as irrigation and application of N fertiliser could shift the timing of critical physiological events. It was therefore decided to make detailed measurements of crop development by monitoring the length and elevation of the young developing apex.

Poor plant establishment of the new experiment sown in July 1973 meant that resowing was necessary in September. Although grain yields were comparatively low as a result of the spring sowing, the experiment did provide some useful agronomic information (Dougherty *et al.* 1975b) as well as some physiological data on the relationship between levels of soluble carbohydrate and grain set (Dougherty *et al.* 1975a).

Overseas research had begun to focus attention on the pattern of grain set and grain growth within the ear (Rawson & Evans 1970; Walpole & Morgan 1970; Evans *et al.* 1972) and possible relationships between early ear development and grain set (Fisher 1973; Lupton *et al.* 1974). Similar investigations were carried out on the 1973-4 experiment and these are presented in Chapters 3 and 4.

CHAPTER 3

AN ANALYSIS OF A WHEAT YIELD DEPRESSION CAUSED BY HIGH SOWING RATE WITH REFERENCE TO THE PATTERN OF GRAIN SET WITHIN THE EAR*

3.1 INTRODUCTION

Most of the differences in grain yields between wheat crops can be accounted for by variation in ear numbers and there is usually an inverse relationship between ear number and grain yield per ear, grain number being particularly sensitive to changes in ear density (Bremner 1969; Scott *et al.* 1973; Dougherty *et al.* 1974). From the limited evidence available, the optimum ear density for grain yield appears to be around 800 ears/m^2. Above this level further increases in ear number are more than offset by reductions in grain number per ear (Scott *et al.* 1973; Dougherty *et al.* 1974). In this paper we analyse a reduction in grain set attributable to high ear populations.

3.2 MATERIALS AND METHODS

Data for this paper were derived from mainstems collected from a large field experiment on wheat grown on the Lincoln College Research Farm as described in detail previously (Dougherty *et al.* 1975b).

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* W.R. Scott, C.T. Dougherty, and R.H.M. Langer
N.Z. Journal of Agricultural Research 18: 209-14 (1975)

The four treatments and their levels were as follows:

Cultivars	C_0	:	Arawa
	C_1	:	Aotea
	C_2	:	Karamu
Irrigation	W_0	:	Not irrigated
	W_1	:	Irrigated 20 November to 18 December
	W_2	:	Irrigated 3 December to 18 December
Sowing rate	S_0	:	250 viable seeds/m^2 (normal)
	S_1	:	500 viable seeds/m^2
Nitrogen fertilisation	N_0	:	None
	N_1	:	200 kg N/ha

Dissection and examination of apices at an early stage in their development showed that Arawa and Aotea both produced a mean spikelet number of 14 and Karamu produced 15. At the early boot stage (Feekes 9+), anthesis (Feekes 1.05), and at maturity five ears per plot bearing the mean number of spikelets for the cultivar were collected. On the first two samplings individual spikelet weights were determined by cutting off the spikelets at their junction with the rachis, drying at 80^{0}C, and weighing. For mature ears, single grains occupying each floret position within each spikelet position were dissected out, dried to constant weight, and weighed. In this way the pattern of grain set within the ear was established.

Spikelets and florets were numbered in an acropetal sequence (Langer & Hanif 1973). Within the spikelet, floret positions one and two were determined by the pattern of overlap of the glumes and by reference to the position of floret 3.

3.3 RESULTS

The grain yield and its components for the mainstem ears were very similar to those recorded for ears derived from the whole crop (Dougherty *et al.* 1975b). Both grain number and size were involved in several interactions (Tables 3.1, 3.2, 3.3). Karamu (C_2) had the most grains per ear and its small superiority over Arawa (C_0) was due to a higher number of spikelets. Aotea (C_1) ears yielded least because the spikelets had fewer and smaller grains. Arawa produced the largest grains and Aotea the smallest, Karamu being in an intermediate position. Nitrogen fertilisation (N_1) reduced grain size in all cultivars and this led to lower ear yields.

The effect of irrigation varied with cultivar and sowing rate. Both irrigated treatments (W_1 and W_2) reduced grain yield per ear in Arawa and Aotea, but in Karamu they increased ear yields (Table 3.2). A larger reduction in grain yield caused by irrigation occurred in wheat grown at the high sowing rate (S_1) (Table 3.3). The early irrigation treatment (W_1) reduced the number of grains per spikelet and grain size, although neither of these effects reached significance (Table 3.1). The sowing rate-nitrogen interaction for grain yield per ear is not presented in detail, as it was largely attributable to variations in the number of spikelets per ear (Table 3.4). Nitrogen (N_1) increased the mean number of spikelets of mainstem ears at the high sowing rate (S_1), but had no effect in wheat grown at the low sowing rate (S_0).

The reduction in grain set (no. grains/spikelet) caused by the high sowing rate occurred in all cultivars, but was most apparent for Arawa, and the responses of only this cultivar will be described in detail. Figure 3.1 presents the effect of sowing rate on the mean

Table 3.1 - Components of grain yield for mainstem ears.

		Grain yield/ear (g)	Weight/grain (mg)	No. grains /ear	No. spikelets /ear	No. grains /spikelet
Cultivar	C_0	1.42	42.6	33.4	13.8	2.38
	C_1	0.98	34.4	28.6	13.7	2.04
	C_2	1.34	37.4	35.7	15.3	2.38
LSD 5%		0.05	1.5	1.6	0.4	0.11
Irrigation	W_0	1.27	38.4	33.1	14.2	2.30
	W_1	1.22	37.7	32.4	14.3	2.25
	W_2	1.24	38.2	32.3	14.3	2.24
LSD 5%		0.05	1.5	1.6	0.4	0.11
Sowing rate	S_0	1.30	37.9	34.0	14.5	2.37
	S_2	1.20	38.3	31.1	14.0	2.17
LSD 5%		0.04	1.2	1.2	0.3	0.09
Nitrogen	N_0	1.28	39.1	32.5	14.2	2.26
	N_1	1.22	37.1	32.7	14.4	2.27
LSD 5%		0.04	1.2	1.2	0.3	0.09
Significant interactions		C x W W x S N x S	None	None	N x S	None

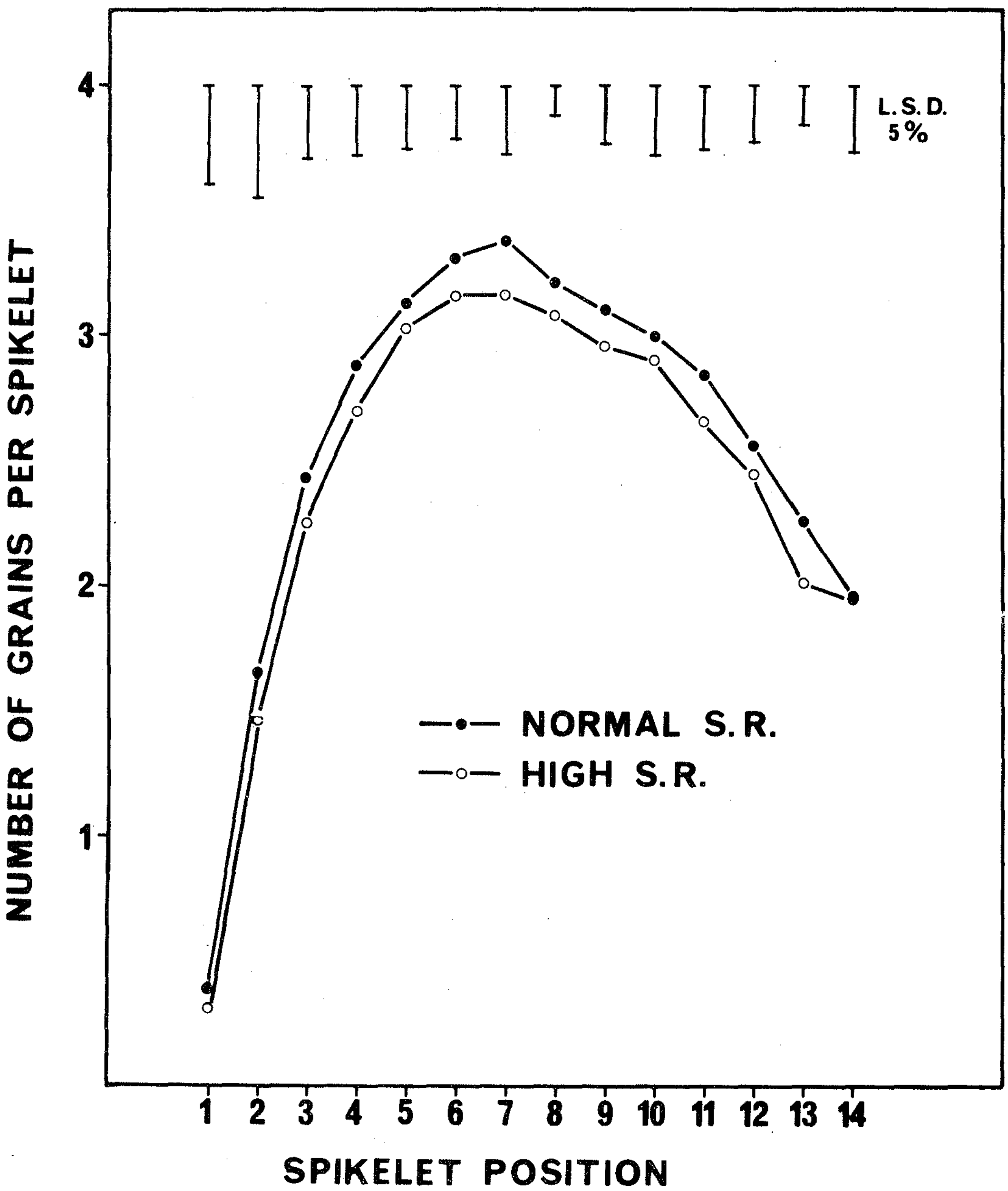

Figure 3.1 - The effect of sowing rate and spikelet position on the number of grains per spikelet of Arawa wheat.

Table 3.2 - The interaction of cultivar and irrigation on grain yield per ear (g).

		Irrigation		
		W_0	W_1	W_2
Cultivar	C_0	1.50	1.38	1.38
	C_1	1.04	0.96	0.95
	C_2	1.30	1.32	1.39
LSD 5%	0.06			

Table 3.3 - The interaction of irrigation and sowing rate for mean grain yield per mainstem ear (g).

		Irrigation		
		W_0	W_1	W_2
Sowing rate	S_0	1.33	1.31	1.25
	S_1	1.23	1.13	1.23

LSD 5% at same sowing rate: 0.06

LSD 5% at same irrigation treatment: 0.05

Table 3.4 - The interaction of nitrogen and sowing rate for the mean number of spikelets per mainstem ear.

		Nitrogen fertilisation	
		N_0	N_1
Sowing rate	S_0	14.54	14.43
	S_1	13.69	14.35
LSD 5%	0.29		

number of grains in each spikelet of Arawa. Spikelets in the low-central position of the ear contained the most grain and those occupying the basal position (1-2) contained very few. Grain set in all spikelets was reduced in wheat grown at the high sowing rate, although this effect reached significance only in the penultimate spikelet (13).

An analysis of grain set in different floret positions within each spikelet position revealed that florets in positions 1 and 2 from the base within each spikelet were usually fertile and little affected by treatment. The fertility of florets in positions 3 and 4 was, however, markedly affected by sowing rate as shown in Figure 3.2. The high sowing rate treatment decreased grain set in floret 3, the depression being most marked and significant in those spikelets near the base and near the apex of the ear. Poor grain set in floret 4 of ears grown at the high sowing rate failed to reach significance, but this floret made only a small contribution to grain yield per ear.

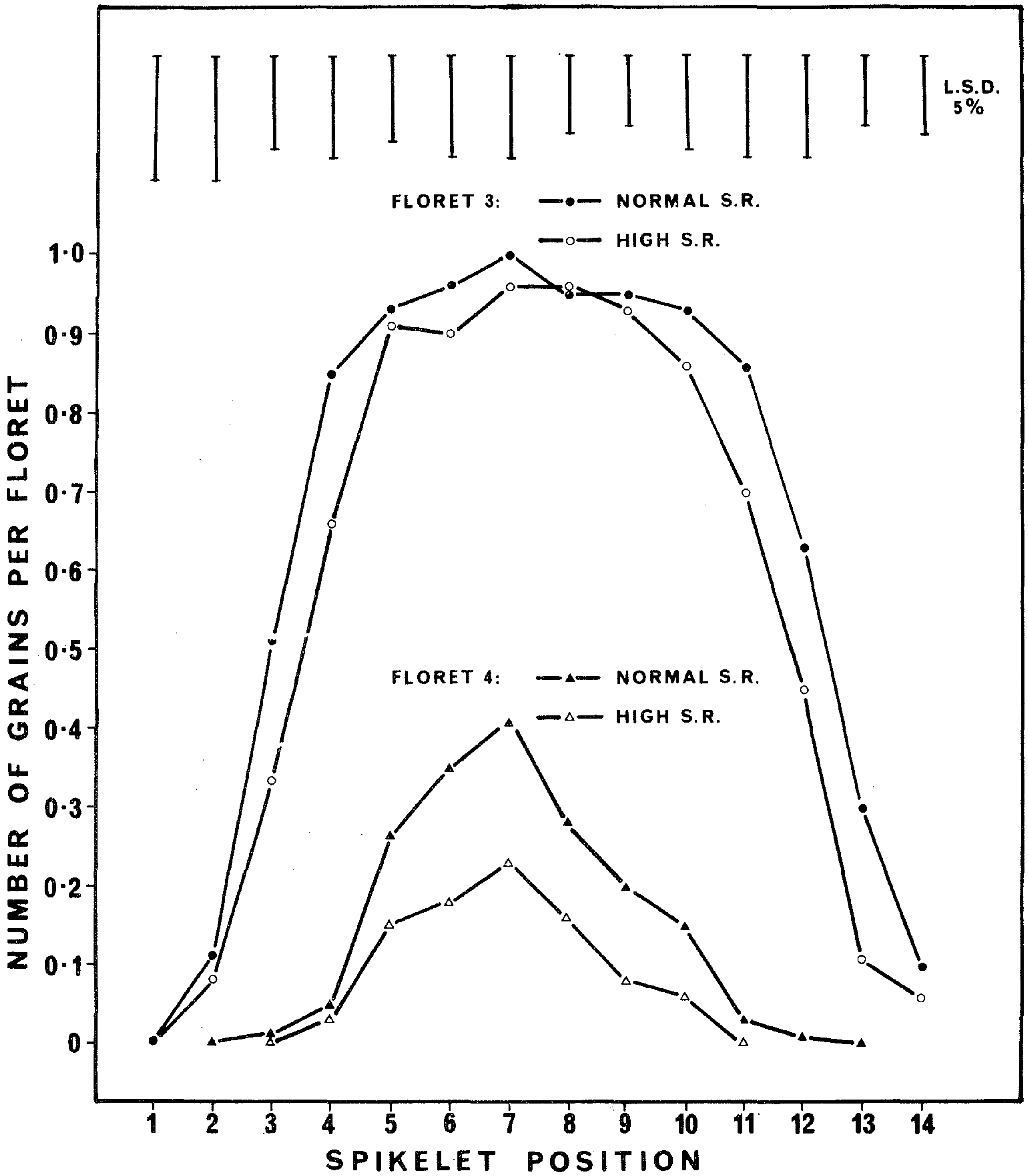

Figure 3.2 - The effect of sowing rate on the fertility of florets 3 and 4 at each spikelet position of Arawa wheat.

On 26 November spikelet dry weights were reduced in wheat grown at the high sowing rate (Fig. 3.3). At this time Arawa wheat was in the very early boot stage (Feekes - Large Scale 9-10) with the ears about 5 cm in length. Ears emerged on 3 December. Shortly after peak anthesis on 17 December dry weight of individual spikelets was unaffected by sowing rate. Differences in sowing rate did not appear to shift the timing of anthesis either.

Regression analysis of the data shown in Figure 3.3 is presented in Figure 3.4 and Table 3.5. The linear relationships between pre-anthesis spikelet dry weight and final grain set were significant for all except the basal and terminal spikelets. Changes in pre-anthesis spikelet dry weight had their biggest effect on grain set in spikelets near the base of the ear (positions 2 and 3) and those in the central and upper portion of the ear were less affected.

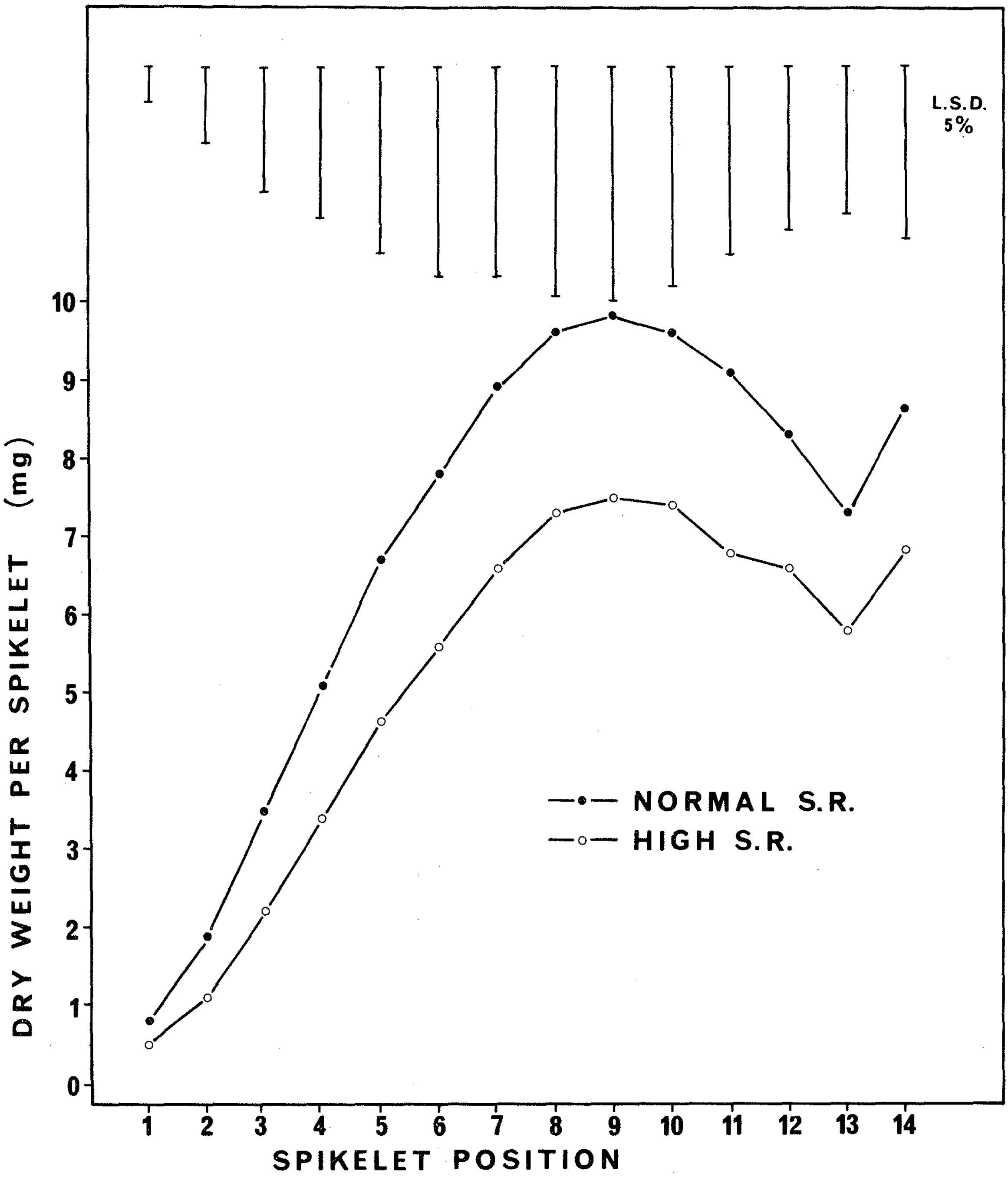

Figure 3.3 - The effect of sowing rate on spikelet weight in the early boot stage of Arawa wheat.

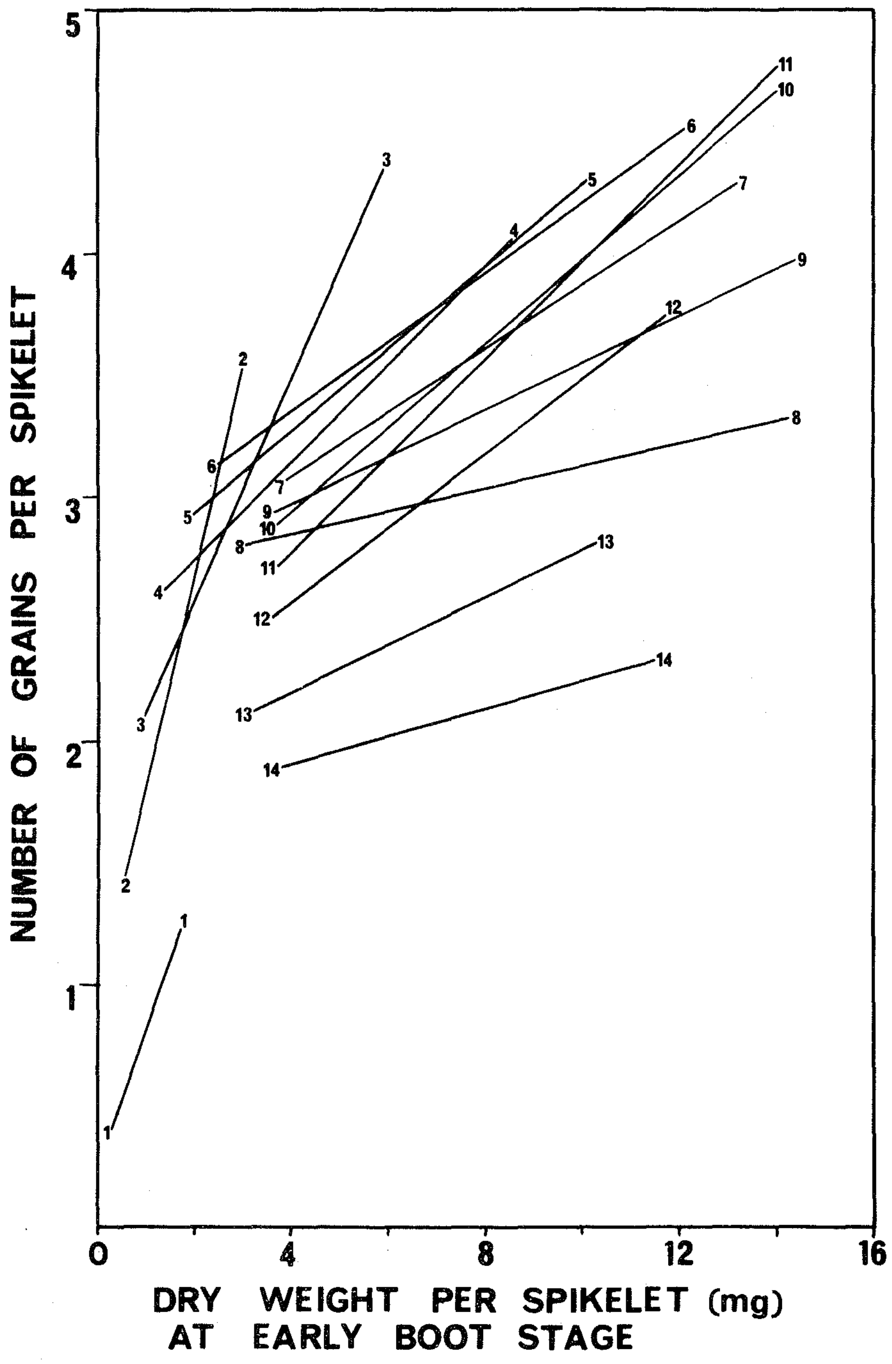

Figure 3.4 - The relationship between spikelet weight in the early boot stage and number of grains per spikelet for each spikelet position of Arawa wheat.

Table 3.5 - Linear regression analysis between spikelet weight in the early boot stage and number of grains per spikelet showing the regression constant, regression coefficient, and correlation coefficient for each spikelet position.

Spikelet Position	Constant	Coefficient†	R^2
1	0.23	0.59 ab	0.25 N.S.
2	0.99	0.76 a	0.54 *
3	1.70	0.46 b	0.74 **
4	2.34	0.21 c	0.62 *
5	2.60	0.17 c	0.58 *
6	2.78	0.14 cd	0.68 **
7	2.57	0.18 c	0.64 **
8	2.66	0.11 cd	0.50 *
9	2.59	0.10 cd	0.65 **
10	2.26	0.17 c	0.76 **
11	1.98	0.19 c	0.72 **
12	1.96	0.15 cd	0.57 *
13	1.82	0.10 cd	0.51 *
14	1.69	0.06 d	0.25 N.S.

† Regression coefficients followed by the same letter do not differ significantly ($P < 0.05$)

3.4 DISCUSSION

Grain setting in wheat has been intensively studied near the time of anthesis by imposing such treatments as floret sterilisation and differing environmental factors (Rawson & Evans 1970; Walpole & Morgan 1973). Walpole and Morgan (1973) suggested that the sequence of anthesis in florets is a critical factor in determining which florets set grain. This sequence, however, is probably a manifestation of events which have occurred during the previous 35 days (Langer & Hanif 1973), and this period has not been so intensively studied. In the present field experiment high sowing rate reduced spikelet dry weight at the very early boot stage (Fig. 3.3) and this parameter was highly correlated with final grain set (Fig. 3.4, Table 3.5). This fact, coupled with the improved grain set brought about by early thinning (Dougherty 1975b), indicates that the initial stages of floret development may influence grain set. Although the spikelets measured at this early boot stage consisted mainly of accessory floral organs, namely glumes, lemmas, and paleas, Fisher (1973) has suggested that rapid early development of accessory floral organs leads to improved grain set. Similar reasoning applied to the present experiment might indicate that the high sowing rate reduced the early development of accessory floral organs which was measured as reduced spikelet weight (Fig. 3.3) and manifested itself as reduced grain set (Table 3.1).

The pattern of grain set for different spikelet positions within the ear of Arawa is very similar to that recorded by other workers with different cultivars (Rawson & Evans 1970; Walpole & Morgan 1973; Kirby 1974). Spikelets in the low-central position of the ear contained the most grains and those at the base contained very few grains, the remaining spikelets being intermediate in fertility (Fig. 3.1). However, it is interesting to note that the relative size of spikelets was determined rather early in their development (Fig. 3.2), and also differences in pre-anthesis spikelet weight had their biggest influence on grain set in those spikelets near the base of the ear, but had very little effect in the terminal spikelet (Table 3.5, Fig. 3.4).

The number of grain-bearing florets is related to the total number of florets initiated and the proportions of these which reach a critical size for fertilisation (Langer & Hanif 1973). The poor grain set in spikelets near the base of the ear shown in this experiment and others (Rawson & Evans 1970; Langer & Hanif 1973) does not appear to be due to fewer florets being initiated in the basal spikelets, but rather due to the higher rate of floret degeneration which occurs in the basal spikelets (Langer & Hanif 1973; Kirby 1974). It is our contention along with other workers (Willey & Holliday 1971; Bingham 1972) that supply of carbohydrate is one of the main factors influencing the fate of initiated florets. As expected it is the terminal florets which suffer in competition for carbohydrate (Fig. 3.2) and it is possible that florets in position 4 fail because they are not connected directly to the vascular system (Hanif & Langer 1972). However, in the present experiment the fertility of floret 3 was also reduced by the high sowing rate, particularly in spikelets near the base and apex of the ear (Fig. 3.2). Recently, Kirby (1974) has shown that the rate of floret initiation does not differ between spikelets, but florets in spikelets near the base and apex of the ear must develop faster to reach anthesis at about the same time. Presumably these rapidly developing florets would be the first to degenerate if the carbohydrate supply was restricted (Dougherty *et al.* 1975a).

In previous experiments we have tried to explain yield depressions caused by high sowing rates on the basis of carbohydrate deficiency during pre-anthesis floret development (Scott *et al.* 1973) and we have shown that in high-yielding wheat crops a high sowing rate may produce a supra-optimal leaf area index, reducing the net assimilation rate and presumably the carbohydrate level. However, it seems highly unlikely that this explanation holds entirely for the present experiment which was concerned with a much lower yielding wheat crop with a lower leaf area. As a result of being spring sown the present crop was also developing at a time in the year when levels of solar radiation were higher.

It seems very likely that spring-sown wheat in Canterbury may be much more susceptible to physiological drought than autumn-sown crops. Dougherty (1973) has pointed out that autumn-sown wheat has a comparatively long time to develop an extensive root system to scavenge for soil water and hence is less susceptible to physiological drought than spring wheat, which has a much shorter period to develop this extensive root system. Mutual shading would have occurred first in plots grown at the high sowing rate, and the effect of shading on restricting root development in grasses and cereals is well documented (Brouwer 1966). Recent Australian work has shown that in wheat high sowing rate reduces root penetration mainly by restricting the growth of seminal roots (Barley *et al.* 1973). In the present experiment irrigation had no effect on the grain set of mainstems (Tables 3.1, 3.2, 3.3) possibly because plants suffering from physiological drought are not always capable of responding to increased supplies of soil water (Dougherty 1972). Wright (1972) showed that very short periods of physiological drought during pre-anthesis floret development reduce grain set in this environment, which Fischer (1973) attributed to the production of abnormal anthers and male sterility. It is suggested that in the present experiment high sowing rate reduced grain set by causing water stress and carbohydrate deficiency within the ear.

What does appear more certain is that the reactions of spring wheat to changes in agronomic and environmental factors are different from those operating in autumn sown crops. The object of further research should be to unravel the complexities surrounding carbohydrate metabolism and water relationships within the young developing ear.

3.5 SUMMARY

Grain set in spikelets of ears was reduced in spring-sown wheat established at high sowing rate (500 viable seeds/m^2) compared with wheat planted at normal rates (250 seeds/m^2), the reduction being greatest in spikelets positioned near the base and near the apex of the ear. Regression analysis revealed a significant and positive relationship between final grain set and spikelet dry weight at the early boot stage. Poor grain set in wheat grown at supra-optimal seeding rates was attributed to a combination of reduced carbohydrate supply and water stress in the young developing ear.

CHAPTER 4

A COMPARISON OF THE PATTERN OF GRAIN SET IN AOTEA AND KARAMU WHEAT*

4.1 INTRODUCTION

Karamu wheat is a New Zealand release of a semi-dwarf hybrid (Lerma Rojo x Norin 10-Brevor 14) Andes[3], bred by the International Centre for maize and wheat improvement (McEwan *et al.* 1972). Extensive trials throughout New Zealand have shown Karamu to be capable of producing very high yields particularly when spring sown (Smith 1974).

The available evidence suggests that the superiority of wheats with Norin 10 in their ancestry lies partly in their ability to produce more grains per ear, this being mainly due to the production of more grains per spikelet (Syme 1970; Fisher 1973; Clements 1974; Dougherty *et al.* 1974). In a recent spring-sown field experiment at Lincoln (Dougherty *et al.* 1975b; Scott *et al.* 1975), Karamu produced more grains per spikelet than Arawa and Aotea. Kirby (1974) has pointed out that in most experiments on cereal yield only the mean number of grains per spikelet is given or can be estimated and this may conceal considerable variation within the ear. The pattern of grain set has been described for several overseas cultivars (Rawson & Evans 1970; Walpole & Morgan 1970; Evans *et al.* 1972; Kirby 1974) but apart from Arawa (Scott *et al.*

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* W.R. Scott and R.H.M. Langer
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1975), there is no such information available for New Zealand cultivars. This paper compares the pattern of grain set in Karamu with that of a standard New Zealand wheat, Aotea.

4.2 MATERIALS AND METHODS

Data for this paper were derived from mainstems collected from a large field experiment as described in detail previously (Dougherty *et al.* 1975b). Arawa, Aotea and Karamu wheat were grown under three irrigation regimes at two sowing rates, and with and without nitrogen fertiliser. A factorial design with two replicates was used, making a total of 24 plots for each cultivar.

Dissection and examination of apices at an early stage in their development showed that Arawa and Aotea both produced a mean spikelet number of fourteen while Karamu produced fifteen. At maturity five ears per plot each bearing the mean number of spikelets for the cultivar were collected and single grains occupying each floret position within each spikelet position were dissected out and dried to constant weight. Spikelets and florets were numbered in an acropetal sequence (Langer & Hanif 1973; Kirby 1974).

As there were no interactions between treatments, the means for each cultivar are made up from a total of 120 ears.

4.3 RESULTS

Only the results for Aotea and Karamu are presented in this paper as the pattern of grain set in Arawa has been described elsewhere (Scott *et al.* 1975). Direct statistical comparisons within each spikelet position are confounded by the fact that Karamu produced one more spikelet than Aotea. However, standard errors for each position are presented and these indicate that within the ear grain number and size were most variable in the basal portion of the ear.

Figure 4.1 shows the pattern of grain set within the ears of Aotea and Karamu. The greatest number of grains per spikelet was found at spikelet positions 5 to 10 for Aotea and 5 to 9 for Karamu. Thus Karamu produced its most fertile spikelets in a slightly lower portion of the ear and had less of a 'fertility plateau' than Aotea. For all spikelet positions Karamu produced more grains per spikelet than Aotea.

A more detailed analysis of the pattern of grain set is presented by reference to floret fertility at each spikelet position. The pattern of grain set in florets 1 and 2 (the basal florets) for each cultivar was very similar, so the mean fertility of these two floret positions is plotted in Figure 4.2. For both cultivars the fertility of the basal florets was depressed in spikelet positions 1 and 2, and the terminal spikelet of Aotea also had reduced fertility. With these exceptions the basal florets within each spikelet were very fertile and, if anything, Aotea was slightly superior to Karamu.

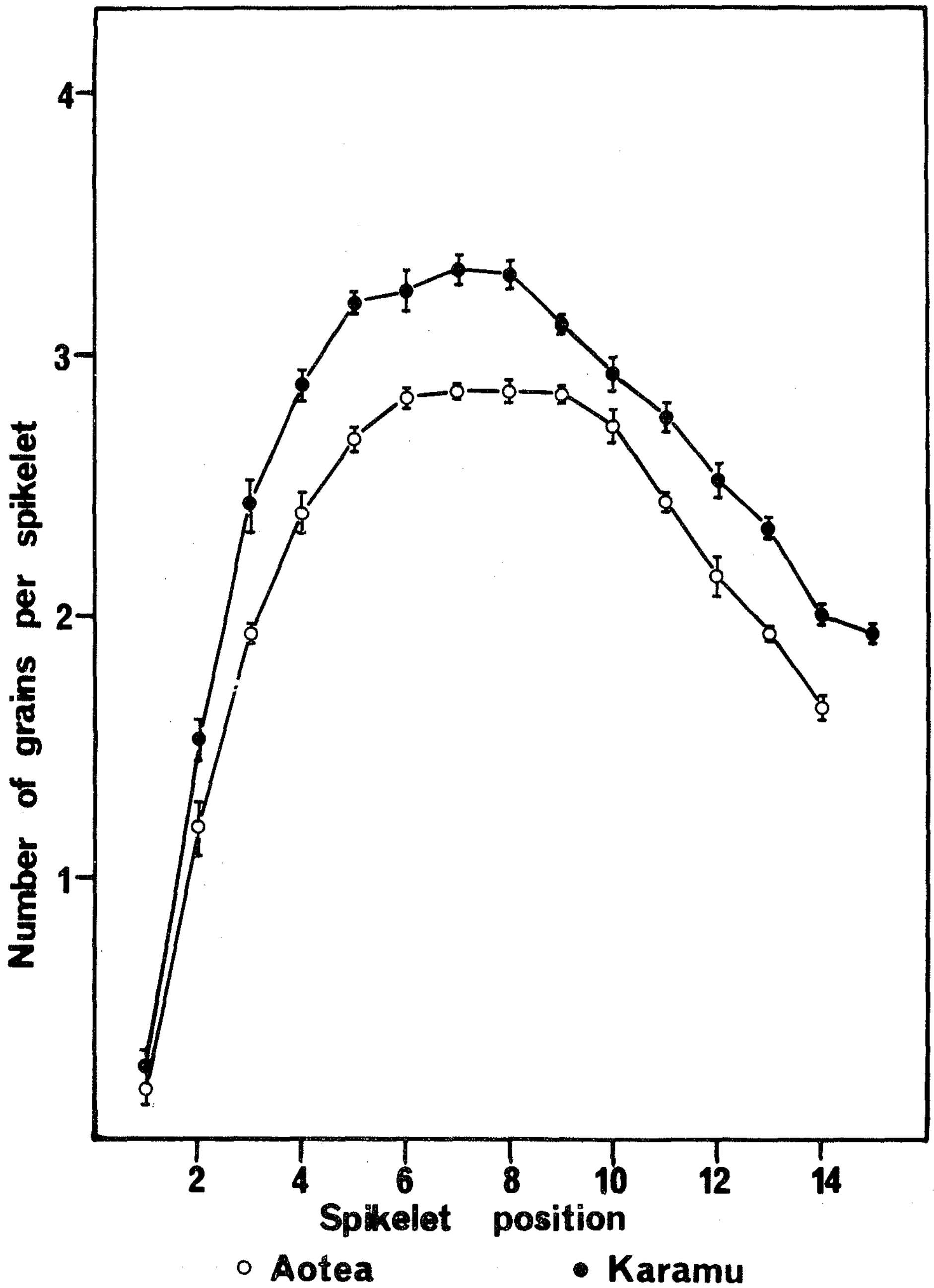

Figure 4.1 - The effect of spikelet position on the number of grains per spikelet of Aotea and Karamu wheat.

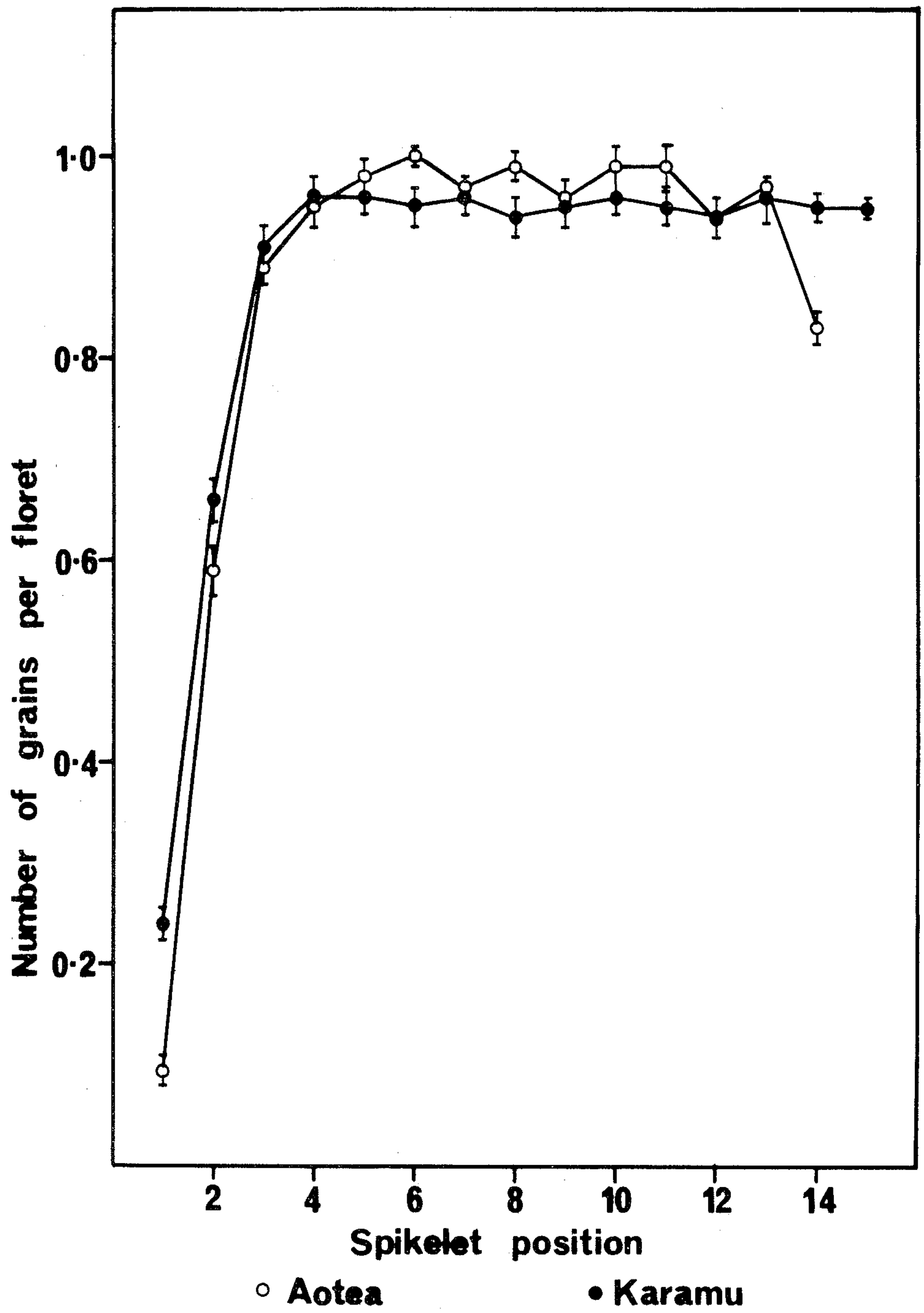

Figure 4.2 - The effect of spikelet position on the mean number of grains in florets 1 and 2 of Aotea and Karamu wheat.

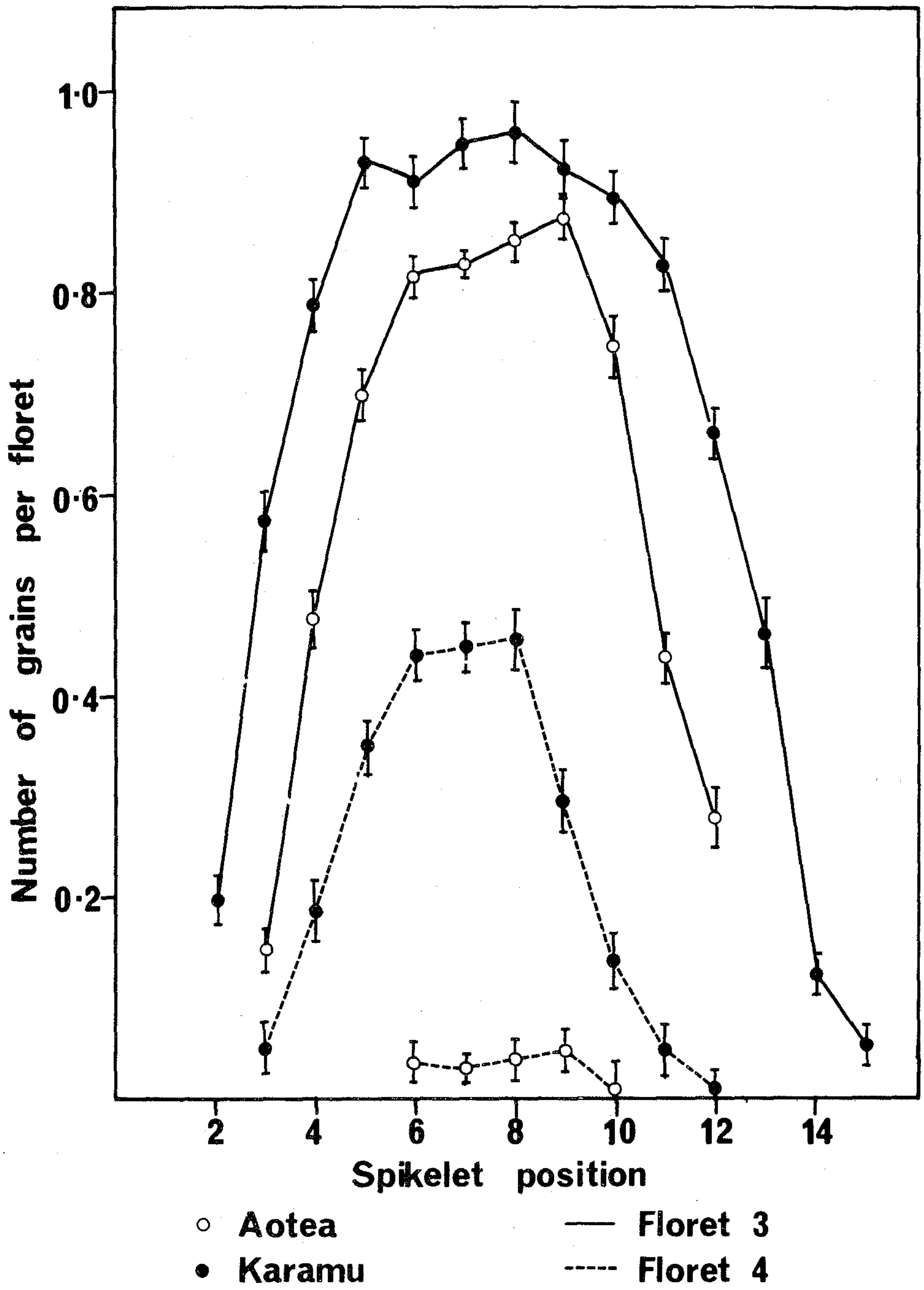

Figure 4.3 - The effect of spikelet position on the mean number of grains in florets 3 and 4 of Aotea and Karamu wheat.

Differences in grain set between cultivars and among spikelet and floret positions were much more marked in the case of florets 3 and 4 (Fig. 4.3) where peak fertility was reached in only a few spikelets near the centre of the ear and declined markedly both basipetally and acropetally. Karamu not only produced more grains in floret positions 3 and 4 but also showed this superior floret fertility in a higher proportion of spikelets. For example floret 3 produced some grain in 14 spikelet positions of Karamu but only in 10 in Aotea (Fig. 4.3). For floret 4 the proportion was 10 in Karamu to 5 in Aotea. For both cultivars floret 3 was much more fertile than floret 4 and neither cultivar produced a grain in floret 5.

Figure 4.4 shows the distribution of mean grain size within ears of Aotea and Karamu. The pattern was very similar for both cultivars with the heaviest grains being produced over about seven spikelets in the centre of the ears. Above and below these spikelets mean grain size declined, with the lightest grains being formed at the base of the ears. Karamu produced heavier grains than Aotea at all spikelet positions.

Examination of grain sizes in floret positions 1 and 2 (Fig. 4.5) revealed a pattern very similar to that shown in Figure 4.4. In Karamu the grain in floret 2 was larger than in floret 1 for spikelet positions 2 to 11 inclusive. For Aotea the range was 3 to 12. Above and below these positions the situation was reversed with grain from floret 1 being larger than that formed in floret 2.

As with grain set differences among spikelet positions for grain weight were much more marked in the case of florets 3 and 4 (Fig. 4.6). In all spikelets, Karamu produced heavier grains than Aotea in floret 3. In floret 4 Karamu showed somewhat less of a peak

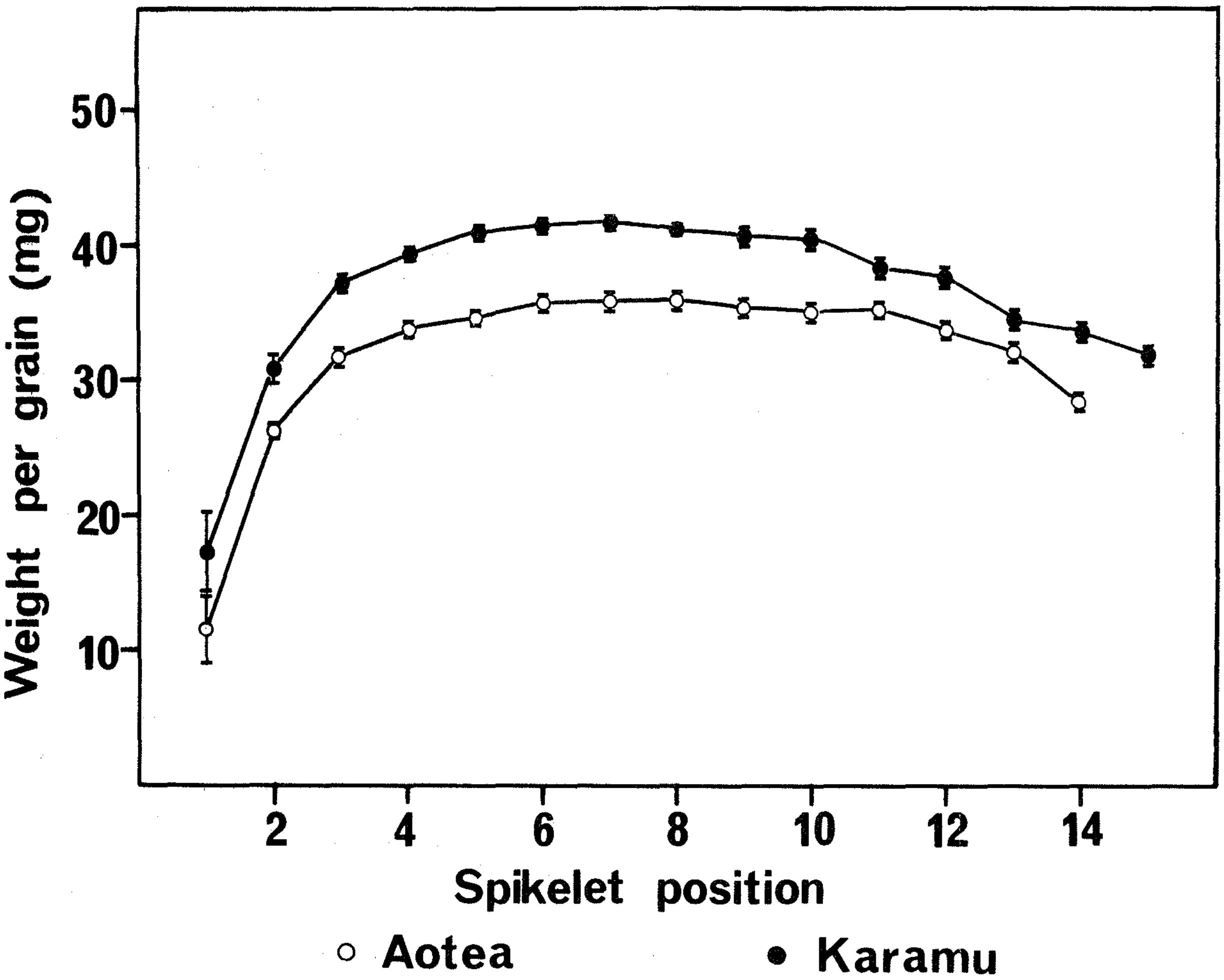

Figure 4.4 - The effect of spikelet position on the mean weight per grain of Aotea and Karamu wheat.

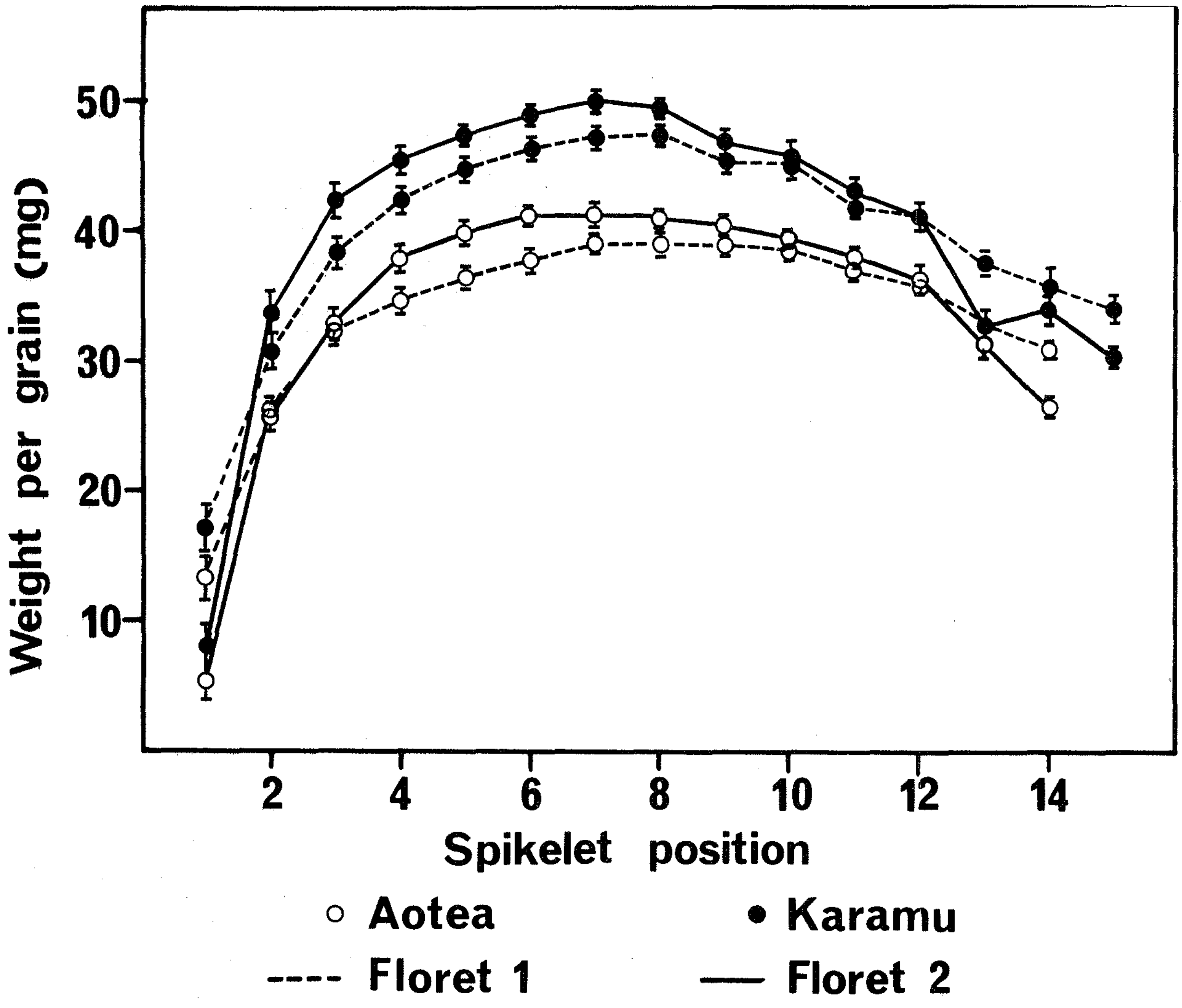

Figure 4.5 - The effect of spikelet position on the mean weight per grain in florets 1 and 2 of Aotea and Karamu wheat.

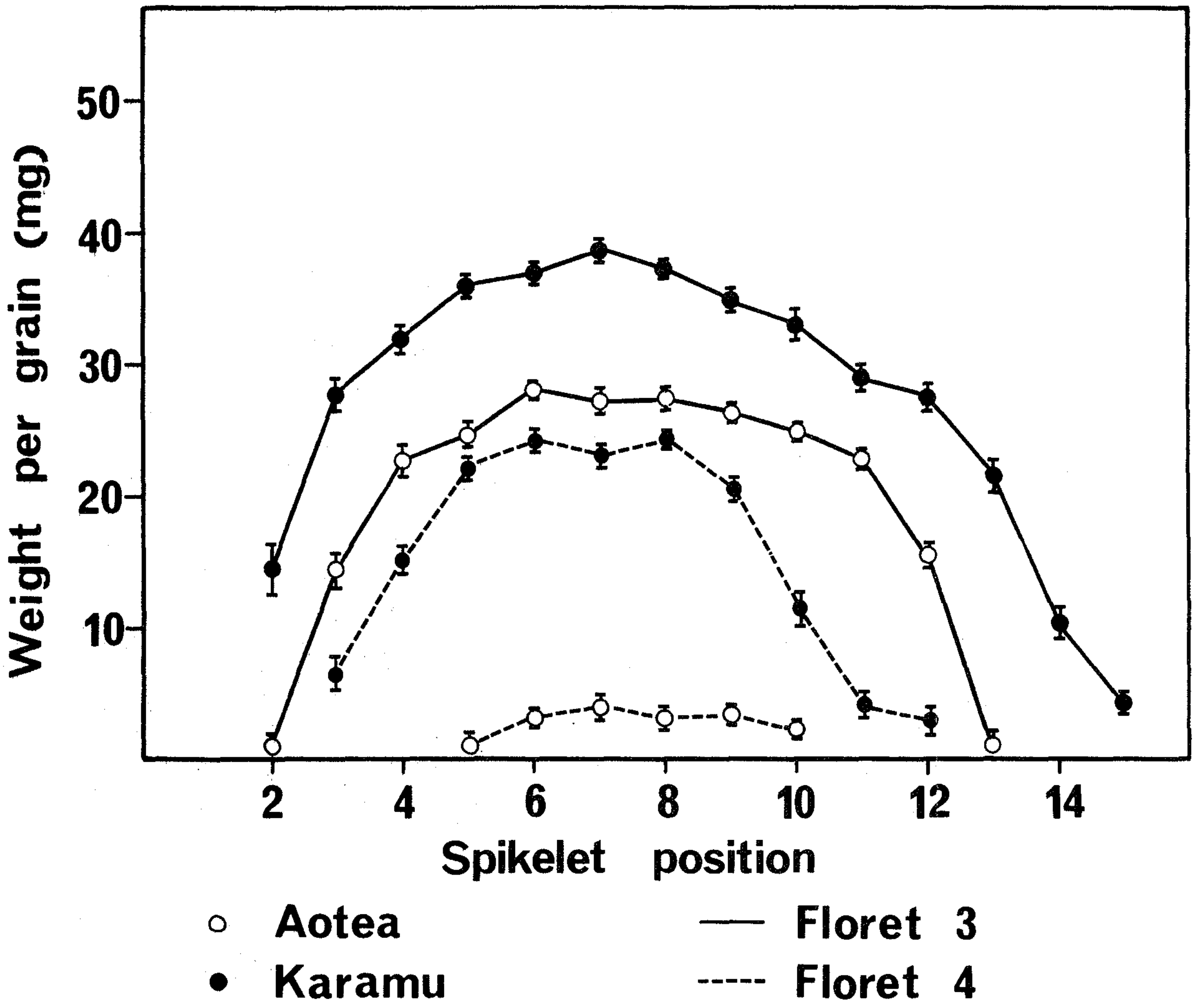

Figure 4.6 - The effect of spikelet position on the mean weight per grain in florets 3 and 4 of Aotea and Karamu wheat.

in its pattern of grain size distribution. The so-called 'grains' from floret 4 of Atoea were all extremely light and would have been classed as screenings. These grains were very pinched and shrivelled and appeared to have been aborted shortly after anthesis. For both cultivars at all spikelet positions floret 3 produced much heavier grains than floret 4.

4.4 DISCUSSION

Aotea and the Norin 10 derivative Karamu differed very little in their general pattern of grain set as shown in Figure 4.1. Both Fisher (1973) and Holmes (1973) found that early spikelet development in Norin 10 derivatives is more synchronised than in standard wheats. The sequence of anthesis in florets and between spikelets is a critical factor in determining which florets set grain (Evans *et al.* 1972; Langer & Hanif 1973; Walpole & Morgan 1973). Thus, synchronised development should result in Norin 10 derivatives producing a number of spikelets of uniformly high fertility in the low-central portion of the ear. This did not occur in the present experiment (Fig. 4.1) and may therefore be an indication that early synchronised development between spikelets mainly influences spikelet number as Karamu produced one more spikelet than Aotea.

The failure of Karamu to produce a number of spikelets of uniformly high fertility (Fig. 4.1) may also mean that grain set is influenced more by floret development occurring between the time the glumes and lemmas cover the apical meristem of the spikelet and ear emergence, a period of about 3 weeks when the ear is elongating rapidly. Apart from the work of Hanif and Langer (1972) and Langer and Hanif (1973) this period of floret development has not been intensively studied due probably to the physical inaccessibility of the small delicate florets at this stage. Spikelet weight at the early boot stage (Feekes 9+) correlates well with the final number of grains set per spikelet (Scott *et al.* 1975).

On average Karamu spikelets contained more grains than those of Aotea (Fig. 4.1) and this was because in Karamu a higher proportion of florets 3 and 4 set grain (Fig. 4.3). The ability of Norin 10 derivatives to produce a large number of grains per spikelet is well documented and has been ascribed to faster rates of floral primordia initiation (Syme 1974) and a smaller degree of "apical dominance" within the spikelet than in standard cultivars (Fisher 1973; Holmes 1973), "apical dominance" signifying the presumed holding in check of basal florets. However, this retarded development of basal florets has been assumed more than observed after they have been enclosed by the accessory floral organs.

An interesting aspect of the present data is the lower grain set of the basal florets of Karamu compared with Aotea (Fig. 4.2). This reduced performance may have resulted from their assumed retarded development during the pre-anthesis period and this could be taken to support the contention of Fisher (1973) and Holmes (1973) that in Norin 10 derivatives the basal florets are held in check even after they have been enclosed by the accessory floral organs.

The lack of difference in grain set between florets 1 and 2 shown jointly in Figure 4.2 is in line with previous work and has been explained on the basis that these basal florets are formed and anthese at about the same time (Evans *et al.* 1972; Walpole & Morgan 1973; Kirby 1974). In contrast, for both cultivars grain set in floret 3 was considerably higher than in floret 4 and this may well be attributed to differences in time of initiation and rate of development as shown by Langer and Hanif (1973).

Grain weight differences between spikelets of both cultivars were relatively small (Fig. 4.4) compared with the differences in grain set (Fig. 4.1). This might indicate firstly, that grain filling in wheat is less affected by spikelet position than is grain set, and secondly, that grain yield per ear may be limited by the capacity of the ear to accumulate sites for grain filling. This second deduction confirms our previous conclusion that in this environment many of the yield differences between crops are caused primarily by grain number rather than grain size (Scott *et al.* 1973; Dougherty *et al.* 1974) so that a knowledge of the factors affecting grain set is of critical importance.

Both Rawson and Evans (1970) and Kirby (1974) found that in intact ears the grain weight of floret 2 was greater than that of floret 1 in all spikelets except the terminal ones. This pattern also existed in the present experiment (Fig. 4.5) except that in the basal spikelet of both Aotea and Karamu the situation was reversed with floret 1 producing a slightly heavier grain than floret 2. The reasons for these differences have been explained on the basis of differences in growth rate between florets (Rawson & Evans 1970), although recently Kirby (1974) has suggested that pre-anthesis floret growth as determined by the duration of the period of ovary formation may determine the potential size of the grain. Times of floret initiation were not recorded in the present experiment but the time between the double-ridge stage and ear emergence was very similar, being approximately 37 and 39 days for Aotea and Karamu respectively.

The spring sowing in this experiment obviously favoured the daylength insensitive Karamu (Rawson 1971) at the expense of Aotea which shows some response to vernalisation and daylength (MacEwan 1959). Stoskopf *et al.* (1974) in Canada concluded that low yields of spring wheat compared with winter wheat were due largely to a reduction in the number of grains per ear, which could be influenced either by changing spikelet number or number of grains per spikelet. In the Lincoln environment with winter sowing, grain weights of Aotea and Karamu are similar, but grain set in the semi-dwarf is still superior (Dougherty *et al.* 1974). Thus the present comparison in grain set between the two cultivars when spring sown probably remains valid.

In conclusion it can be said that the superior grain setting ability of Karamu wheat compared with Aotea is due to its ability to set grains in a higher proportion of florets 3 and 4, and that this more than offsets the reduced grain set which occurs in florets 1 and 2. Although this study does not explain the physiological reasons for these differences it does suggest the need for more detailed studies of floret development from the time the accessory floral organs close over the florets until about one week after ear emergence. This time span of about 3 weeks covers the most rapid period of ear growth which multiple regression analysis (Lupton *et al.* 1974) has shown to be highly correlated with grain yield.

4.5 SUMMARY

The pattern of grain set and grain size distibution within mainstem ears of a standard New Zealand wheat Aotea was compared with that in a Norin 10 derivative Karamu when both cultivars were spring sown. Karamu produced one more spikelet and heavier grains than Aotea. The higher number of grains per spikelet produced by Karamu was due to superior grain set in florets 3 and 4 of the central spikelets. Florets 1 and 2 of Karamu spikelets had slightly lower fertility than those of Aotea and this was attributed to retarded development of the basal florets during pre-anthesis floret development.

4.6 POSTSCRIPT

The studies on the pattern of grain set and grain growth of Aotea, Arawa and Karamu wheat both indicated that events occurring before anthesis had a major influence on the number of grains produced in each spikelet. In particular, Chapter 3 showed that the potential number of fertile florets was probably determined even before ear emergence as there was a significant correlation between spikelet dry weight at the early boot stage and final grain number per spikelet. This pre-anthesis development appeared to be related to the supply of carbohydrate reaching the young developing ear (Dougherty *et al.* 1975a) and was restricted by any treatments which encouraged vegetative growth. These findings were somewhat surprising in view of the fact that the crops were comparatively low yielding with restricted leaf development and spike populations. Physiological drought may have been a confounding influence in this spring sown crop.

The original objective in 1973 was to establish a potentially high yielding wheat crop that contained treatments which would modify both ear number and grain set, and to monitor the length and height of the apex. Owing to the failure of the autumn sowing this remained the main objective for the 1974-5 season with some additions. The 1972-3 experiment with Aotea had demonstrated the importance of ear number and LAI in determining final yield but more information was required on the relationship between ear number, LAI and grain set in a high yielding crop. Rothamsted research reviewed by Thorne (1973) also stressed the importance of LAI, and the relationship between flag leaf area and grain yield, an aspect which had not yet been adequately researched in New Zealand. Thus for the 1973-4 season it was decided to monitor both total leaf area and flag leaf area and relate these to the components of grain yield. These aspects are reported in Chapter 5.

CHAPTER 5

DEVELOPMENT AND YIELD COMPONENTS OF HIGH-YIELDING WHEAT CROPS*

5.1 INTRODUCTION

New Zealand's national average wheat yield in the 1972-73 season was 2.98 t/ha (N.Z. Farm Production Statistics 1972-73), although yields of over 6 t/ha are possible under both commercial and trial-plot conditions (Scott *et al.* 1973). Recent research on high-yielding wheat crops has examined the relationship between yield components (Fisher & Kertesz 1976) as well as leaf area (Thorne 1973).

There is little published information available on the development and yield components of high-yielding wheat crops in New Zealand, apart from that recorded previously by Scott *et al.* (1973). This paper presents data from a factorial field experiment in which the mean wheat yield was 6.6 t/ha, more than double the national average. In other research conducted on this experiment, water and nitrogen profiles, plant water relations, and 14-C fixation of flag leaves were monitored at intervals.

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* W.R. Scott, C.T. Dougherty and R.H.M. Langer
N.Z. Journal of Agricultural Research *20*: in press (1977).

5.2 MATERIALS AND METHODS

Experimental techniques were similar to those described previously (Dougherty *et al.* 1975b). A 2 x 3 x 2 x 2 factorial experiment was laid out in two randomised blocks on Wakanui silt loam on the Lincoln College Research Farm. Previously the site was in irrigated freezer peas and, before that, irrigated permanent pasture composed mainly of white clover and perennial ryegrass. The treatments and their levels were:

Cultivars	C_0	:	Aotea
	C_1	:	Arawa
Irrigation	W_0	:	Not irrigated
	W_1	:	Early irrigation
	W_2	:	Late irrigation
Nitrogen fertilisation	N_0	:	None
	N_1	:	140 kg/ha
Sowing rate	S_0	:	250 viable seeds/m^2
	S_1	:	500 viable seeds/m^2

The plots (30 x 3 m) were sown 22 May 1974 in 15 cm rows at a depth of 3 cm with superphosphate at 250 kg/ha.

Control plots were not irrigated and, like the others, no attempt was made to exclude rain. Plots on the early irrigation schedule were first irrigated on 11 November and by the end of this treatment on 13 December 234 mm of water had been applied. The late irrigation treatment started on 26 November and also ended on 13 December after 161 mm of irrigation. Soil water content was determined gravimetrically at weekly intervals to a depth of 20 cm and at irregular intervals to depths of 90 cm and expressed on a dry-weight basis after drying to 105°C.

Nitrogen Fertilisation

Nitrogen as nitrolime (26:0:0) was broadcast at 100 kg N/ha on 22 August on all N_1 treatments. Soil nitrate and ammonium levels were analysed routinely by T.E. Ludecke, Department of Soil Science, Lincoln College. In late September these analyses revealed low levels of plant-available N to depths of 90 cm in both unfertilised and fertilised plots (Table 5.1). Subsequently, on 14 October additional N (40 kg/ha) was applied as nitrolime to all N_1 plots.

Measurements

On 28 June plant numbers were counted by sampling six 0.1 m^2 quadrats per plot. At fortnightly intervals starting on 12 September one 0.1 m^2 quadrat was cut from each plot, living tillers were counted, and all green laminae removed at the junction of the leaf sheath. Leaf area was determined with a planimeter and leaf area index (LAI) calculated. The methods used for determination of grain yield have been described previously (Dougherty *et al.* 1975b).

5.3 RESULTS

Plant Establishment

Plant establishment counts on 28 June showed that proportionally fewer seeds established at the high sowing rate but there was no significant difference between cultivars (Table 5.2).

Table 5.1 - Available N (kg/ha) in soils under wheat grown with and without fertiliser N.

Treatment	Soil Zone (cm)	6 August	28 August	28 Sept	23 Oct	19 Nov
N_0	0-20	8	2	0	6	0
	20-90	83	54	13	77	0
N_1	0-20	-	-	9	27	0
	20-90	-	-	41	100	7

Table 5.2 - Establishment of Aotea and Arawa as affected by sowing rate (plants/m^2); LSD 5%, 51.

	S_0	S_1	Mean
C_0	236	413	325
C_1	225	416	321
Mean	231	415	

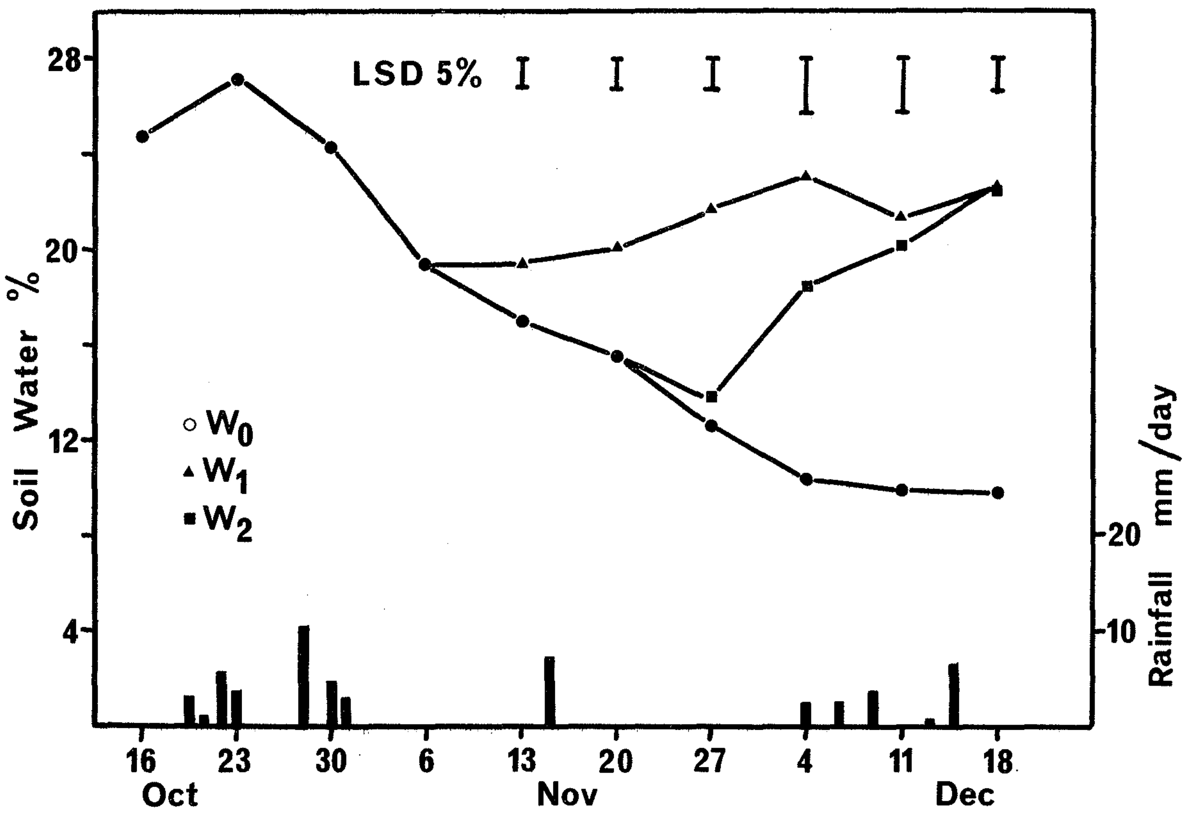

Figure 5.1 - Effect of irrigation and rainfall on soil water (%) in the 0-20 cm zone.

Reproductive Development

Nitrogen delayed ear emergence by about 3 days in both cultivars, hence the range shown in Table 5.3. However, the timing of 50% anthesis was not influenced by N. Both irrigation and sowing rate had no effect on the timing of these events.

Soil Moisture

In the 0-20 cm zone Wakanui silt loam has a field capacity of 28.8% moisture and a wilting point of 11.3% (Dougherty 1973). After the build-up of soil moisture over winter all plots were near field capacity in October but, without irrigation, soil moisture dropped to wilting point in late November (Fig. 5.1). This drop in soil water level in November was prevented by early irrigation, and late irrigation increased soil water levels from late November onwards.

Irrigation was not the only treatment that affected soil water levels (Fig. 5.2). Soils fertilised with N contained about 2% less soil water than unfertilised plots in the 0-20 cm zone during November and December.

Available soil water levels in the 60-90 cm zone were higher than in the 0-2 cm zone (Table 5.4). The 60-90 cm zone of this soil has a field capacity of 14.8% and a wilting point of 4.4% (J.B. Judd, unpublished data).

LAI

High sowing rate significantly increased LAI only on 12 September and these data are not presented. However, there were large differences in LAI caused by cultivar and N (Fig. 5.3). Peak

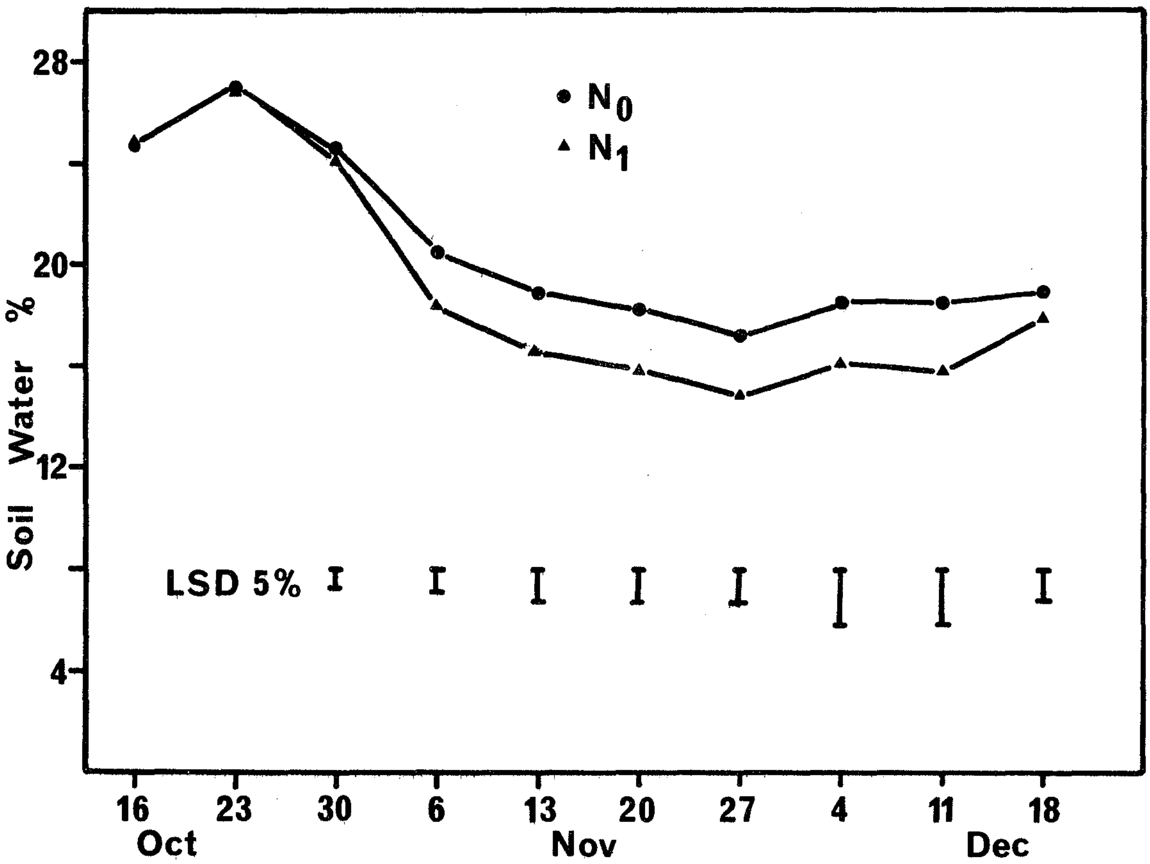

Figure 5.2 - Effect of nitrogen on soil water (%) of the 0-20 cm zone.

Table 5.3 - Timing of reproductive events

	Double Ridge	Ear Emergence	Anthesis
Aotea (C_0)	13 Sept	19-21 Nov	26 Nov
Arawa (C_1)	10 Sept	12-15 Nov	21 Nov

Table 5.4 - Soil water (%) in the 60-90 cm zone (T.E. Ludecke, unpublished data).

6 Aug	29 Aug	23 Sept	23 Oct	19 Nov
19.7	21.5	19.6	19.6	15.5

LAI in Arawa occurred on 7 November and timing was unaffected by N. In Aotea peak LAI was reached on 24 October without N and a week earlier with N.

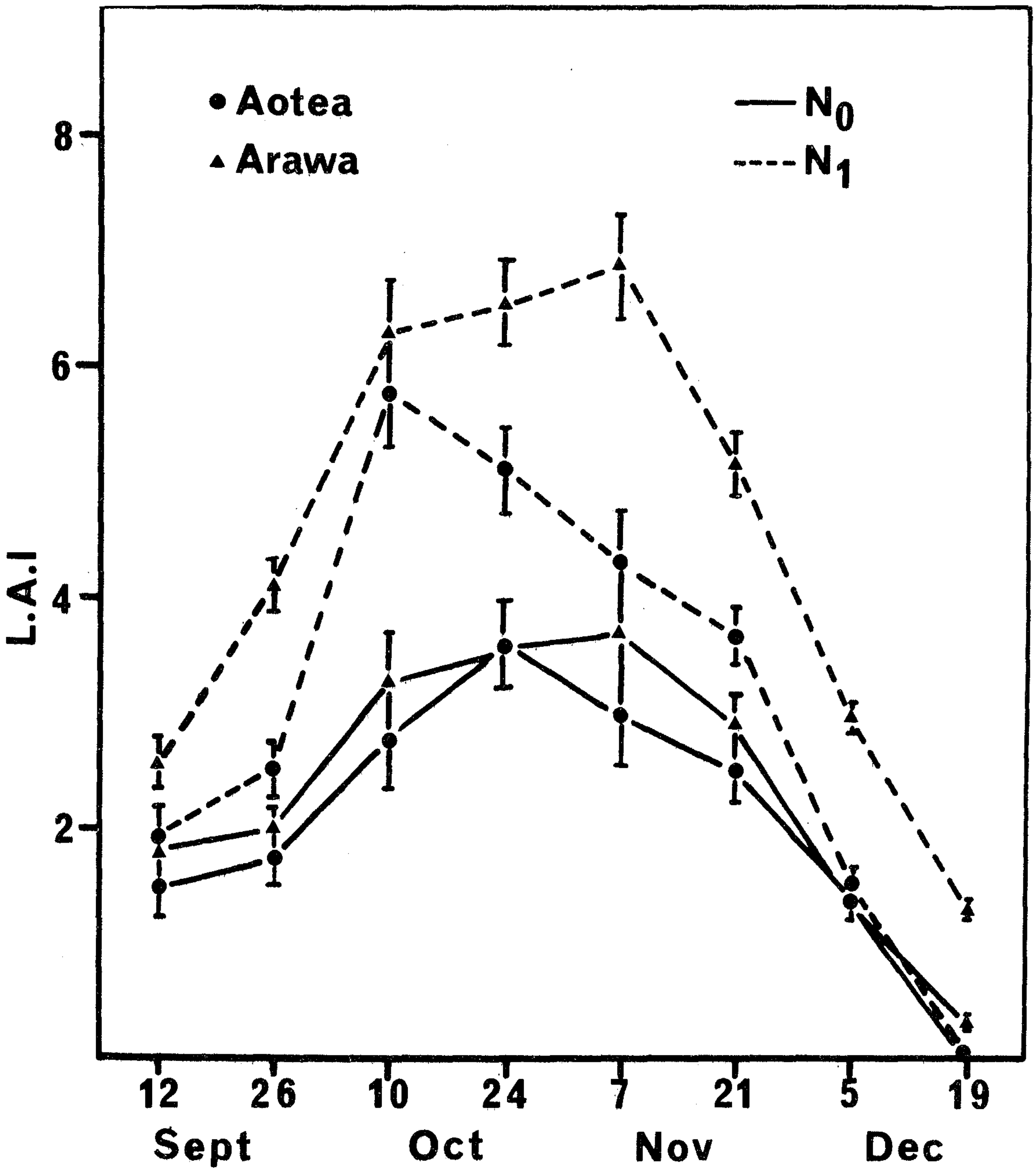

Figure 5.3 - Effect of cultivar and nitrogen on LAI.

Grain Yield, Tiller, and Ear Populations

Mean grain yields for both cultivars were high, Arawa significantly outyielding Aotea (Table 5.5).

Table 5.5 - Effect of cultivar, irrigation, N, and sowing rate on grain yields and ear population at harvest.

		Grain yield (kg/ha)	No. ears/m^2
Cultivar	C_0	6292	656
	C_1	6920	539
LSD 5%		600	33
Irrigation	W_0	6414	600
	W_1	6793	621
	W_2	6611	572
LSD 5%		735	41
Nitrogen	N_1	6038	543
	N_2	7174	652
LSD 5%		600	33
Sowing rate	S_0	6743	572
	S_1	6469	623
LSD 5%		600	33
Significant interactions		None	C x N**

Irrigation and sowing rate failed to produce a significant grain yield response, even though high sowing rate signficiantly increased ear numbers. Nitrogen increased overall grain yield by 19%, but it affected ear number of Arawa more than Aotea (Table 5.6).

Table 5.6 - Interaction of cultivar and N on ears/m^2; LSD 5%, 67.

	N_0	N_1
C_0	624	688
C_1	461	617

A similar interaction between cultivar and N also occurred with live tiller numbers (Fig. 5.4) late in the season (19 December). At other times N increased tiller numbers in both cultivars. The timing and rate of tiller mortality differed between cultivars and was markedly influenced by N (Fig. 5.4).

Yield Components of the Ear

Arawa produced a much larger ear than Aotea in all respects (Table 5.7). Arawa produced much larger grains than Aotea, but no agronomic treatment influenced grain weight. Thus the interaction between N and sowing rate on grain yield per ear was largely due to differences in grain number per ear, and Table 5.8 shows that high sowing rate reduced grain number per ear only when N was not applied (Table 5.9).

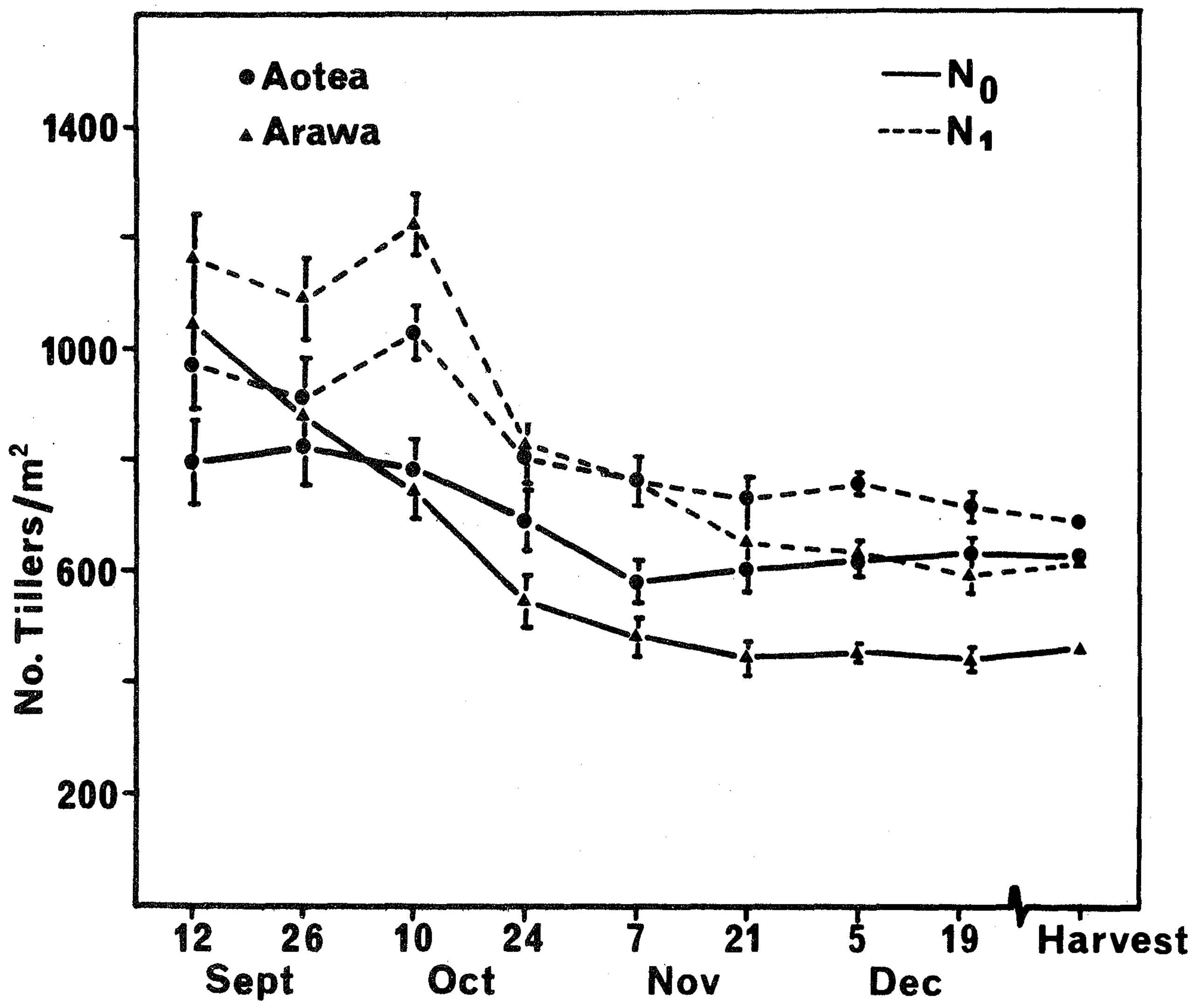

Figure 5.4 - Effect of cultivar and nitrogen on tiller and ear numbers.

Table 5.7 - Effect of cultivar, irrigation, N, and sowing rate on yield components of the ear.

		No. spikelets/ear	No. grains/spikelet	No. grains/ear	Wt/grain (mg)	Grain wt/ear (g)
Cultivar	C_0	17.0	1.40	23.8	40.6	0.96
	C_1	17.5	1.61	28.1	46.2	1.29
LSD 5%		0.27	0.16	2.8	1.45	0.11
Irrigation	W_0	17.4	1.47	25.5	43.1	1.10
	W_1	17.1	1.51	25.8	43.5	1.12
	W_2	17.2	1.54	26.6	43.7	1.16
LSD 5%		0.34	0.19	3.4	1.78	0.13
Nitrogen	N_0	16.7	1.56	26.2	43.6	1.14
	N_1	17.7	1.45	25.8	43.2	1.11
LSD 5%		0.27	0.16	2.8	1.45	0.11
Sowing rate	S_0	17.4	1.58	27.5	44.0	1.20
	S_1	17.0	1.43	24.5	42.8	1.05
LSD 5%		0.27	0.16	2.8	1.45	0.11
Significant interactions		C x S*	N x S*	N x S*	None	N x S*

Table 5.8 - Interaction of N and sowing rate on mean number of grains per ear; LSD 5%, 4.0.

	N_0	N_1
S_0	29.1	25.9
S_1	23.3	25.6

To aid in the interpretation of data from all the ears, the yield components of main-stem ears are presented in Table 5.9, and some differences are apparent. The interaction between irrigation and sowing rate on grain yield per ear was because at low sowing rate late irrigation reduced grain weight (Table 5.10). N had no effect on grain weight per ear on main stems, but it did influence the yield components in that the increase in spikelet number caused by N was offset by a significant decrease in the number of grains per spikelet.

Table 5.9 - Yield components of mainstem ears.

		No. spikelets/ear	No. grains/spikelet	No. grains/ear	Wt/grain (mg)	Grain wt/ear (g)
Cultivar	C_0	17.7	1.88	33.3	40.2	1.34
	C_1	18.3	2.22	40.7	46.9	1.91
LSD 5%		0.3	0.15	2.7	1.5	0.14
Irrigation	W_0	18.0	2.11	38.0	43.9	1.68
	W_1	17.9	2.03	36.3	43.5	1.58
	W_2	18.1	2.02	36.8	43.3	1.60
LSD 5%		0.4	0.19	3.3	1.8	0.17
Nitrogen	N_0	17.4	2.19	38.3	43.8	1.69
	N_1	18.6	1.91	35.7	43.4	1.56
LSD 5%		0.3	0.15	2.7	1.5	0.14
Sowing rate	S_0	18.3	2.11	38.6	44.2	1.72
	S_1	17.7	2.00	35.4	42.9	1.53
LSD 5%		0.3	0.15	2.7	1.5	0.14
Significant interactions		None	None	None	W x S*	W x S*

Table 5.10 - Interaction of irrigation and sowing rate on mean weight per grain (mg) for mainstem ears; LSD 5%, 2.0.

	S_0	S_1
W_0	45.5	42.2
W_1	44.4	42.7
W_2	42.7	44.0

Flag-Leaf-Area Duration

Flag-leaf-area duration (FLAD) showed no response to irrigation or sowing rate, but there was a significant interaction between cultivar and N (Table 5.11).

Table 5.11 - Interaction of cultivar and N on flag-leaf-area duration (m^2 week); LSD 5%, 0.26.

	N_0	N_1
C_0	2.06	3.44
C_1	1.80	3.79

Simple linear correlation between FLAD and grain yield showed a significant relationship (r = +0.53**). However, FLAD showed no significant correlation with either grains per spikelet (r = -0.16) or mean grain weight (r = -0.05).

Relationships Between Components of Yield

Simple linear correlations between grain yield and its components revealed that both grains per spikelet and spikelets per ear accounted for the largest amount of variation in grain yield, although mean grain weight and ear number had much lower correlation coefficients (Table 5.12). Grains per spikelet and mean weight per grain were both inversely related to ear number.

Table 5.12 - Simple correlation matrix for components of yield.

Component	1	2	3	4
1. Ears/m^2	1.00			
2. Spikelets/ear	+0.07	1.00		
3. Grains/spikelet	-0.53**	+0.23	1.00	
4. Grain weight	-0.60**	+0.28*	+0.29*	1.00
5. Grain yield	+0.22	+0.45**	+0.54**	+0.24

When fitted against grain yield by stepwise linear regression the components were ranked in the order shown in Table 5.13. Differences in grains per spikelet and ears/m^2 combined accounted for 65% of the variation in grain yield. Inclusion of grain weight and spikelets per ear increased this figure to 90 and 94% respectively.

Table 5.13 - Stepwise multiple regression of components of yield.

Variable	Coefficient	SE of Coefficient
(Constant - 1951.73)		
Grains/spikelet	391.32	19.10
Ears/m^2	1.13	0.06
Grain weight	16.62	1.66
Spikelets/ear	36.28	6.99

5.4 DISCUSSION

Cultivars

Arawa produced a higher grain yield than Aotea largely because its larger spikelets contained heavier grains, but both cultivars produced very high yields (Tables 5.5, 5.7). If 97% plant survival is assumed, as found by Clements *et al.* (1974), it can be estimated from Table 5.2 that mainstem ears of Arawa produced 86% of the total grain yield, but in Aotea they produced only 69%, proportions similar to those found by Clements *et al.* (1974) and Ishag and Taha (1974) in much lower-yielding crops. It seems therefore that even in high-yielding wheat crops, mainstem ears still contribute the bulk of the yield.

Peak tiller numbers in Arawa ($1103/m^2$) were higher than in Aotea ($909/m^2$), but tiller survival was 49 and 72% respectively, so that Aotea produced a much higher ear population at harvest (Table 5.5, Fig. 5.4), results similar to those found by Langer (1964) in lower-yielding crops.

Arawa is generally recommended for autumn sowing under high-fertility conditions (Smith 1974). In the present experiment Arawa was more responsive to N than Aotea in terms of ear numbers (Table 5.5) and LAI in the initial stages (Fig. 5.3), but not in terms of grain yield (Table 5.5). These responses follow the general pattern frequently observed in taller wheats which have a greater capacity to respond to favourable conditions by increasing vegetative growth at the expense of reproductive growth and grain yield (Dougherty & Langer 1974).

Irrigation

The outstanding feature of the irrigation treatments was the complete lack of grain yield response despite the fact that soil water levels in the 0-20 cm zone of the control plots fell to low levels in November and December (Fig. 5.1). Previous irrigation trials on this soil with winter wheat have given various responses ranging from 30% yield depressions (Dougherty & Langer 1974) to 12% yield increases (Scott *et al.* 1973). On a less moisture-retentive Templeton soil, Wilson (1974) obtained a mean yield increase of 17% in winter wheat, and on shallow Lismore soils at Winchmore yield increases of up to 150% have been recorded on crops lower-yielding than those described here (Drewitt & Rickard 1970). The explanation for these differential responses probably lies in the availability and exploitation of subsoil moisture. In the present experiment available subsoil moisture levels were high (Table 5.4) after a wet winter, and after excavation wheat roots were clearly visible at a depth of 90 cm. The 60-90 cm zone of this soil has a field capacity of 14.8% and a wilting point of 4.4%. Thus even in November the water content of the subsoil was above field capacity (Table 5.4).

Nitrogen fertiliser significantly increased crop water use in November and December as evidenced by soil water content (Fig. 5.2). In pasture species (Johns & Lazenby 1973) and lucerne (Ritchie & Burnett 1971) it has been found that water use is insensitive to changes in LAI above 3.0. LAI of unfertilised wheat in the present experiment fell to below 3 in early November (Fig. 5.3), the same time at which N depressed soil water levels (Fig. 5.2).

Accelerated use of soil water of N-fertilised wheat did not result in any yield reduction through the process of "haying off", but this phenomenon may explain some of the fertiliser-induced yield depressions recorded in the past (Walker 1969; Ludecke 1972) on soils of lower water-holding capacity and in years when soil moisture deficits in the root zone induce crop water stress.

Nitrogen and Sowing Rate

Nitrogen responses in this experiment are consistent with those in England. Watson *et al.* (1963) found that in winter wheat N increased the LAI and tiller number in a pattern similar to that described here. However, in measuring LAI both Watson *et al.* (1963) and Fischer (1975) included leaf sheaths, culms, and ears, Fischer referring to this overall measurement as photosynthetic area index (PAI). Both these authors obtained maximum PAI values of about 8 near ear emergence, 50% of which was made up of laminae (Watson *et al.* 1963). If we assume that crop structure is similar, peak PAI values in the present experiment may have reached the very high value of 14 for Arawa with N (Fig. 5.3). Fischer (1975) showed that very high grain yields could be obtained with a PAI of 8, but Scott *et al.* (1973) showed that very high values of LAI could even depress grain yield. Thus it would appear the the N-induced grain yield response was not directly related to the increase in LAI attributable to increased N availability.

In both treatments Arawa reached peak LAI at the normal time, around ear emergence, but in Aotea peak LAI was reached 4 and 6 weeks before ear emergence in the N_0 and N_1 treatments respectively (Table 5.3, Fig. 5.3). This early reduction in LAI of Aotea, particularly when N was applied may have been assisted by the moderate infection of powdery mildew (*Erysiphe graminis* D.C) which occurred despite application of benomyl. Nitrogen caused a flush of tillers in early October in both cultivars at a time when tiller numbers were already declining in unfertilised plots (Fig. 5.4). It seems highly likely that these late-formed tillers died soon after (Bremner 1969). Available N declined markedly between 23 October and 19 November (Table 5.1), indicating perhaps that wheat at this time is capable of absorbing ammonium and nitrate N at a faster rate than it is made available by mineralisation. This also implies that nitrogen may have limited growth and yield during parts of early reproductive growth and development.

Unlike some previous results (Scott *et al.* 1973, 1975; Dougherty & Langer 1974; Dougherty *et al.* 1975a, b) the decrease in grain set caused by N and high sowing rate was not sufficient to reduce overall yield, which was increased 19% by N fertiliser because of its effect on spike population (Table 5.7). This indicates that in the Canterbury environment a high-yielding wheat crop can be achieved with only a moderate 1.5 grains per spikelet, provided that at least 600 ears/m^2, each bearing at least 17 spikelets, are also produced.

Without detailed measurements of soil N levels such a dramatic grain yield increase in response to N would not have been predicted on this fertile soil cultivated out of vining peas ex. pasture (Wright 1969). Of the nitrogen available in August, 52 kg/ha to a depth of 60 cm was in the nitrate form (T.E. Ludecke, unpublished). At this level of nitrate N, Ludecke's (1974) model would predict a 30% grain yield response to applied N. The increase was 19%, possibly because of mineralisation of organic N which occurred subsequently (Table 5.1).

Relationships Between Yield Components

Mean weight per grain was poorly correlated with grain yield (Table 5.12) and, apart from differences between cultivars, no other treatment affected this component (Table 5.7). A significant correlation ($r = +0.53^{**}$) between grain yield and FLAD has been found by several other workers (Fischer & Kohn 1966; Simpson 1968; Puckridge 1971) and initially indicates that the crops were source-limited. During grain filling daily solar radiation levels were much higher (25.9 MJ/m^2) than the 12-year mean (22.5 MJ/m^2). This value is nearly double that recorded by Welbank *et al.* (1966) during grain filling in England and even higher than the 24.3 MJ/m^2 recorded for an equivalent period in Mexico by Fischer (1975). Gifford *et al.* (1973) calculated a factor to estimate the extent to which grain growth was limited by source. It is not possible to calculate the source limitation factor for the present experiment, but comparison of the data with those of Fisher (1975) and Welbank *et al.* (1966) suggests that mean weight per grain in the present experiment was not source-limited despite the high grain number (> 15,000/m^2). Strong supporting evidence comes from the fact that mean weight per grain was unrelated to FLAD (r = -0.05). The results therefore support the conclusion of Langer and Dougherty (1976) that in this environment, it is differences in grain number which cause the major variations in yield.

Differences in grain number per unit area are attributable mainly to differences in grain number per spikelet and ears/m^2 (Tables 5.5, 5.7), and when fitted against grain yield by stepwise linear regression these two yield components combined accounted for 65% of the variation in grain yield (Table 5.13). In this experiment the number of ears/m^2 did not contribute significantly to variations in yield (Table 5.12), and this supports our previous conclusion (Scott *et al.* 1973) that once a yield of about 6 t/ha is approached, ear number becomes less important as a yield-limiting component. At this yield level the optimum ear population is 600-700 ears/m^2, depending on cultivar (Table 5.5, Scott *et al.* 1973). Once this ear population is reached grain set or the number of grains per spikelet usually becomes an important yield-limiting factor. In the present experiment grains per spikelet alone was positively correlated with yield (r = +0.54**) but negatively correlated with ear number (r = -0.53**).

5.5 CONCLUSION

The experiment has demonstrated that high-yielding wheat crops in Canterbury result from the production of a large number of grains per unit area, and the most obvious method of achieving this number is by improving grain number per spikelet and maintaining high ear densities, perhaps by reducing tiller mortality. Wheat yields of Arawa and Aotea do not appear to be limited by tillering capacity or leaf area.

Two practical conclusions can also be drawn. Firstly, irrigation of winter wheat on deep, moisture-retentive soils is unlikely to result in substantial increases in grain yield, particularly in years when subsoil moisture has been built up by heavy winter rains. Secondly, grain yield increases from N fertiliser may occur even on fertile soils when excessive rainfall causes leaching of mineral N.

5.6 SUMMARY

In a field experiment, Arawa wheat outyielded Aotea by 10% through the production of a higher grain yield per ear. Irrigation had no effect on grain yield because of plant uptake of subsoil moisture. Nitrogen increased grain yield by 19% mainly by increasing ear number. Sowing rate had no effect on yield. Mean yield for the experiment was 6.6 t/ha, the mean yield components being 600 ears/m^2, each composed of just over 17 spikelets containing 1.5 grains, which weighed 43 mg. Arawa produced larger grain than Aotea; no other treatment influenced mean weight per grain, which was unrelated to flag-leaf duration. It is suggested that further yield increases

will best be achieved by increasing grain number per unit area, probably by increasing grains per spikelet, the component most highly correlated with yield in this experiment.

5.7 POSTSCRIPT

Up until the 1975 harvest all experiments had been carried out on Wakanui silt loam soils. For the 1975-6 experiment it was decided to move the experimental site approximately 5 km north-east on to a Templeton silt loam. Two factors influenced this decision. Firstly, bird damage was becoming a problem and, secondly, it was decided to start experimenting on a soil of lower water holding capacity than the Wakanui silt loam where all previous experiments had been carried out. By the harvest of the 1974-5 season it appeared that responses to nitrogen fertiliser were much more predictable and reliable than previously with the aid of Ludecke's (1974) soil test for available N. The results of previous trials had suggested that under conditions of high natural fertility New Zealand wheat cultivars sometimes produced supra-optimal leaf growth, although it was not known to what extent this occurred with nitrogen fertiliser. Unlike in previous experiments a number of rates of nitrogen were applied, these rates covering those that were used commercially.

By the 1975 season Kopara and Karamu were becoming more widely grown (section 1.2) and it was decided to compare these two cultivars directly under conditions of autumn sowing to examine the relationship between spike production and grains per spikelet. Previous experiments with Kopara at Lincoln (Dougherty & Langer 1974) and elsewhere (Douglas *et al.* 1971) indicated that the effects of N on grain yield of Kopara were variable so that more information of this aspect was required, preferably with concurrent measurements on levels of available soil N. It was not possible to include an irrigation treatment in the 1975-6 experiment as none was available on the site. The 1975-6 experiment is written up in Chapter 6.

CHAPTER 6

GROWTH AND YIELD OF KOPARA AND KARAMU WHEAT UNDER DIFFERENT RATES OF NITROGEN*

6.1 INTRODUCTION

Previous experiments on high yielding wheat crops (Scott *et al.* 1973, 1977) have demonstrated the importance of grain number in determining yield differences, and that once an ear population of $600/m^2$ is established it is variation in the number of grains per spikelet or grain set which influences grain number per unit area. While high levels of available soil nitrogen can assist in the establishment of high ear populations, grain set may be so reduced that yield reductions occur (Dougherty & Langer 1974).

Whereas the timing and rate of application of fertiliser N can be controlled, the supply of N from the soil is more variable and, until recently, has not been adequately monitored in N fertiliser experiments. The aim of the present experiment was to investigate the effects of several rates of nitrogen on the growth and yield of a standard New Zealand wheat Kopara, in comparison with the semi-dwarf Karamu.

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* W.R. Scott and C.T. Dougherty

6.2 MATERIALS AND METHODS

The experiment was carried out on the Lincoln College Research Farm on a Templeton silt loam soil. Ryegrass seed was harvested off the paddock the previous year and, before that, several successive cereal crops. A 2 x 4 x 2 factorial design with 3 replicates was used. Treatments and their levels were as follows:

Cultivars	C_0	:	Kopara
	C_1	:	Karamu
Nitrogen	N_0	:	Control
	N_1	:	25 kg N/ha
	N_2	:	50 kg N/ha
	N_3	:	100 kg N/ha
Sowing rate	S_0	:	250 viable seeds/m^2
	S_1	:	500 viable seeds/m^2

The experiment was sown on 12 June 1975 using the same plot size, fertiliser, pest and disease control as that described previously (Dougherty *et al.* 1975). Nitrogen was applied as ammonium nitrate on 18 August. Levels of soil nitrogen and plant available soil moisture were regularly measured by Mr T.E. Ludecke of the Department of Soil Science of Lincoln College.

Tiller numbers, leaf area and final yield components were measured as described previously (Dougherty *et al.* 1975; Scott *et al.* 1977) and grain yields expressed at 14% moisture.

6.3 RESULTS

Rainfall during August, October and November was above average and maintained the soil well above wilting point throughout the growth of the crop (T.E. Ludecke, unpublished data). Thus, it is unlikely that water stress sufficient to reduce grain yield was caused by soil water deficits. Early reproductive development was about one week later than normal (Table 6.1).

Table 6.1 - Timing of key physiological events.

	Double Ridge	Ear Emergence	Anthesis
Kopara	26 Sept	27 Nov	7 Dec
Karamu	19 Sept	6 Nov	13 Nov

Levels of available soil N (Table 6.2) were increased by the addition of nitrogen fertiliser but the differences between rates had disappeared by December. As expected nitrogen had a big influence on the growth of the crop and more than doubled peak LAI (Fig. 6.1). Peak tiller numbers were increased by 50% (Fig. 6.2) and a high proportion of these survived so that by harvest the highest rate of N (N_3) gave a 44% increase in the number of ears (Table 6.3).

Mean grain yield for the experiment was moderately high being just over 6 t/ha (Table 6.3) with nitrogen having the biggest effect of all the treatments, the response being linear up

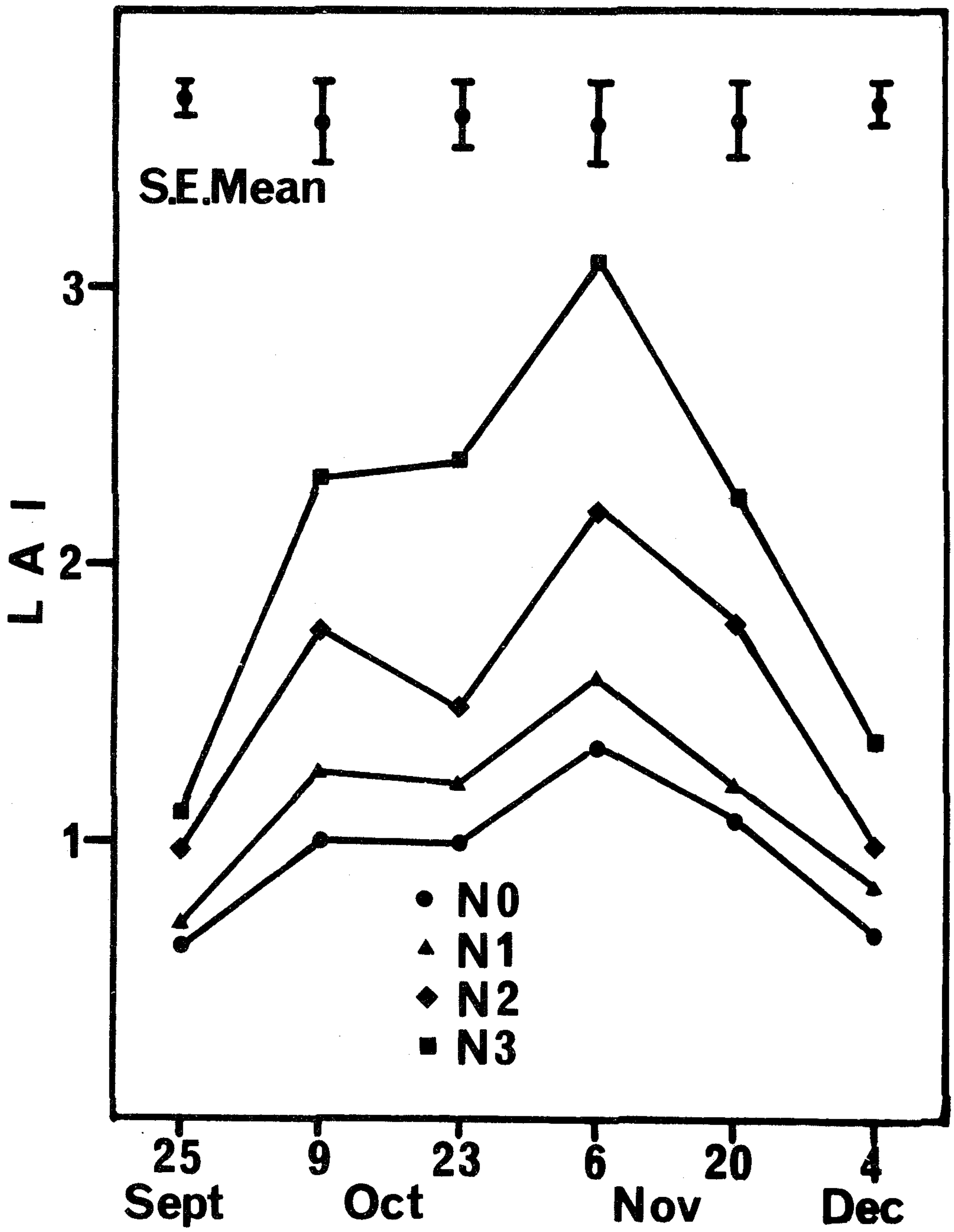

Figure 6.1 - Effect of rates of nitrogen on LAI.

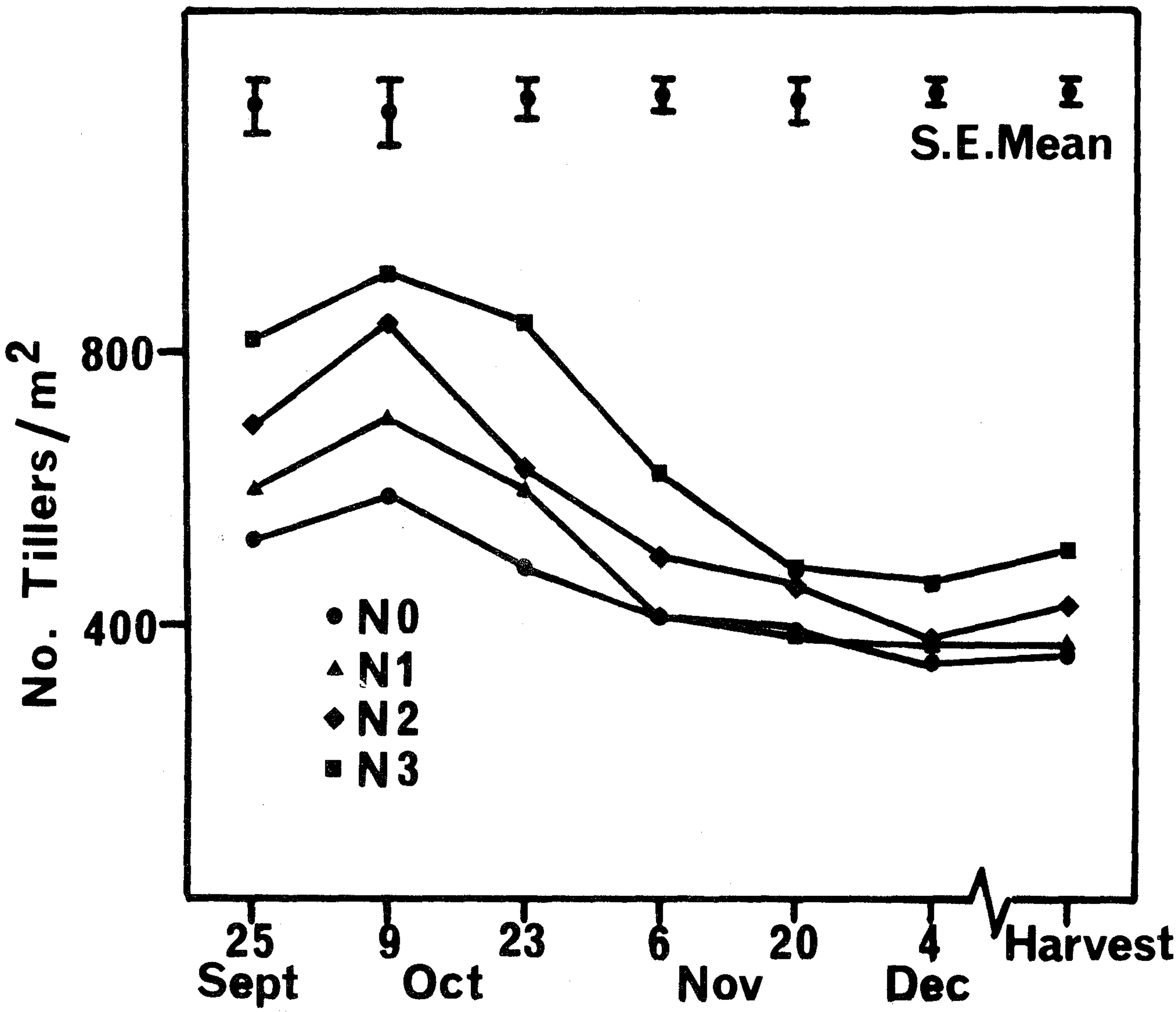

Figure 6.2 - Effect of rates of nitrogen on tiller and ear numbers.

Table 6.2 - Levels of available soil N (kg/ha) in the 0-90 cm zone. T.E. Ludecke (unpublished data)

N Treatment	Date:	14/7	6/8	15/9	24/9	9/10	23/10	6/11	20/11	4/12
N_0		58	44	71	48	85	48	19	23	20
N_1		-	-	-	86	61	30	24	35	0
N_2		-	-	-	158	93	45	47	51	14
N_3		-	-	-	133	77	66	45	64	15

Table 6.3 - Effects of cultivar, nitrogen, and sowing rate on components of grain yield.

	Grain Yield (kg/ha)	No. ears/m^2	No. spikelets/ear	No. grains/spikelet	No. grains/ear	Mean wt/grain	Grain wt/ear
Kopara	6067	411	18.1	1.87	34.0	44.0	1.50
Karamu	5962	426	17.6	1.84	32.6	43.2	1.41
LSD 5%	410	35	0.2	0.11	2.0	0.8	0.10
N_0	4620	356	16.9	1.81	30.7	43.9	1.35
N_1	5177	375	17.5	1.81	31.8	44.4	1.41
N_2	6443	431	18.3	1.86	34.2	44.0	1.50
N_3	7818	512	18.7	1.96	36.6	42.2	1.54
LSD 5%	580	50	0.3	0.16	2.8	1.1	0.14
S_0	6079	384	18.1	1.99	36.1	44.2	1.59
S_1	5950	453	17.6	1.72	30.5	43.1	1.31
LSD 5%	410	35	0.2	0.11	2.0	0.8	0.10
Interactions	None	None	C x N*	None	None	None	None

to 100 kg/ha of N. Apart from increasing ear number, nitrogen also increased spikelet number and grain number per spikelet resulting in up to 6 more grains/ear, although the highest rate of N significantly reduced mean weight/grain.

There was no significant difference between cultivars with regard to total grain yield and although Karamu (C_1) produced slightly smaller grains than Kopara (C_0), Kopara produced more spikelets/ear than Karamu in response to nitrogen (Table 6.4).

Table 6.4 - The interaction of cultivar and nitrogen on mean number of spikelets/ear; LSD 5%, 0.3.

	N_0	N_1	N_2	N_3
C_0	16.8	17.8	18.8	19.1
C_1	17.0	17.2	18.0	18.3

As with differences between cultivars, sowing rate had no effect on total grain yield despite its influence on some of the yield components. The increase in ear number produced by the high sowing rate (Fig. 6.2, Table 6.3) was offset by a decrease in spikelet number, grains/spikelet and mean grain weight.

Relationships Between Components of Yield

The simple linear correlations presented in Table 6.5 showed that ears/m^2 and spikelets/ear accounted for most of the variation in grain yield. When fitted against grain yield by stepwise linear regression the components were ranked in the order shown in Table 6.6 with differences in spikelets/ear and ears/m^2 combined accounting for 83% of the variation in grain yield. When grains/ spikelet and grain weight were included this figure was increased to 94 and 96% respectively.

Table 6.5 - Simple correlation matrix for components of yield.

Component	1	2	3	4
1. Ears/m^2	1.00			
2. Spikelets/ear	+0.45**	1.00		
3. Grains/spikelet	-0.34*	+0.34*	1.00	
4. Grain weight	-0.69**	-0.10 NS	+0.32*	1.00
5. Grain yield	+0.76**	+0.79**	+0.28 NS	-0.36*

Table 6.6 - Stepwise multiple regression of components of yield.

Variable	Coefficient	S.E.
Constant: -1796.56		
Spikelets/ear	39.75	7.11
Ears/m^2	1.43	0.09
Grains/spikelet	269.11	24.45
Grain weight	13.44	3.95

6.4 DISCUSSION

The results of the present experiment and those reported previously (McEwan *et al.* 1972; Dougherty *et al.* 1974; 1975) suggest that at Lincoln, Karamu is superior to New Zealand-bred cultivars only when spring sown. In Australia semi-dwarf wheats are more responsive to applied nitrogen (Beech & Norman 1968; Syme *et al.* 1976) although this does not appear to be the case in the United Kingdom (Thorne & Blacklock 1971). Previous New Zealand work (Dougherty *et al.* 1974; 1975b), together with this experiment indicate that Karamu is no more responsive to nitrogen than standard New Zealand cultivars.

Both cultivars gave linear grain yield responses up to the highest rate of N applied (100 kg/ha), a rate which is high by commercial standards. On 15 September 1975, 24 kg N/ha was available in the top 60 cm soil (T.E. Ludecke, unpublished data). From this figure Ludecke's (1974) model would predict a grain yield response greater than 50% to an application of 40 kg N/ha. The actual response was about 35%.

From a physiological viewpoint the most interesting aspect of the data is the fact that yields in excess of 6 t/ha were obtained from a very low LAI of 3 (Table 6.3, Fig. 6.1) or the equivalent of a photosynthetic area index of 6 (Watson *et al.* 1963; Fischer 1975). The 1975-76 season was generally wetter and cooler than average (Lucas *et al.* 1976) and this may have restricted leaf growth (Friend 1966). These high yields were obtained from a moderate population of about 500 ears/m^2 each bearing less than 19 spikelets (Table 6.3). However, the mean number of grains per spikelet was very high at 1.96 and, unlike previous experiments (Dougherty *et al.* 1975; Scott *et al.* 1977), was increased by the application of nitrogen fertiliser (Table 6.3).

The number of grains/spikelet appeared to be closely related to the level of available N in the soil during pre-anthesis floret development in November (Table 6.1, 6.2). These results reinforce our view, expressed previously (Scott *et al.* 1973; 1977), that the leaf area of many wheat crops is supra-optimal so that attempts to increase yield by irrigation or nitrogen applications leads to further leaf growth and depressions in grain yield because of reduced grain set. Unfortunately, obtaining a high ear population and low LAI under conditions of adequate levels of soil N, as in this experiment, could prove very difficult to reproduce in practice as the objectives seem mutually exclusive. A possible alternative is for plant breeders to select for less leafy cultivars, a suggestion also made by Donald (1968).

The mean ear population for the experiment was 419/m^2 and was highly correlated ($r = +0.76^{**}$) with yield, suggesting that yields may have been increased even further with a higher ear population. Previous experiments in this environment have indicated that 600-800 ears/m^2 is about optimal (Scott *et al.* 1973; 1977). However, the high yields obtained in the present experiment, with this moderate ear density, reflect the plasticity and partial compensation that exists between the yield components of wheat.

In practical terms it seems that profitable responses to high rates of nitrogen may be obtained from wheat and that Ludecke's (1974) model gives a reasonably accurate prediction of these responses. However there is no evidence to suggest that Karamu is more responsive to nitrogen than the standard cultivars Aotea and Kopara.

6.5 SUMMARY

Autumn-sown Kopara and Karamu wheat (*Triticum aestivum* L.) gave linear responses in grain yield to rates of nitrogen up to 100 kg/ha. There was no evidence to show that the semi-dwarf Karamu responded more to nitrogen than Kopara. Yields in excess of 6 t/ha were obtained with peak LAI values of 3 and ear populations of 500/m^2 due to the production of many grains per spikelet. These results are discussed in relation to wheat breeding.

CHAPTER 7

GENERAL DISCUSSION

7.1 YIELD COMPONENTS

To understand the causes of differences in grain yield it is necessary not only to divide yield into its various components but also define the time period over which the components are determined. In this way the effects of both environmental factors and agronomic treatments applied at different times become more meaningful. In Figure 7.1 an attempt is made to define the time of occurrence of the critical growth parameters for an autumn sown wheat crop in the Lincoln environment, and to relate these to levels of soil moisture and available soil N. Data for this figure were derived from Langer and Khatri (1965) and from the experiments described in Chapters 2, 5 and 6.

A recent review on the physiology of grain yield in cereals (Evans & Wardlaw 1976) emphasised that research on cereals has shown that in many instances the capacity of the grain to store assimilates (the size of the sink) may limit yield as much as the capacity of the crop to provide them during grain filling (the amount of photosynthesis). In the experiments described in this thesis grain size was only changed slightly by the treatments imposed (Tables 2.3, 5.7, 6.3). Although there were differences among cultivars (Table 3.1, 5.7), weight/grain was not related to flag leaf area duration (section 5.3), indicating that the amount of photosynthate was adequate to fill the grains which had been set. The detailed analysis of the

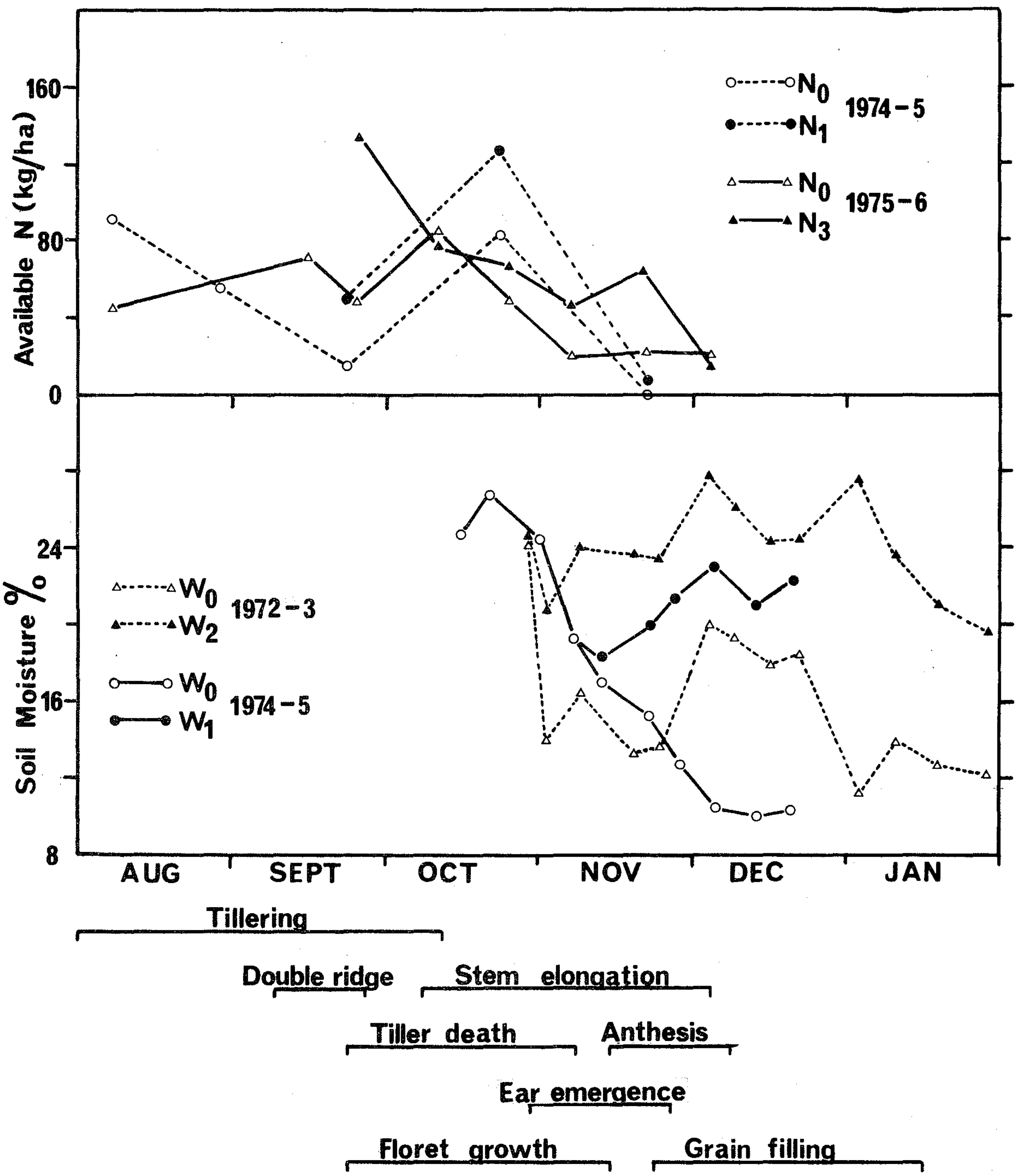

Figure 7.1 - Growth parameters of autumn wheat at Lincoln in relation to soil moisture and available soil N.

pattern of grain set and grain size within the ear (Chapter 4) showed that grain weight differences between spikelets of both Aotea and Karamu were relatively small compared with the differences in grain set, again indicating that grain yield per spike was probably limited by the capacity of the spike to accumulate sites for grain filling.

For most non-irrigated wheat crops the bulk of the grain filling occurs in December, a time when there are usually low levels of available water in the top 30 cm of soil (Fig. 7.1). Fischer (1973) found that water stress during grain filling decreased grain size only when leaf area was reduced sufficiently to develop a source limitation. Presumably in the Lincoln environment on moisture retentive soils, water stress during grain filling seldom reduces leaf area to this critical level.

Grain filling also occurs at a time when levels of available N are low (Fig. 7.1). In view of the limited effects of applied N on grain size (Tables 5.7, 6.3) it would appear that most of the N is taken up by the commencement of grain filling to be redistributed into the grains subsequently, a suggestion also made by Williams (1955) and Langer and Liew (1973).

The results of the present study therefore support the view of Langer and Dougherty (1976) that, in this environment, it is differences in grain number per unit area which bring about the major differences in yield for any one cultivar. Grain number per unit area can be influenced by the number of spikes, the number of spikelets/spike and the number of florets within each spikelet that actually set grain.

Rawson and Bremner (1976) stated that a productive spike population of $800/m^2$ was required under conditions where high yields were to be expected. Similarly Dougherty *et al.* (1975b) suggested that 800 spikes/m^2 was about optimum and that above this level the number of grains per spikelet was drastically reduced. In an endeavour to verify the validity of these assertions and in order to characterise the yield components of high yielding Kopara crops, samples were taken from five commercial wheat crops growing in mid-Canterbury during the 1975-6 season. Five separate 0.2 m^2 quadrats were sampled from what appeared to be the highest yielding portions of these crops. The results are presented in Table 7.1.

Table 7.1 - Yield components of high yielding Kopara wheat crops.

Crop Number	Grain Yield t/ha	Spikes/m^2	Spikelets/spike	Grains/spikelet	Wt/grain (mg)
1	10.14	667	18.7	1.94	41.9
2	9.47	578	18.8	2.03	43.1
3	8.55	570	20.9	1.59	45.2
4	7.55	561	19.0	1.75	40.7
5	7.44	497	19.3	1.83	42.6
CV %	7.2	10.7	1.5	4.6	2.9

Although these crops all produced very high yields, none developed 800 spikes/m^2. The results of the 1972-3 experiment presented earlier also suggest that 800 spikes/m^2 may be too high for maximum yields while both the 1974-5 and 1975-6 experiments showed that yields in excess of 6 t/ha could be produced with spike populations of 650 and

430 spikes/m^2 respectively. Collectively, these results suggest that 800 spikes/m^2 is supra-optimal with present cultivars in the Lincoln environment.

The final spike population is a reflection of the total number of tillers produced and the proportion of these which survive to produce an ear. In autumn wheat, tillers are produced most rapidly in September, reaching their peak number in late September-early October (Fig. 7.1). In all the crops studied in this thesis a high proportion of the tillers died, with most of the deaths occurring during October and corresponding with the onset of rapid stem elongation (Fig. 7.1). Rawson and Bremner (1976) discussed the possible deleterious effects of unproductive tillers, emphasising that it was a question "of long standing". Results of the present study (Tables 2.3, 2.7, 5.7, Fig. 5.4) suggest that these unproductive tillers may interfere with floret development in the remaining fertile tillers, an aspect which is discussed in detail in a later section. What does seem certain is that the yield of New Zealand wheats is not limited by their ability to produce tillers, since it is possible for high yields to be obtained by relatively sparse populations of ears. Although abundant tillering may partially compensate for adequate or irregular plant establishment resulting from poor drilling techniques, these are not conditions which are likely to be encountered regularly in the high-yielding situation.

The number of spikelets/spike does not seem to offer a great deal of scope as a means of increasing yield. Although up to two additional spikelets/spike could usually be produced by the addition of N, such increases were not always accompanied by an increase in grain yield (Tables 5.7, 6.3). In the 1975-6 experiment N gave a big increase in spikelet number and grain yield (Table 6.3) and, although spikelet number was highly correlated with grain yield in this experiment (Table 6.5), the effect of N on yield was largely due to an increase in the spike population. This experiment was the only one where the mean number of spikelets per ear approached 20, the number that Rawson and Bremner (1976) suggested as being optimal for a high yielding wheat crop. It is also interesting to note that the highest yielding commercial crops sampled in the same season produced only slightly fewer than 20 spikelets/ear (Table 7.1).

The final yield component to be considered, namely the number of grains/spikelet was inversely related to spike population, particularly when it exceeded 700/m^2 (Tables 2.1, 2.2, 2.3). This relationship has occurred elsewhere and has been attributed to a reduction in the assimilate supply to the florets prior to anthesis, and contributed to by excessive vegetative growth (Dougherty & Langer 1974; Dougherty *et al.* 1974, 1975a, 1975b). During the initial stages of floret development before the florets become enclosed by the accessory floral organs and while the spike is about 1 cm in length (Fisher 1973; Holmes 1973; Kirby 1974) it seems rather unlikely that the supply of assimilate would restrict floret growth due to the very small amount of material involved. However the pattern of grain set described in Chapters 3 and 4 strongly suggest that the amount of floret development that occurs in the three weeks prior to anthesis is critical in determining which florets set grain. In morphological terms this period is from the time the accessory floral organs close over the florets until about one week after ear emergence and covers the period of most rapid ear growth when one would expect competition between florets to be most intense. For autumn wheat this critical period is in late October-early November, the time when the rapidly elongating stem is also a competing sink for assimilate (Fig. 7.1).

It is possible that the inverse relationship between spike number and grain set is not due to differences in spike numbers *per se*, but is a manifestation of high LAI values that usually accompany such populations (Table 2.6, Fig. 5.3). As light interception in most cereal crops exceeds 95% once an LAI of about 4 is obtained (Evans & Wardlaw 1976), further increases in LAI have little effect on crop photosynthesis. In the experiments described in this thesis LAI values sometimes exceeded 4 at high ear populations (Table 2.6, Fig. 5.3) and were associated with depressions in grain set. It is suggested that further increases in the grain yield of wheat might possibly be achieved by selecting wheat cultivars with smaller more vertically inclined leaves, a suggestion also made by Evans and Wardlaw (1976). With such plants it may be possible to marry the two objectives of high spike population with high grain set, instead of the inverse relationship which appears to operate with present cultivars. Donald and Hamblin (1976) have recently pointed out that such plants may not always appear highly productive when grown as spaced plants.

The mean number of grains per spikelet recorded in the present series of experiments ranged from 1.2 to 2.0 (Tables 2.3, 7.1). Even the highest value of 2 falls short of the 3 or more grains produced by the central spikelets in mainstem ears (Fig. 4.1) and is less than one quarter of the 7-9 florets produced in each spikelet (Langer & Hanif 1973). In theory at least, there appears to be considerable scope for improvement here.

7.2 CULTIVARS

The experiments described in this thesis as well as those published elsewhere (McEwan & Vizer 1970; Douglas *et al.* 1971; Clements *et al.* 1974; Dougherty *et al.* 1974, 1975b) would suggest that when autumn sown the semi-dwarf Karamu is not generally superior to the standard New Zealand cultivars Aotea and Kopara. The superior grain yield of spring sown Karamu appears to be largely due to the production of more spikelets and more grains per spikelet than the other cultivars. Under conditions of spring sowing, Karamu produced a mean number of 14.5 spikelets/spike compared with a mean of 13.4 for Aotea and Arawa (Dougherty *et al.* 1975b), an increase of about 8%. Similar calculations for the number of grains per spikelet showed that Karamu had a 9% advantage over the other cultivars. The superiority of Karamu was therefore split evenly between spikelets/spike and grains/spikelet. The sequence of anthesis in florets and between spikelets is a critical factor in determining which florets set grain (Evans *et al.* 1972; Langer & Hanif 1973; Walpole & Morgan 1973) while both Fisher (1973) and Holmes (1973) found that early spikelet development in Norin 10 derivatives such as Karamu is more synchronised than in standard wheats. Indeed, the comparison of the pattern of grain set in Karamu and Aotea described in Chapter 4 suggests that the semi-dwarf does have more synchronised development within the spike and within the spikelet. Although florets in positions 1 and 2 of Karamu were slightly less fertile than those of Aotea (Fig. 4.2), Karamu still produced more grains/spikelet due to superior fertility in floret positions 3 and 4.

The New Zealand cultivars Aotea and Arawa showed the characteristics described by McEwan (1959), being high yielding under conditions of autumn sowing (Tables 2.1, 5.5) but rather low yielding when spring sown (Dougherty *et al.* 1975a). Although Kopara was not compared directly with Aotea and Arawa in these experiments it undoubtedly has a high yield potential (Douglas *et al.* 1971; Tables 6.3, 7.1). Whereas Kopara is more responsive to P than Aotea (Douglas *et al.* 1971) its responses to N appear to be more variable. Kopara showed a marked response to N in the 1975-6 season although Dougherty and Langer (1974) found that heavy applications of N (200 kg/ha) to irrigated Kopara wheat gave a 30% reduction in yield. Further research on the nitrogen nutrition of this high yielding cultivar should prove rewarding.

7.3 NITROGEN

It has been mentioned previously that the yield components of wheat tend to be compensatory (section 1.1), and this becomes very evident when one examines the effects and interactions of N on the different yield components for the various experiments described in this thesis.

N increased the number of spikelets/spike in all experiments but in the 1974-5 experiment this was accompanied by a decline in the number of grains/spikelet so that overall there was little or no increase in the number of grains/spike (Table 5.7), an effect which has been noted elsewhere and attributed to a reduction in assimilate supply to the florets prior to anthesis (Dougherty *et al.* 1974, 1975a, 1975b; Dougherty & Langer 1974) and which is associated with increased leaf growth (section 7.1). The 1975-6 experiment has been the only one at Lincoln where N increased the number of grains/spikelet and it is suggested that this occurred because the LAI was less than 4 (Fig. 6.1), the level where light interception has been shown to exceed 95% (Evans & Wardlaw 1976). An alternative explanation for N increasing the number of grains/spikelet in 1975-6 could be that in this season levels of available N remained high well into November, the time of pre-anthesis floret development (Fig. 7.1). The profiles of available soil N plotted in Figure 7.1 also indicate that even in a very fertile soil where the 1974-5 crop was grown, the rate of mineralisation of soil N may not occur fast enough to supply the rapidly growing crop in November.

The effects of N on tiller production and survival were consistent with those occurring in England (Watson *et al.* 1963), particularly for the 1974-5 experiment where N gave a 22% increase in peak tiller numbers but had little effect on tiller survival, the proportions being 59% and 57% for N_0 and N_1 respectively (Fig. 5.4). For the 1975-6 experiment 56% and 61% of the tillers survived for the N_0 and N_3 treatments respectively but here N gave a 60% increase in peak tiller number (Fig. 6.2). This bigger increase in spike number resulting from N application came under conditions of very low levels of available N which occurred during the 1975-6 season (Table 6.2, Fig. 7.1).

The soil test and predictive model based on available soil N described by Ludecke (1974) have been of considerable assistance not only in explaining the responses of the various crops to N fertiliser but also in deciding on the timing of application (section 5.2). Increases in grain yield occurred when available N levels in August fell to below 60 kg/ha in the top 60 cm of soil (Tables 5.1, 6.2). In the 1974-5 season low levels of available nitrogen were caused by extensive leaching while low total N was responsible in the 1975-6 season. In both cases the increases in grain yield could largely be attributed to N increasing the spike population.

However, despite the use of this predictive model, more information is still required on the fate of both mineralised and applied N within the soil and plant systems. Such information would require more regular measurements of N in both the soil and the plant than those which were carried out in the present studies. In particular, there is a need for detailed studies on the factors controlling the amount of N actually reaching the grain. Although levels of grain N were not measured in the present experiments, this aspect is of critical importance in view of its relationship with baking quality (Wright 1969).

7.4 IRRIGATION

The results of the 1972-3 experiment on Aotea wheat showed that it is possible to increase the yield of autumn wheat on deep soils by the use of irrigation but that the increases are far less than are possible on soils of low water retention (Drewitt 1974a, 1974b). This experiment also confirmed that irrigation increases yield mainly by increasing tiller survival as found by Barley and Naidu (1964).

The subsequent experiment in 1974-5 showed that one of the reasons for the limited response to irrigation on deep moisture retentive soils was that wheat could scavenge for soil moisture at depths greater than 90 cm where the soil was at field capacity even although the topsoil was below wilting point (Fig. 5.2, Table

5.4). Other aspects of the water relations of the wheat grown in this particular experiment were described by Martin and Dougherty (1975), although it is interesting to note from Figure 7.1 that in the 1972-3 season the drop in level of soil water occurred earlier than in 1974-5. This could be another explanation for the differing response between seasons.

One of the reasons suggested for the lack of grain yield response to applied N and sometimes the occurrence of yield depressions has been that the increased vegetative growth caused by N leads to accelerated use of soil water (Ludecke 1972, 1974; Stephen 1973). N fertiliser did cause accelerated use of soil water in the 1974-5 experiment (Fig. 5.2) presumably because the increased leaf biomass (Fig. 5.3) increased the amount of transpiration. Although this did not cause a yield depression, it does confirm that N can lead to accelerated use of soil water and this may help explain some of the N fertiliser induced yield depressions recorded in the past (Walker 1969; Ludecke 1972, 1974; Stephen 1973) on soils of lower water holding capacity.

From the practical viewpoint it seems that on deep moisture retentive soils, irrigation water is probably better applied to crops such as peas (Anderson & White 1974), ryegrass and white clover seed (Scott 1973), in which economic responses are more likely than in autumn sown wheat.

7.5 SOWING RATE

The results of the present study suggest that higher than normal sowing rates are not required to exploit the bountiful growing conditions produced by irrigation and nitrogen fertiliser. Indeed they suggest that where more than 250 plants/m^2 are established, grain yield may be depressed even though the spike population is increased (Tables 1.2, 2.1, 5.5).

Spikelet number was reduced by high sowing rate (Tables 2.3, 3.1., 5.7, 6.3) although there was evidence to show that this could be alleviated to some extent by the application of N (Table 3.4, 5.7) except that this must be applied no later than the double ridge stage (Langer & Liew 1973).

The main yield component reduced by high sowing rate was the number of grains per spikelet (Tables 2.3, 3.1), an effect also reported by Willey and Holliday (1971) in England. The physiological explanation for this reduction in grain set caused by high sowing rate is probably similar to that produced by high levels of available N (section 7.3), again indicating the effects that excessive leaf growth can have on grain set.

The seed size of commercial New Zealand seed wheat can vary from 30 to 50 mg depending on cultivar and the amount of screening that has occurred (Dougherty *et al.* 1974, 1975b). Assuming a 90% field establishment (Dougherty *et al.* 1975b) a plant population of 250/m^2 would require sowing rates of 85 and 140 kg/ha respectively for this range of seed sizes. These figures not only bring this discussion into practical perspective but also demonstrate that, in scientific terms, plant population is probably more meaningful than sowing rate, especially in non-experimental conditions.

CONCLUSIONS

1. The yield of Canterbury wheat crops is probably limited by spike number when the population is below about 500 spikes/m^2. Above this level the number of grains per spikelet becomes an increasingly important component and is then usually inversely related to the spike population. Once the spike population exceeds 700/m^2, grain yields may decline. It is suggested that further yield increases may be achieved by selecting cultivars that are less leafy particularly under high fertility conditions. The weight per grain is not considered an important yield component, and is rather difficult to change by agronomic treatments, except severe water stress.

2. The superiority of the semi-dwarf Karamu as a spring wheat lies in its ability to produce more spikelets/spike and grains/spikelet than other cultivars. These characteristics appear to be due to more synchronised development both within the spike and within the spikelet. There is no evidence to show that Karamu is more responsive to N than Aotea, Arawa or Kopara.

3. The likely responses in grain yield to applied N are best predicted through the use of a soil test to measure the amount of available soil N in August. Yield increases caused by N in these experiments were due mainly to an increase in the spike population. Yield depressions due to N fertiliser on

deep moisture retentive soils were attributable mainly to a reduction in the number of grains/spikelet. This was possibly caused by a reduced assimilate supply to the florets prior to anthesis and was generally associated with supra-optimal leaf development.

4. There was no evidence to suggest that on moisture retentive soils yield reductions caused by N fertiliser were due to water stress although this phenomenon probably occurs on soils of low moisture retention. Yield increases of autumn wheat on moisture retentive soil, in response to irrigation, are likely to be small and are largely due to increased tiller survival.

5. Wheat grown under high fertility, irrigated conditions requires a similar plant population to that growing under dryland conditions and medium fertility. The optimum plant population appears to be around 250 plants/m^2.

SUMMARY

Between 1972 and 1976 a series of field experiments were conducted to investigate the factors limiting grain yield in wheat (*Triticum aestivum* L.). Spike population restricted yield when it was below about 500 spikes/m^2 but once it exceeded 700/m^2 grain yield declined due to a reduction in the number of grains per spikelet. Irrigation, high sowing rate, and nitrogen fertiliser generally increased spike number but the effects on the number of grains/spikelet were variable, apparently depending on processes related to leaf area index.

The semi-dwarf Karamu outyielded New Zealand wheats when spring-sown because it produced more spikelets/spike and more grains/spikelet than the other cultivars. The superior grain set of Karamu was because more of the distal florets within each spikelet produced grain than in the other cultivars.

The results are discussed in relation to cultural practices and plant breeding.

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REFERENCES

Adams, M.W.; Grafius, J.E. 1971: Yield component compensation - alternative interpretations. Crop Science 11: 33-5.

Anderson, J.A.D.; White, J.G.H. 1974: Yield of green peas. II. Effects of water and plant density. New Zealand Journal of Experimental Agriculture 2: 165-71.

Barley, K.P.; Alston, A.M.; Ponsana, P.; Lungley, D.R.; Meyer, W.; Rathjen, A.J. 1973: Relationships between root system geometry and the uptake of water and nutrients. Biennial Report of the Waite Agricultural Research Institute: 25-6.

Barley, K.P.; Naidu, N.A. 1964: The performance of three Australian wheat varieties at high levels of nitrogen supply. Australian Journal of Experimental Agriculture and Animal Husbandry 4: 39-48.

Barnard, C. 1955: Histogenesis of the inflorescence of *Triticum aestivum* L. Australian Journal of Botany 3: 1-20.

Beech, D.F.; Norman, M.J.T. 1968: A preliminary assessment of the adaptation of semi-dwarf wheat varieties to the Ord River Valley. Australian Journal of Experimental Agriculture and Animal Husbandry 8: 349-57.

Bingham, J. 1972: Physiological objectives in breeding for grain yield in wheat. Proceedings of the Sixth Congress of Eucarpia 1971: The way ahead in plant breeding. pp. 15-29.

Bonnett, O.T. 1936: The development of the wheat spike. Journal of Agricultural Research 53: 445-51.

Bremner, P.M. 1969: Growth and yield of three varieties of wheat with particular reference to the influence of unproductive tillers. Journal of Agricultural Science 72: 281-87.

Bremner, P.M. 1972: Accumulation of dry matter and nitrogen by grains in different positions of the wheat ear as influenced by shading and defoliation. Australian Journal of Biological Sciences 25: 657-68.

Brouwer, R. 1966: Root growth of grasses and cereals. In 'The Growth of Cereals and Grasses', F.L. Milthorpe and J.D. Ivins (Eds.), pp. 153-66, Butterworths, London.

Clements, R.J.; Cross, R.J.; Sanders, P. 1974: Effect of sowing rate on the growth and yield of standard and semidwarf wheat cultivars. New Zealand Journal of Experimental Agriculture 2: 139-44.

Coles, G.D.; Wrigley, C.W. 1976: Laboratory methods for identifying New Zealand wheat cultivars. New Zealand Journal of Agricultural Research 19: 499-503.

Copp, L.G. 1956: Arawa wheat. New Zealand Wheat Review 5: 48-51.

Copp, L.G. 1958: Aotea, a replacement for Cross 7 wheat. New Zealand Journal of Agriculture 96: 210-14.

Copp, L.G. 1972: Kopara wheat. New Zealand Journal of Agriculture 125: 26-7.

Copp, L.G.; Lobb, W.R. 1956: Arawa, a new wheat to replace Dreadnought. New Zealand Journal of Agriculture 94: 221-3.

Denmead, O.T.; Shaw, R.H. 1960: The effects of soil moisture stress at different stages of growth on the development and yield of corn. Agronomy Journal 52: 272-4.

Donald, C.M. 1962: In search of yield. Journal of the Australian Institute of Agricultural Science 28: 171-8.

Donald, C.M. 1968: The breeding of crop ideotypes. Euphytica 17: 385-403.

Donald, C.M.; Hamblin, J. 1976: The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Advances in Agronomy 28: 361-405.

Dougherty, C.T. 1972: Water stress in Turoa red clover under Aotea wheat. New Zealand Journal of Agricultural Research 15: 706-11.

Dougherty, C.T. 1973: Water relations of wheat as affected by irrigation and nitrogen fertilisation. New Zealand Journal of Agricultural Research 16: 12-18.

Dougherty, C.T.; Langer, R.H.M. 1974: An analysis of a nitrogen-induced depression of yield in irrigated 'Kopara' wheat. New Zealand Journal of Agricultural Research 17: 325-31.

Dougherty, C.T.; Rooney, K.R.; Scott, W.R.; Langer, R.H.M. 1975a: Levels of water-soluble carbohydrate in the pre-anthesis ear of wheat, and grain set per spikelet. New Zealand Journal of Agricultural Research 18: 351-6.

Dougherty, C.T.; Scott, W.R.; Langer, R.H.M. 1975b: Effects of sowing rate, irrigation, and nitrogen on the components of yield of spring-sown semidwarf and standard New Zealand wheats. New Zealand Journal of Agricultural Research 18: 197-207.

Dougherty, C.T.; Scott, W.R.; Langer, R.H.M.; Meijer, G. 1974: The effects of irrigation and fertilizer on the yields of Arawa, Aotea and Karamu wheats. New Zealand Journal of Agricultural Research 17: 241-9.

Douglas, J.A. 1970: Fertilisers and wheat. New Zealand Wheat Review 11: 80-82.

Douglas, J.A.; Cossens, G.G.; McLeod, C.C.; Nixon, G.W.; Risk, W.H.; Stephen, R.C.; Dyson, C.B. 1971: Performance of the wheat cultivar Kopara in South Island field trials. Proceedings Agronomy Society of New Zealand 1: 173-81.

Drewitt, E.G. 1967: Irrigation of wheat can increase yield but reduce quality. New Zealand Journal of Agriculture 115: 28-9.

Drewitt, E.G. 1974a: The influence of sowing time on wheat yields at two irrigation levels. Proceedings Agronomy Society of New Zealand 4: 38-40.

Drewitt, E.G. 1974b: Irrigating wheat. New Zealand Journal of Agriculture 128: 44-7.

Drewitt, E.G.; Rickard, D.S. 1970: Annual Report of Research Division. New Zealand Department of Agriculture: 168-9.

Drewitt, E.G.; Rickard, D.S. 1971: The effects of irrigation and applied nitrogen on the growth, grain yields and nitrogen content of wheat. Proceedings Agronomy Society of New Zealand 1: 147-57.

Drewitt, E.G.; Rickard, D.S. 1973: The effect of irrigation on the yield components and nitrogen uptake of three wheat cultivars. Proceedings Agronomy Society of New Zealand 3: 73-80.

Evans, L.T.; Bingham, J.; Roskams, M.A. 1972: The pattern of grain set within ears of wheat. Australian Journal of Biological Science 25: 1-8.

Evans, L.T.; Wardlaw, I.F. 1976: Aspects of the comparative physiology of grain yield in cereals. Advances in Agronomy 28: 301-59.

Fischer, R.A. 1973: The effect of water stress at various stages of development on yield processes in wheat. UNESCO, 1973. Plant response to climatic factors. Proceedings of the Uppsala Symposium 1970. (Ecology & Conservation, 5): p. 233-41.

Fischer, R.A. 1975: Yield potential of dwarf spring wheat and the effect of shading. Crop Science 15: 607-14.

Fischer, R.A.; Hagen, R.M. 1965: Plant water relations, irrigation management and crop yield. Experimental Agriculture 1: 161-77.

Fischer, R.A.; Kertesz, Z. 1976: Harvest index in spaced populations and grain weight in microplots as indicators of yielding ability in spring wheat. Crop Science 16: 55-9.

Fischer, R.A.; Kohn, G.D. 1966: The relationship of grain yield to vegetative and post flowering leaf area in the wheat crop under conditions of limited soil moisture. Australian Journal of Agricultural Research 17: 281-95.

Fisher, J.E. 1973: Developmental morphology of the inflorescence in hexaploid wheat cultivars with and without the cultivar Norin 10 in their ancestry. Canadian Journal of Plant Science 53: 7-15.

Frankel, O.H.; Hullett, E.W. 1948: Hilgendorf wheat of outstanding baking quality. New Zealand Journal of Agriculture 76: 117-9.

Friend, D.J.C. 1966: The effects of light and temperature on the growth of cereals. In 'The Growth of Cereals and Grasses', F.L. Milthorpe and J.D. Ivins (Eds.), pp. 181-99, Butterworths, London.

Gifford, R.M.; Bremner, P.M.; Jones, D.B. 1973: Assessing photosynthetic limitations to grain yield in a field crop. Australian Journal of Agricultural Research 24: 297-307.

Hanif, M.; Langer, R.H.M. 1972: The vascular system of the spikelet in wheat (*Triticum aestivum* L.). Annals of Botany 36: 721-7.

Hilgendorf, F.W. 1938: 'Wheat in New Zealand'. Whitcombe and Tombs, Wellington. 136 p.

Holford, F.H. 1927: 'Wheat for Profit'. Andrews, Baty and Co. Ltd, Christchurch. 84 p.

Holmes, D.P. 1973: Inflorescence development of semidwarf and standard height wheat cultivars in different photoperiod and nitrogen treatments. Canadian Journal of Botany 51: 941-56.

Holmes, J.C.; Tahir, W.M. 1956: The effect of some factors on growth, development and yield of winter wheat. Journal of Agricultural Science 48: 115-23.

Hsiao, C. 1973: Plant responses to water stress. Annual Review of Plant Physiology 24: 519-70.

Ishag, H.M.; Taha, M.B. 1974: Production and survival of tillers of wheat and their contribution to yield. Journal of Agricultural Science 83: 117-24.

Janson, C.G.; Knight, T.L. 1973: Establishment of lucerne with cover crops under different soil moisture conditions. New Zealand Journal of Experimental Agriculture 1: 243-51.

Jewiss, O.R. 1972: Tillering in grasses - its significance and control. Journal of the British Grassland Society 27: 65-82.

Johns, G.G.; Lazenby, A. 1973: Defoliation, leaf area index, and the water use of four temperate pasture species under irrigated and dryland conditions. Australian Journal of Agricultural Research 24: 783-95.

Kirby, E.J.M. 1974: Ear development in spring wheat. Journal of Agricultural Science 82: 437-47.

Langer, R.H.M. 1959: Growth and nutrition of timothy (*Phleum pratense* L.). IV. Growth and flowering at different levels of nitrogen. Annals of Applied Biology 47: 740-51.

Langer, R.H.M. 1965: A study of New Zealand wheats. I. Growth and yield characteristics. New Zealand Journal of Agricultural Research 8: 10-14.

Langer, R.H.M. 1972: Leaf growth. In 'How Grasses Grow', pp 6-16. Edward Arnold (Publishers) Ltd, London.

Langer, R.H.M.; Ampong, A. 1970: A study of New Zealand wheats. III. Effects of soil moisture stress at different stages of development. New Zealand Journal of Agricultural Research 13: 869-77.

Langer, R.H.M.; Dougherty, C.T. 1976: Physiology of grain yield in wheat. In 'Perspectives in Experimental Biology', Volume 2, Botany, pp. 59-67. N. Sunderland (Ed.), Pergamon Press, Oxford & New York.

Langer, R.H.M.; Hanif, M. 1973: A study of floret development in wheat (*Triticum aestivum* L.). Annals of Botany. 37: 743-51.

Langer, R.H.M.; Khatri, M.I. 1965: A study of New Zealand wheats. II. Flower initiation and development. New Zealand Journal of Agricultural Research 8: 213-22.

Langer, R.H.M.; Liew, F.K.Y. 1973: Effects of varying nitrogen supply at different stages of the reproductive phase on spikelet and grain production and on grain nitrogen in wheat. Australian Journal of Agricultural Research 24: 647-56.

Langer, R.H.M.; Olugbemi, L.B. 1970: A study of New Zealand wheats. IV. Effects of extreme temperature at different stages of development. New Zealand Journal of Agricultural Research 13: 878-86.

Langer, R.H.M.; Prasad, P.C.; Laude, H.M. 1973: Effects of kinetin on tiller bud elongation in wheat (*Triticum aestivum* L.). Annals of Botany 37: 565-71.

Lazenby, A.; Matheson, E.M. 1975: 'Australian Field Crops', Volume 1: Wheat and other temperate cereals. Angus and Robertson. 552 p.

Lucas, R.J.; Pownall, D.B.; Herbert, S.J. 1976: October-sown *Lupinus angustifolius* in Canterbury. Proceedings Agronomy Society of New Zealand 6: 75-7.

Lucas, Daphne. 1972: The effect of daylength on primordia production of the wheat apex. Australian Journal of Biological Science 25: 649-56.

Ludecke, T.E. 1972: Nitrogen fertilisers for wheat in Canterbury. Proceedings of the Lincoln College Farmers Conference, p. 85-91.

Ludecke, T.E. 1974: Prediction of grain yield responses to nitrogen fertilisers. Proceedings Agronomy Society of New Zealand 4: 27-9.

Lupton, F.G.H.; Oliver, R.H.; Ruckenbauer, P. 1974: An analysis of the factors determining yields in crosses between semidwarf and taller wheat varieties. Journal of Agricultural Science, Cambridge 82: 483-96.

McEwan, J.M. 1959: The wheat varieties of New Zealand. New Zealand Department of Scientific and Industrial Research Bulletin 131.

McEwan, J.M. 1975: Takahe. DSIR Cereal News 1: 8-9.

McEwan, J.M.; Vizer, K.J.; Douglas, J.A. 1972: Karamu - a new spring wheat. New Zealand Journal of Agriculture 125: 50-1.

McLeod, C.C. 1960: Rate of seeding wheat trials in South Canterbury. New Zealand Journal of Agriculture 101: 126-7.

McLeod, C.C. 1973: Phosphate and nitrogen responses in first, second and third successive wheat crops in South Canterbury. New Zealand Wheat Review 12: 44-7.

New Zealand Year Book 1972: N.Z. Official Year Book, 1972. Department of Statistics, Wellington. 1082 p.

Puckridge, D.W. 1971: Photosynthesis of wheat under field conditions. III. Seasonal trends in carbon dioxide uptake of plant communities. Australian Journal of Agricultural Research 22: 1-9.

Puckridge, D.W.; Donald, C.M. 1967: Competition among wheat plants sown at a wide range of densities. Australian Journal of Agricultural Research 18: 193-211.

Rawson, H.M. 1970: Spikelet number, its control and relation to yield per ear in wheat. Australian Journal of Biological Science 23: 1-15.

Rawson, H.M.; Bremner, P.M. 1976: Development in relation to grain yield in the temperate cereals. In 'Crop Physiology', U.S. Gupta (Ed.), I.B.H. & Oxford, New Delhi (in press).

Rawson, H.M.; Evans, L.T. 1970: The pattern of grain growth within the ear of wheat. Australian Journal of Biological Science 23: 753-64.

Rawson, H.M.; Ruwali, K.N. 1972a: Branched ears in wheat and yield determination. Australian Journal of Agricultural Research 23: 541-9.

Rawson, H.M.; Ruwali, K.N. 1972b: Ear branching as a means of increasing uniformity in wheat. Australian Journal of Agricultural Research 23: 551-9.

Ritchie, J.T.; Burnett, E. 1971: Dryland evaporation flux in a sub-humid climate. II. Plant influences. Agronomy Journal 63: 56-62.

Ryde, B.J.P. 1965: The wheat-white clover rotation. Canterbury Chamber of Commerce Agricultural Bulletin No. 427.

Salter, P.J.; Goode, J.E. 1967: Crop responses to water at different stages of growth. Commonwealth Bureau of Horticulture and Plantation Crops, East Malling, Maidstone, Kent (Research Review 2).

Santhirasegaram, K.; Black, J.N. 1965: Agronomic practices aimed at reducing competition between cover crops and undersown pasture. Herbage Abstracts 35: 221-5.

Scott, W.R. 1973: Pasture seed production. In 'Pastures and Pasture Plants', R.H.M. Langer (Ed.), pp. 291-321. A.H. & A.W. Reed, Wellington.

Scott, W.R.; Dougherty, C.T. 1977: Development and yield components of high yielding wheat crops. New Zealand Journal of Agricultural Research 20: in press.

Scott, W.R.; Dougherty, C.T.; Langer, R.H.M. 1975: An analysis of a wheat yield depression caused by high sowing rate with reference to the pattern of grain set within the ear. New Zealand Journal of Agricultural Research 18: 209-14.

Scott, W.R.; Dougherty, C.T.; Langer, R.H.M.; Meijer, G. 1973: Wheat yield as affected by sowing rate, irrigation, and time of white clover introduction. New Zealand Journal of Experimental Agriculture 1: 369-76.

Simpson, G.M. 1968: Association between grain yield per plant and photosynthetic area above the flag-leaf node in wheat. Canadian Journal of Plant Science 48: 253-60.

Single, W.V. 1964: The influence of nitrogen supply on the fertility of the wheat ear. Australian Journal of Experimental Agriculture and Animal Husbandry 4: 165-8.

Smith, H.C. 1974: Recommended wheat varieties. New Zealand Journal of Agriculture 128: 50-55.

Stephen, R.C. 1973: What yield responses to applied fertiliser in mid and north Canterbury. New Zealand Wheat Review 12: 48-9.

Stoskopf, N.C.; Nathaniel, R.K.; Reinbergs, E. 1974: Comparison of spring wheat and barley with winter wheat: yield components in Ontario. Agronomy Journal 66: 747-50.

Syme, J.R. 1970: A high-yielding Mexican semi-dwarf wheat and the relationship of yield to harvest index and other varietal characteristics. Australian Journal of Experimental Agriculture and Animal Husbandry 10: 528-31.

Syme, J.R. 1972: Features of high-yielding wheats grown at two seed rates and two nitrogen levels. Australian Journal of Experimental Agriculture and Animal Husbandry 12: 165-70.

Syme, J.R. 1974: Leaf appearance rate and associated characters of some Mexican and Australian wheats. Australian Journal of Agricultural Research 25: 1-7.

Syme, J.R.; Mackenzie, J.; Strong, W.M. 1976: Comparison of four wheat cultivars for yield and protein response to nitrogen fertilizer. Australian Journal of Experimental Agriculture and Animal Husbandry 16: 407-10.

Thorne, G.N. 1962: Effect of applying nitrogen to cereals in the spring or at ear emergence. Journal of Agricultural Science 58: 89-96.

Thorne, G.N. 1966: Physiological aspects of grain yield in cereals. In 'The Growth of Cereals and Grasses', pp. 88-105. F.L. Milthorpe and J.D. Ivins (Eds.), Butterworths, London.

Thorne, G.N. 1973: Physiology of grain yield in wheat and barley. Rothamsted Experimental Station, Report for 1973, Part 2: p. 5-25.

Thorne, G.N.; Blacklock, J.C. 1971: Effects of plant density and nitrogen fertilizer on growth and yield of short varieties of wheat derived from Norin 10. Annals of Applied Biology 78: 93-111.

Walker, T.W. 1969: Nitrogen fertilisers in Canterbury. Proceedings of the Lincoln College Farmers Conference, p. 99-104.

Walpole, P.R.; Morgan, D.G. 1970: A quantitative study of grain filling in *Triticum aestivum* L. cultivar Maris Widgeon. Annals of Botany 34: 309-18.

Walpole, P.R.; Morgan, D.G. 1973: The effects of floret sterilization on grain number and grain weight in wheat ears. Annals of Botany 37: 1041-8.

Ward, R.C. 1971: Nitrate nitrogen soil test. Communications in Soil and Plant Analysis 2: 61-71.

Watson, D.J. 1936: The effect of applying a nitrogenous fertilizer to wheat at different stages of growth. Journal of Agricultural Science 26: 391-414.

Watson, D.J.; Thorne, G.N.; French, S.A.W. 1958: Physiological causes of differences in grain yield between varieties of barley. Annals of Botany 22: 321-52.

Watson, D.J.; Thorne, G.N.; French, S.A.W. 1963: Analysis of growth and yield of winter and spring wheats. Annals of Botany 27: 1-22.

Welbank, P.J.; French, S.A.W.; Witts, K.J. 1966: Dependence of yields of wheat varieties on their leaf-area durations. Annals of Botany 30: 291-99.

Williams, R.F. 1955: Redistribution of mineral elements during development. Annual Review of Plant Physiology 6: 25-42.

Williams, R.F. 1966: Development of the inflorescence in Gramineae. In 'The Growth of Cereals and Grasses', p. 74-87. F.L. Milthorpe and J.D. Ivins (Eds.), Butterworths, London.

Willey, R.W.; Holliday, R. 1971: Plant population, shading and thinning studies in wheat. Journal of Agricultural Science, Cambridge 77: 453-61.

Wilson, D.R. 1974: Comparative responses to irrigation of five wheat cultivars. Proceedings of the Agronomy Society of New Zealand 4: 34-8.

Wright, G.M. 1969: Effect of nitrogenous fertiliser on wheat yield and baking quality. New Zealand Journal of Agricultural Research 12: 727-46.

Wright, G.M. 1972: Drought injury in wheat ears. New Zealand Journal of Agricultural Research 15: 43-7.

APPENDIX

"ESTABLISHMENT OF UNDERSOWN WHITE CLOVER AS AFFECTED BY WHEAT SOWING RATE, TIME OF WHITE CLOVER INTRODUCTION, AND IRRIGATION"

"EFFECTS OF IRRIGATION AND FERTILISER ON THE YIELDS OF ARAWA, AOTEA AND KARAMU WHEATS"

"LEVELS OF WATER-SOLUBLE CARBOHYDRATE IN THE PRE-ANTHESIS EAR OF WHEAT, AND GRAIN SET PER SPIKELET"

"EFFECTS OF SOWING RATE, IRRIGATION, AND NITROGEN ON THE COMPONENTS OF YIELD OF SPRING-SOWN SEMIDWARF AND STANDARD NEW ZEALAND WHEATS"

Establishment of undersown white clover as affected by wheat sowing rate, time of white clover introduction, and irrigation

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ABSTRACT

Establishment of undersown white clover was unaffected by differences in sowing rate of 'Aotea' wheat between 50 and 150 kg/ha. Clover sown with wheat in June established at a higher density than when overdrilled the following spring. Irrigation increased the survival of undersown clover without increasing plant size. It is suggested that the growth of irrigated clover was restricted by low light intensity.

INTRODUCTION

Sowing white clover under a cereal is a common practice in the forage seed producing areas of New Zealand, but little agronomic research has been carried out on the cereal - white clover association. Scott (1973) described the cultural techniques commonly employed for white clover establishment and Dougherty (1972) reviewed the factors affecting red clover establishment under wheat. A previous paper (Scott *et al.* 1973) reported on the effects of various agronomic treatments on the wheat component of this wheat - white clover association. This paper describes how the treatments affected the establishment of undersown white clover.

MATERIALS AND METHODS

The trial site and experimental design have been described in detail previously (Scott *et al.* 1973). A 3 × 3 × 3 factorial design with two-fold replication was used and each plot measured 30 × 3 m. The three levels of wheat sowing rate, time of white clover introduction, and irrigation were as follows:

Sowing rate of wheat	S_0	50 kg/ha
	S_1	100 kg/ha
	S_2	150 kg/ha
Time of white clover introduction	T_0	26 June 1972 with wheat
	T_1	overdrilled 5 Sept 1972
	T_2	overdrilled 8 Oct 1972
Irrigation treatments	W_0	not irrigated
	W_1	irrigated to 2 weeks after anthesis of wheat
	W_2	irrigated to wheat harvest

Wheat (*Triticum aestivum* L. cv. 'Aotea') was sown in 15 cm rows by a combine drill together with superphosphate at 250 kg/ha on 26 June 1972. 'Grasslands Huia' white clover (*Trifolium repens* L.) planted at the same time as the wheat was broadcast behind the coulters and lightly harrowed. For later times of planting the clover was direct-drilled in 15 cm rows in the same direction as the wheat rows. The sowing rate of clover was 3 kg/ha for all times of sowing. In irrigated plots, soil water was restored to field capacity through a microtube trickle system whenever soil water was depleted to −0.5 bars according to tensiometers permanently installed in representative plots at depths of 30 cm.

After the wheat harvest in early February 1973 all plots were mown and the straw removed by baling. On 15 February the whole trial area was spray irrigated.

MEASUREMENTS

At monthly intervals starting in November, white clover seedling numbers and size were recorded on one 1000 cm² quadrat per plot. For the final establishment count on 5 March 1973 ten 1000 cm² quadrats were sampled per plot.

TABLE 1 — Effects of wheat sowing rate, time of white clover introduction, and irrigation on white clover plants per m^2

Treatment	Date 15/11/72	11/12/72	10/1/73	22/3/73
S_0	201	139	106	55
S_1	179	102	81	59
S_2	182	77	88	44
T_0	143	131	109	74
T_1	133	104	96	44
T_2	269	84	70	41
W_0	104	91	48	32
W_1	196	93	68	57
W_2	246	134	159	69
L.S.D. 5%	105	54	38	18

TABLE 2 — Effects of wheat sowing rate, time of white clover introduction, and irrigation on clover plant size (mg DM/plant)

Treatment	Date 15/11/72	11/12/72	10/1/73	22/3/73
S_0	8.94	7.44	8.02	52.3
S_1	3.82	3.92	5.78	42.5
S_2	2.83	3.21	5.30	47.6
T_0	8.01	7.88	7.19	44.8
T_1	5.27	2.85	6.26	44.9
T_2	2.31	3.84	5.65	52.8
W_0	7.80	5.34	5.30	37.3
W_1	3.74	4.01	7.92	41.7
W_2	4.04	5.22	5.89	63.5
L.S.D. 5%	5.46	2.64	2.65	14.8
Significant interactions	None	S × T*	None	None

After counting, the plants were dried to constant weight at 70°c and weighed.

Light transmission through the wheat crop was measured with an EEL Lightmaster light meter by taking a reading at ground level and above the crop canopy in quick succession on calm, cloudy days. Three sets of readings were taken per plot. Soil-water levels were measured gravimetrically at approximately weekly intervals as described previously (Scott *et al.* 1973).

RESULTS

As there were no significant interactions of treatments on clover plant numbers through the growing season, only main effects are presented in Table 1.

For the first three sampling dates the data were extremely variable and for the final count in March part of this problem was reduced by sampling a greater area and number of plants.

Wheat sowing rate had little effect on white clover numbers except in December, when they were significantly reduced at the high sowing rate. The effect of clover sowing time changed with time, as initially there were more plants in the plots over-drilled in October; but by March, clover sown in June had established at a significantly higher density. Irrigation had no significant effect on plant numbers until December, but by March all irrigated plots contained significantly more plants. Irrigation to near harvest (W_2) did not give significantly more plants than irrigation to 2 weeks after anthesis (W_1). In all treatments there was a marked decline in clover numbers as the season progressed. The effects of treatments on plant size are presented in Table 2 and the only significant interaction in Table 3.

Compared with the low wheat sowing rate (S_0), the high sowing rate (S_2) significantly depressed white clover size through most of the season, but by March the differences had disappeared (Table 2). In December this depression was significant only for clover that had been

TABLE 3 — Interaction of wheat sowing rate and time of white clover introduction on clover dry weight per plant (mg) on 11 December 1972

	T_0	T_1	T_2	Mean
S_0	14.60	3.20	4.53	7.44
S_1	4.83	3.13	3.80	3.92
S_2	4.21	2.23	3.20	3.21
Mean	7.88	2.85	3.85	

L.S.D. 5% Between main effect means, 2.64
Between treatments at same or different levels, 4.57

TABLE 4 — Effects of wheat sowing rate, time of white clover introduction, and irrigation on light transmission (%)

Treatment	Date 30/11/72	9/1/73
S_0	6.9	16.5
S_1	4.5	16.8
S_2	4.5	13.9
T_0	4.9	15.2
T_1	5.5	15.8
T_2	5.5	16.2
W_0	7.2	19.3
W_1	4.3	15.0
W_2	4.4	12.9
L.S.D. 5%	1.5	N.A†

† Not available

sown in June (Table 3). Variations in clover size caused by sowing time were also significant in the early stages, but disappeared with time. Clover plants in plots that had been irrigated to early January (W_2) were significantly larger in March, although in November there was a tendency for both irrigated treatments to decrease plant size.

Table 4 presents the main effects of treatments on light transmission through the canopy. There were no significant interactions.

No statistical analysis is available for the January reading, as only one block was recorded due to the onset of windy conditions. In November the lowest sowing rate of wheat gave a significant increase in light transmission, but both irrigated treatments gave a significant depression. Time of clover introduction had no effect. By January the effect of sowing rate had largely disappeared, but irrigation still appeared to be reducing light transmission.

DISCUSSION

For white clover seed production under New Zealand conditions, the optimum plant density is not well defined. For British conditions Zaleski (1961, 1964) recommended a plant density of 60–70 plants per m^2, and in California a density of 110–160 plants per m^2 is recommended for seed production of Ladino white clover (Marble *et al.* 1970). Specialist seed producers in New Zealand say that 20–30 robust clover plants per m^2 is sufficient. At flowering, individual clover plants are very difficult to identify, however, and the population of stolon apices is probably the critical factor for flower and seed production As considerable cool-season growth of white clover may occur in New Zealand, a satisfactory population of stolon apices at flowering may be obtained from a density of about 30 plants per m^2. If this assumption is correct, then all plots in the present experiment contained sufficient white clover plants for seed production, although some of the treatments produced large differences in the final population.

Santhirasegaram & Black (1965) concluded that one method of increasing the establishment of undersown species was to sow the cover crop at a reduced seeding rate. In the present experiment sowing rate had no effect on white clover establishment (Table 1) or size (Table 2), even though the low rate of 50 kg/ha was half the conventional sowing rate and caused reductions in wheat grain yield (Scott *et al.* 1973). Low sowing rates produced large and significant reductions in the leaf area index of the wheat crop up until the end of October (Scott *et al.* 1973), and even in November levels of light transmission were significantly greater in plots from the low sowing rate (Table 4). However, in all treatments the levels of light transmission were extremely low compared with the levels recorded by other workers with similar crops (Genest & Steppler 1973; Janson & Knight 1973). Levels of light reaching the clover canopy may well have been even lower than measured as a result of taking the readings during cloudy conditions (Santhirasegaram & Black 1968).

The very low levels of light transmission recorded within the wheat crop explain the limited growth of clover that occurred in the irrigated plots from November to January (Table 2). The final differences in clover size caused by irrigation probably reflect growth made between the wheat harvest and the commencement of post-harvest irrigation. The growth characteristics of white clover which make is extremely tolerant of severe frequent grazing are obviously a distinct disadvantage under low light intensity, particularly at the seedling stage. Whereas lucerne seedlings with an erect growth habit have the capacity to etiolate under conditions of low light intensity (Janson & Knight 1973), etiolation in white clover is restricted to the petioles (Mitchell 1956). Thus white clover has only very limited ability to extend its leaf canopy into the zones of higher light intensity nearer the top of the cover crop (Santhirasegaram & Black 1968). Although irrigated white clover plants did not grow much when subjected to severe shading, irrigation increased plant survival.

For maximum establishment of undersown species it is generally agreed that the cover crop and the undersown species should be sown at the same time (Santhirasegaram & Black 1965). Results from this experiment confirm this belief. The idea that clover sown with wheat in May – June may suffer from frost heave (Ryde 1965) is probably ill-founded in all but the coldest seed-producing areas at higher altitudes closer to the Southern Alps than Lincoln. However, the higher rainfall in these areas should aid establishment and survival of clover undersown in the spring.

The variability of the numbers and size of white clover recorded in this trial appeared to be due to the heterogeneity of this outcrossing species (Davies 1969) being compounded by the variable micro-environment beneath the wheat cover crop. Clover plants derived from seeds already present in the soil may have added to the variability. In spite of this variability, several practical conclusions can be drawn from this trial and the one described previously (Scott *et al.* 1973). When sowing rates of wheat much below 100 kg/ha are used with the objective of aiding establishment of undersown white clover, wheat yields on high-fertility, moisture-retentive soils may be reduced without a concurrent improvement in clover establishment. Clover sown at the same time as the wheat establishes at a higher density than when introduced in spring, although introduction can be delayed until early October with no deleterious effects on wheat yields. In dry years irrigation is beneficial to white clover establishment and may also increase wheat yields.

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REFERENCES

Davies, W. Ellis 1969: *Proceedings of the British Grassland Society Occasional Symposium No. 6*: 99–122.

Dougherty, C. T. 1972: *N.Z. Journal of Agricultural Research 15*: 706–11.

Janson, C. G.; Knight, T. L. 1973: *N.Z. Journal of Experimental Agriculture 1*: 243–51.

Genest, J.; Steppler, H. 1973: *Canadian Journal of Plant Science 53*: 285–90.

Marble, V. L.; Jones, L. G.; Goss, J. R.; Jeter, R. B.; Burton, U. E.; Hall, D. H. 1970: *California Agricultural Experiment Station Extension Circular 554.*

Mitchell, K. J. 1956: *N.Z. Journal of Science and Technology 37B*: 395–413.

Ryde, B. J. P. 1965: *Canterbury Chamber of Commerce Agricultural Bulletin 427.*

Santhirasegaram, K.; Black, J. N. 1965: *Herbage Abstracts 35*: 221–5.

———— 1968: *Journal of the British Grassland Society 23*: 1–12.

Scott, W. R. 1973: *In* "Pastures and Pasture Plants". Ed. R. H. M. Langer. A. H. and A. W. Reed, Wellington. 428 pp.

Scott, W. R.; Dougherty, C. T.; Langer, R. H. M.; Meijer, G. 1973: *N.Z. Journal of Experimental Agriculture 1*: 369–76.

Zaleski, A. 1961: *Journal of Agricultural Science, Cambridge 57*: 199–212.

———— 1964: *Journal of the British Grassland Society 19*: 237–47.

Effects of irrigation and fertiliser on the yields of 'Arawa', 'Aotea', and 'Karamu' wheats

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ABSTRACT

Grain yields of 'Aotea', 'Arawa', and 'Karamu' wheats were depressed by irrigation during early stages of reproductive development which reduced the number of grains per spikelet and slowed the rate of reproductive development. Nitrogen fertiliser increased the ear population at harvest but had little effect on the dry weight or leaf area of the tillers during the critical pre-anthesis stage or on the mean values of the components of yield of the ears. There were no interactions between fertiliser and irrigation treatments. 'Karamu', a Mexican semi-dwarf, was similar to the New Zealand-bred wheats except that it had slightly more spikelets per ear and grains per spikelet, but it had smaller grains. An antitranspirant applied to irrigated wheat had no effect on any of the components of grain or straw yield. Responses were interpreted on the basis that pre-anthesis assimilate levels were modified by agronomic treatments and affected grain set.

INTRODUCTION

Soil-moisture deficits during spring have been recognised as the main limiting factor of wheat yields in Canterbury for many years (Frankel 1935; Walker 1956). Soil fertility, particularly nitrogen status, influences yield and quality of New Zealand wheats (Ludecke 1972; Wright 1969) by modifying the relative values of one or more of the four main components of yield (Langer & Liew 1973). In high-yielding wheat crops in Canterbury the importance of these components in accounting for variations in grain yield usually ranks in the following descending order: ear density, grains per spikelet, grain size, and spikelets per ear. Frankel (1935) thought that the environment of the wheatlands of Canterbury was generally unfavourable for the full yield development of ears of British wheats, and he noted that successful cultivars were characterised by an erect growth habit, sparse tillering with high tiller survival, and many small to intermediate-sized ears. He attributed the success of these wheat types to their ability to adapt to drought and yet to respond to favourable conditions.

In a factorial experiment on Wakanui silt loams of the Lincoln College Research Farm in 1972–73 wheat yields were lowest in plots receiving high levels of nitrogen fertiliser and non-limiting water supply (Dougherty 1973a). When nitrogen and water are readily available, growth increases the number and size of both non-reproductive and reproductive sinks, but generally the size and competitiveness of the non-reproductive sinks are affected more (Langer & Liew 1973; Scott *et al.* 1973; Dougherty 1973b).

The wheat ear may encounter nutrient or water deficiency after a period of unrestricted growth when all parts of the plant develop at optimal rates. Non-reproductive sinks may thus increase in size and capacity during favourable conditions, but later, as the environment deteriorates, these sinks become competitive with reproductive structures to the detriment of grain yield (Brouwer 1962). Tillers, for example, may withdraw carbohydrates from the main stem when their own level of assimilation cannot satisfy their internal demand (Bremner 1969). Modern New Zealand cultivars have been selected for yield and quality in the absence of irrigation and under medium levels of soil fertility; they are thus adapted to some nutritional or water stress which prevents excessive vegetative growth.

The yield depressions which concerned us here are not the well-known responses associated with high nitrogen or irrigation. Irrigation may reduce crop yields if water is applied at an excessive rate to cause flooding, for when soil-water levels are above field capacity soil oxygen tensions decline and root permeability is reduced (Kramer 1969). The development and activity of the root system may be modified so that water and nutrient uptake is severely restricted. Similarly, under moist conditions high levels of plant-available nitrogen may predispose the crop to lodging.

Research at Winchmore (Drewitt & Rickard 1971) has shown that wheat responds to irrigation on the less moisture-retentive soil series of the Canterbury Plains and that one application at flowering suffices.

TABLE 1 — Seed characteristics and plant densities on 6 September 1972

A Cultivar	Germination (%)	Seed size (mg)	Sowing rate (kg/ha)	Plant density (plants/m²)
0 'Arawa'	100	47	112	183
1 'Aotea'	97	41	100	190
2 'Karamu'	80	38	112	217

Irrigation responses are usually better on the shallower, less fertile soils than on the deeper, fertile ones (Scott *et al.* 1973).

The factorial experiment described here was designed to provide information on the response of wheat to various irrigation and nitrogen treatments. Three cultivars, the relatively tall 'Arawa', intermediate 'Aotea', and the semi-dwarf 'Karamu', were sown to provide crops with potentially different source - sink relationships. Ear differentiations occur when the primary competing sink is the extending stem and, consequently, the semi-dwarf was expected to have a weaker sink (Patrick 1972). Irrigation treatments were also intended to modify source - sink relationships. One irrigation treatment was included which represented the recommended farm practice of one application at flowering, but two were scheduled before ear emergence in an endeavour to influence the source - sink relations of grain set. An antitranspirant was applied to one of the treatments in this irrigation schedule to assess the effects of physiological water stress (Wright 1972). Fertiliser was applied in another treatment in an attempt to modify source - sink relations by nutrition.

MATERIALS AND METHODS

A 3 × 4 × 2 factorial experiment was laid out in two randomised blocks on Wakanui silt loams on the Lincoln College Research Farm. Cereals had been grown on the trial site during the three previous seasons and before that a perennial ryegrass - white clover pasture. The treatments and levels of each were:

A. Cultivar	(*Triticum aestivum* L.) 0 'Arawa' 1 'Aotea' 2 'Karamu'
B. Irrigation	0 None 1 Early 2 Early plus antitranspirant 3 Late
C. Fertiliser	0 None 1 N + K

TABLE 2 — Crop parameters measured on 13 November 1972

Main effects	Tillers (no./m²)	Mean tiller wt. (g)	Leaf area (cm²/tiller)	Stem wt. (g/m)	Leaf wt. (g/m²)	Leaf & stem wt. (g/m²)	LAI
A *Cultivar*							
0 'Arawa'	522	1.47	50.7	637	126	763	2.67
1 'Aotea'	601	1.01	43.9	491	117	608	2.64
2 'Karamu'	555	1.27	24.3	632	71	703	1.35
LSD(5%)	57	0.10	6.0	67	17	70	0.4
B *Irrigation*							
0 None	545	1.31	36.4	601	101	702	2.02
1 Early	588	1.16	40.4	573	102	674	2.37
2 Antitranspirant	534	1.22	43.3	543	110	653	2.33
3 Late	570	1.31	38.3	629	106	735	2.15
LSD(5%)	66	0.11	7.0	78	19	75	0.5
C *Fertilisation*							
0 None	510	1.28	37.5	557	88	645	1.91
1 N + K	608	1.22	41.8	615	122	737	2.52
LSD(5%)	46	0.08	4.9	55	14	64	0.4
CV (%)	14	11	21	16	22	25	27

There were no significant interactions

A Cultivars

All plots (30 × 3 m) were sown in 15 cm rows by a combine drill with superphosphate at 250 kg/ha on 28 June 1972. A sowing rate of 100 kg/ha was selected for 'Aotea', and the rates of 'Arawa' and 'Karamu' were adjusted for seed size and viability (Table 1). 'Karamu' wheat is a New Zealand release of a semi-dwarf hybrid (Lerma Rojo × Norin 10 — Brevor 14) Andes[3], bred by the International Centre for Maize and Wheat Improvement in Mexico City (McEwan *et al.* 1972). This wheat was introduced into Australia in 1963 by wheat breeders of the Wagga Wagga Research Institute and given the local accession number WW15. Descriptions of 'Aotea' and 'Arawa' wheats are readily available (McEwan 1959; Langer 1965; Langer & Khatri 1965).

B Irrigation

B_0; none — In this treatment no water was applied and the plots were not reticulated with a trickle system. In this and all other irrigation treatments rainfall was not excluded.

B_1; early — Soil water was restored to field capacity through a microtube trickle reticulation system whenever soil-water levels were depleted to −0.5 bars according to tensiometers buried at 30 cm in representative plots. Between 6 October and 26 November 230 mm were applied, coinciding with the period until anthesis.

B_2; early plus antitranspirant — Plots received the same irrigation treatments as those in B_1. However, a stabilised emulsion of finely divided wax particles in water (Mobilcer C) was sprayed to form a wax layer of at least 1 μ over all transpiring surfaces. All antitranspirant plots were sprayed on 18 and 30 October. 'Karamu' plots were treated for the third time on 13 November soon after anthesis, 'Arawa' plots at anthesis on 20 November, but 'Aotea' plots not until 28 November, 5 days after anthesis, because of rain.

B_3; late — Plots in this treatment received no additional water except that from rainfall until after ear emergence when soil-water levels were restored to field capacity by the trickle irrigation system. 'Karamu' received 85 mm water during 3–26 November. 'Arawa' and 'Aotea' were irrigated with 55 mm on 24–26 November.

C Fertiliser

Fertilised plots (C_1) were broadcast with 50 kg N/ha as nitrolime (23 : 0 : 0) and 50 kg K/ha as potassium sulphate (0 : 0 : 40) on 22 August 1972. Plots additional to the main design were fertilised with 50 kg N/ha of nitrolime alone to assist in the analysis of confounding between nitrogen and potassium fertilisers. Soil tests of control plots sampled on 28 August 1972 gave the following results: pH 5.6, Ca 7, K 5, Truog P 10, Olson P 45.

Pest control

A MCPA-dicamba herbicide mixture (6 : 1) was applied at the rate of 2.45 l/ha on 26 September 1972. Grain-eating birds were discouraged. The crop was not treated with insecticide, but fungicide was applied to seeds before sowing.

Measurements

On 6 September 1972, plant numbers were counted by sampling six separate 1000 cm² quadrats per plot. On 13 November and at ear emergence one 1000 cm³ quadrat was cut from each plot and separated into a "leaf" and "stem" fraction. The "leaf" fraction consisted of all living laminae removed at the junction with the leaf sheath, and the "stem" fraction consisted of all the remaining material. Live tillers were counted and leaf area determined on a leaf area planimeter. After oven drying at 75°c the separate fractions were weighed.

Just before combine harvesting 10 separate 1000 cm² quadrats per plot were selected at random and cut to ground level for determination of straw yield and components of grain yield. Ears were counted and recorded. Spikelets per spike were counted on a random sample of 20 ears per plot. Grain was threshed and cleaned mechanically, weighed, and expressed at 14% moisture. Mean grain weight was established by counting and weighing a sample of 400 grains. Straw was weighed after drying to a constant weight at 75°c and expressed at 14% moisture. Combine yields were determined by direct heading one 30 m strip down the centre of each plot after trimming and discarding 1 m off each end. After machine dressing the grain was weighed and the yields corrected to 14% moisture content. Soil water was monitored regularly by a gravimetric method based on three 0–20 cm soil cores per plot. Soil-water content was expressed on a dry-weight basis after drying to a constant weight at 105°c.

RESULTS

When above-ground material was harvested on 13 November 'Karamu' was at ear emergence and the other cultivars at the boot stage. Data obtained from this harvest are presented in Table 2. There were no significant interactions. Plants from 'Arawa' plots generally had fewer tillers per square metre but these were heavier and had a greater leaf area so that the dry-matter yields per square metre and leaf area indices were higher than those of the two shorter-strawed cultivars. The semi-dwarf 'Karamu', which was the most advanced, was characterised by higher proportions of stem and lowest leaf areas per tiller and leaf area indices. At this time the two early irrigation treatments (B_1 and B_2) resulted in lower dry-matter yields mainly because the stem fractions were lighter. Leaf area per tiller was increased by these treatments as were leaf area indices.

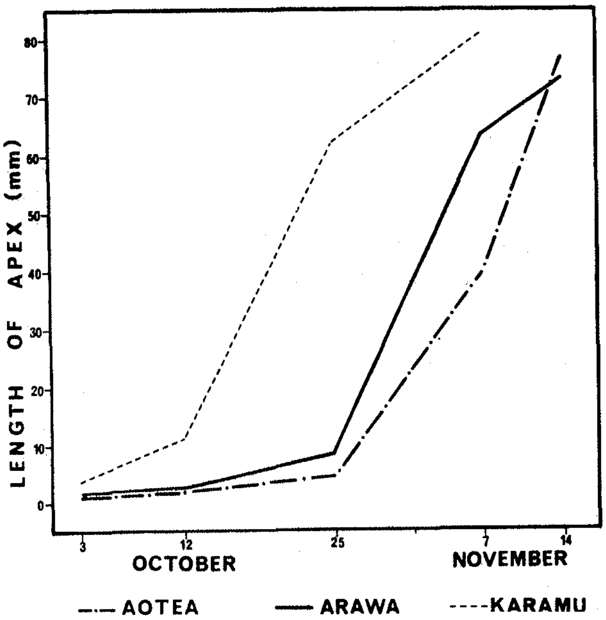

Fig. 1 — Mean lengths of 'Aotea', 'Arawa', and "Karamu' apices.

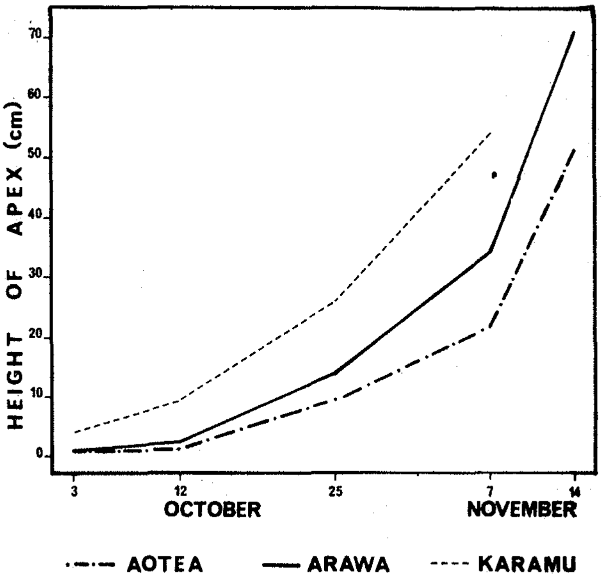

Fig. 2 — Mean height of mainstem apices of 'Aotea', 'Arawa', and 'Karamu' above roots.

TABLE 3 — Components of grain yield of wheat at harvest for all main treatments

	Ear density (no./m²)	No. spikelets/ ear	No. grains/ spikelet	No. grains/ ear	Grain wt. (mg)	Grain yield/ ear (g)
A Cultivar						
0 'Arawa'	412	15.4	1.59	24.5	50.4	1.23
1 'Aotea'	569	15.5	1.47	23.0	46.7	1.07
2 'Karamu'	501	15.8	1.68	26.6	44.2	1.15
LSD(5%)	24	0.3	0.10	2.1	2.4	0.07
B Irrigation						
0 None	478	15.4	1.72	26.5	47.1	1.24
1 Early	505	15.6	1.50	23.4	46.7	1.08
2 Antitranspirant	506	15.8	1.52	24.1	45.9	1.09
3 Late	486	15.6	1.58	24.8	48.7	1.20
LSD(5%)	28	0.3	0.12	2.3	2.7	0.08
C Fertilisation						
0 None	474	15.6	1.57	24.5	47.4	1.15
1 N + K	514	15.6	1.59	24.8	46.8	1.15
LSD(5%)	19	0.2	0.08	1.9	1.9	0.05
CV (%)	7	3	9	8	7	8

There were no significant interactions

Early irrigation delayed reproductive development and this may have caused the lower stem fraction. The fertiliser treatment (C_1) increased dry-matter yields and leaf area index roughly in proportion to the effect on tiller density. Tiller dry weights were slightly depressed and leaf area per tiller slightly increased by fertiliser.

The components of dry-matter yields on 13 November were modified by the stage of development of the wheat. 'Karamu' plots were most advanced and this was reflected in their high proportion of non-leaf. 'Aotea' plots were slowest and 'Arawa' intermediate. The relative rates of reproductive development of the three cultivars may be deduced from data from Fig. 1, which shows the length of the stem apex in its transformation to become an ear. The height of the apex above the roots (Fig. 2) serves as a measure of stem elongation. The early irrigation treatments (B_1 and B_2) also tended to delay stem growth, and this reduced yields of non-leaf dry matter. The fertiliser treatment (C_1) increased the proportion of leaf, but retarded development to a lesser extent.

At the final harvest grain yields were similar for plots of the shorter cultivars 'Aotea' and 'Karamu' (Tables 3, 4). 'Aotea' yields were characterised by the highest ear density and lowest grain weight per ear. 'Aotea' also had generally fewer grains per spikelet and per ear than the other cultivars, and its grains were intermediate in weight. 'Aotea' had a similar straw yield to 'Arawa' and considerably more straw than the semi-dwarf, so that its total biological yield at harvest was the highest of the three wheats. 'Karamu' produced slightly less grain than 'Aotea', although it had more grain per spikelet and per ear; its mean grain weight was lowest, and this reduced its mean grain yield per ear. A low straw yield resulted in a high harvest index. The tallest cultivar, 'Arawa', yielded least grain because it had the lowest population of ears, but its grain production per ear was the highest, primarily because of its greater mean grain weight. 'Arawa' produced the most straw and had the lowest harvest index.

The irrigation treatments gave the most interesting results (Tables 3, 4). Plots which were not irrigated (B_0) and those plots which were irrigated after ear-emergence (B_3) had similar responses except that the latter had slightly fewer grains per spikelet and therefore grains per ear and slightly lower grain yields per ear and per square metre. In non-irrigated plots (B_0) soil-water levels in the top 15 cm fell steadily (Fig. 3) during the period of reproductive development until rainfall raised levels to about 15% in late November (Table 5). The timing of application of water to the late irrigation (B_3) plots depended on the different rates of development of the three cultivars. Soil-water percentage in 'Karamu' plots was similar to that of B_0 plots until irrigation in early November restored it to a level similar to

TABLE 4 — Mean grain and straw yields (14% moisture), harvest index, and height of wheat at harvest for all main treatments

Main effects	Grain (g/m²)	Straw (g/m²)	Grain and straw (g/m²)	Harvest index (%)	Height (cm)
A Cultivar					
0 'Arawa'	507	952	1460	35.2	100.1
1 'Aotea'	606	944	1550	39.3	90.6
2 'Karamu'	581	678	1259	46.1	73.8
LSD(5%)	30	66	78	2.2	1.6
B Irrigation					
0 None	591	807	1397	42.7	84.7
1 Early	547	923	1470	37.6	91.6
2 Antitranspirant	546	906	1451	38.3	91.4
3 Late	577	797	1374	42.3	85.0
LSD(5%)	35	76	90	2.6	1.9
C Fertilisation					
0 None	541	813	1354	40.2	87.1
1 N + K	588	903	1492	40.2	89.2
LSD(5%)	25	54	64	1.8	1.4
CV (%)	7	11	8	8	3
Significant interactions	none	B × C* A × B*	none	none	A × B** B × C*

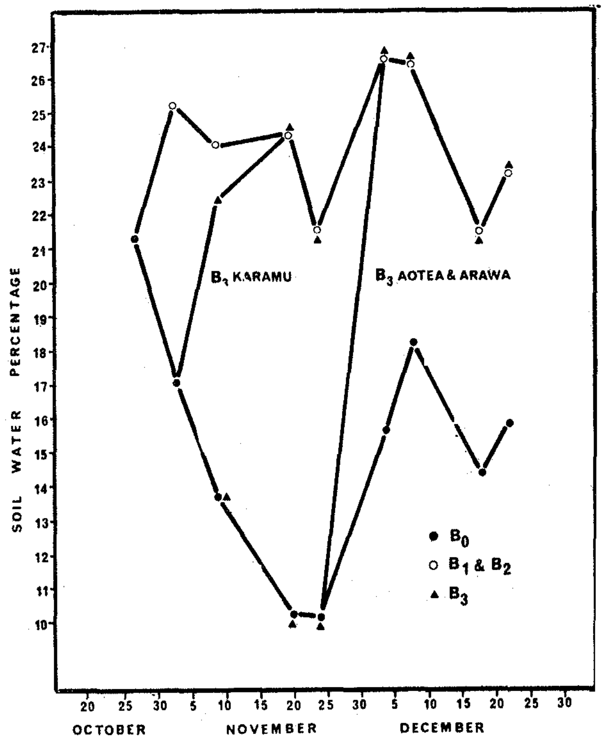

Fig. 3 — Mean soil-water contents of plots subjected to non-irrigated and irrigation treatments.

those in B_1 and B_2 plots (Fig. 3). 'Aotea' and 'Arawa' plots of the B_3 treatment were irrigated soon after ear emergence and were thus subjected to decreasing soil water for most of November. The effect of the late irrigation treatment (B_3) in reducing the number of grains per spikelet was greater in 'Karamu' (14%) than in the later-developing New Zealand-bred cultivars ('Arawa' 3.4%; 'Aotea' 7.6%).

Wheat which was irrigated before ear emergence with (B_1) or without (B_2) antitranspirant yielded less grain than the other two treatments (Table 4). These early irrigations increased ear density at harvest, had little effect on the mean number of spikelets per ear, but significantly decreased the mean number of grains per spikelet and the mean grain weight so that yield per ear and per square metre was lower. In these plots soil-water levels were maintained above 21% by irrigation until the end of November and by precipitation during early stages of grain-filling (Fig. 3, Table 5). These two treatments also boosted vegetative growth apparently at the expense of reproductive growth so that straw yields and crop height increased but the harvest index was lowered. Use of the antitranspirant (B_2) had no significant effect that could be attributed to this treatment.

The fertiliser treatment increased the number of ears per square metre at harvest, but had no significant effect on any of the other components of grain yield. Thus fertiliser increased grain yields by increasing the ear population. Straw yields, crop height, and total dry-matter yields were also increased (Tables 3, 4). Comparison of these yield data with those of additional plots receiving nitrogen but no potassium indicates that the observed response was attributable to the nitrogen component.

DISCUSSION

Irrigation of wheat before and just after ear emergence on these moisture-retentive Wakanui silt loams reduced grain yields mainly because of poor grain set (Tables 3, 4). Irrigation may raise the proportion of less productive lower-order tillers and so depress the mean ear size (Bremner 1969), but this was not the case, as ear numbers at harvest were only slightly affected (Table 3). Irrigation treatments associated with reduced grain set had little effect on other components of yield, but they did increase straw yields and crop height and depress harvest index (Table 4).

Grain set appears to be particularly sensitive to changes in crop-water status. Bingham (1966), for

TABLE 5 — Rainfall and pan evaporation data (mm) for Lincoln College for 5-day periods from August 1972 to January 1973

	August		September		October		November		December		January	
Days	Rain	Evap.	Rain	Evap.	Rain	Evap.	Rain	Evap.	Rain	Evap.	Rain	Evap.
1–5	3.4	3.0	0.1	10.5	—	20.2	0.3	21.4	18.0	14.5	2.9	38.3
6–10	1.1	3.7	0.9	18.3	54.9	5.1	0.6	26.0	0.2	21.3	—	29.8
11–15	3.3	5.4	2.2	19.5	11.7	22.2	0.4	32.9	17.8	29.7	18.1	29.7
16–20	2.2	7.0	7.7	20.8	2.5	17.6	2.3	29.4	4.2	28.1	—	30.9
21–25	6.3	10.1	—	27.6	—	22.3	1.5	26.3	3.7	21.6	4.3	40.9
26–31	10.7	8.4	1.6	16.5	5.1	32.0	11.6	18.3	0.6	41.0	3.6	42.9
Total	26.9	37.5	12.5	113.2	74.2	119.4	16.7	154.3	44.5	156.2	28.9	212.5

example, has shown that water stress preceding pollen meiosis by a few days may result in male sterility and poor seed set. Campbell *et al.* (1969), in contrast, observed that wheat grown in soil just below field capacity suffered male sterility apparently caused by changes in metabolism induced by low rates of soil oxygen diffusion. In the field, however, a substantial failure of grain set because of male sterility is unlikely because the wheat flower is female fertile and cross-pollination is possible (Campbell *et al.* 1969). Cross-pollination, however, usually is not as efficient as self-pollination in wheat, and some reduction in grain set would occur (Khan *et al.* 1973).

Partitioning of dry-matter yields near ear emergence and at harvest also revealed that reproductive growth had been retarded by the application of water (Tables 2, 4). Brouwer (1962) has noted that, generally, conditions which favour rapid growth tend to suit vegetative processes more than reproductive ones. Applications of water before ear emergence also increased leaf area indices during the period before anthesis, which is critical for grain set (Willey & Holliday 1971; Scott *et al.* 1973).

The late irrigation treatment had little influence on the wheat crop, but was associated with a reduction in grain set which was compensated by slightly larger mean grain weight (Table 3). In view of these responses it can be assumed that during the 1972–73 season soil water did not limit grain-filling. The application of water soon after ear emergence also reduced grain set, but to a lesser degree than the early irrigation treatments.

The antitranspirant treatment (B_2) had no effect on the vegetative or reproductive growth despite the high rates of pan evaporation after applications began in mid October (Table 5). It could be concluded that, in this season, water stress during ear determination either did not occur or had no measurable effect. Fuehring (1973) reported that in New Mexico, grain yields were raised by 5–17% by pre-boot applications of antitranspirants to irrigated sorghum crops.

The fertiliser treatment did not affect the mean values of yield components of the ear, and raised grain yield by increasing ear populations (Table 3). It is, however, possible that nitrogen had two counteracting effects on the components of ear yield. Nitrogen fertiliser may have increased the proportions of less productive ears of lower-order tillers (Bremner 1969) and at the same time increased grain set (Langer & Liew 1973). It is also possible that the applied nitrogen was taken up by the crop or lost by leaching (Ludecke & Tham 1971) before grain set, as it was applied in August and exposed to heavy rains soon after irrigation to field capacity in October (Table 5).

'Karamu' was sown in June even though it was released as a spring wheat in New Zealand (McEwan *et al.* 1972) and, probably because of its lower sensitivity to vernalisation and photoperiod (Syme 1968), it was earlier than 'Arawa' and 'Aotea' (Figs 1, 2). Although spikes of 'Karamu' generally had more spikelets and grains per spikelet than the New Zealand cultivars, the grains were smaller (Table 3). Fisher (1973) noted that Norin 10 derivatives (such as 'Karamu') initiated more spikelets than conventional varieties, and he also suggested that stronger apical dominance within the individual spikelet presumably prevented the precocious development of the basal florets so that more distal florets were able to grow to the critical size for grain set (Langer & Hanif 1973).

'Karamu' grains tended to be smaller than those of 'Arawa' and 'Aotea' (Table 3). Syme (1969) has suggested that maximum grain size of semi-dwarf wheats is inherently less than in normal wheats. The absence of an effect of late irrigation on grain size supports our previous observation (Scott *et al.* 1973) that, normally, grain filling is not limited by soil-water availability on Wakanui silt loams. Grain-filling in Canterbury wheat occurs at a time of high and rising levels of solar radiation and when the crop architecture is conducive to efficient light utilisation. Semi-dwarf wheats generally have a high ratio of grain weight to post-anthesis leaf area (Syme 1969) and appear to have, in our situation at least, a faster rate of maturation. Thus grain size of 'Karamu' may also reflect deficiencies in carbohydrate supply during grain-filling and its early senescence.

Grain yields of 'Karamu' and 'Arawa' suffered from insufficient ear populations compared with 'Aotea' (Table 3). In favourable circumstances on this soil type grain yields increase with ear densities up to 800 ears/m^2 (Scott *et al.* 1973). In 'Aotea' a high proportion of tillers survive and produce ears, but in 'Arawa' fewer tillers do so (Langer 1965). 'Aotea' is classified by McEwan (1959) as a freely tillering wheat and 'Arawa' as one with moderate tillering capability. 'Arawa' also tends to suffer more from plant mortality or poor establishment in the field (Table 1), (Langer 1965). Poor establishment, a characteristic of semi-dwarf wheats, has been associated with reduced coleoptile elongation and seedling emergence, but this was not observed in 'Karamu' (Table 1) (Allan *et al.* 1965). Individual plants of 'Karamu' had a limited time for tiller production because this process ceases at or about flowering. 'Karamu' may have benefited from higher sowing rates, but this is not necessarily so, for Thorne & Blacklock (1971) observed in England that semi-dwarf spring wheats were relatively insensitive to changes in sowing rate between 120 and 240 kg/ha.

'Karamu' did not appear to differ from 'Aotea' and 'Arawa' in its responses to nitrogen fertiliser (Tables 2, 3, 4). Thorne & Blacklock (1971) found no evidence that short-strawed wheats required more nitrogen or responded better to nitrogen than tall wheats, but in New South Wales, Syme (1970) found that WW15 ('Karamu') was adapted to high-yielding environments. Under the comparatively low fertility conditions of this experiment 'Karamu' appeared to have no superior agronomic features. These results imply that the semi-dwarf and New Zealand wheats are subject to, and equally susceptible to, the same limitations in our environment.

The results obtained from this experiment and our concurrent one (Scott *et al.* 1973) are consistent with the hypothesis of Willey & Holliday (1971) that agronomic treatments may reduce grain set by limiting the availability of carbohydrates before anthesis. The early irrigation treatments retarded development and promoted vegetative growth at the expense of reproductive growth. These responses are, according to Brouwer (1962), indicative of plants which have low levels of soluble carbohydrate. Mild water stress, perhaps as experienced in wheat from non-irrigated and late-irrigated plots, may have improved grain set by increasing the supply of carbohydrate to the ear before anthesis (Willey & Holliday 1971), as utilisation of carbohydrates in water-stressed plants is likely to be less affected than their assimilation (Brouwer 1962; Hsiao 1973). Growth may be maintained at low tissue-water potentials if the osmotic potential is lowered by the transport of solutes from other less essential parts of the plant (Meyer & Boyer 1972). Either or both of these mechanisms may have contributed to the observed differences in grain set.

The semi-dwarf 'Karamu's' responses could also be interpreted on the basis that carbohydrate limits grain set. Before anthesis 'Karamu' plots had lower leaf area indices (Table 2) and plants may have had higher net assimilation rates and, presumably, higher soluble carbohydrate status than the New Zealand cultivars (Scott *et al.* 1973). During grain set there should also have been considerably less competition for assimilates from the stem sink of the semi-dwarf (Patrick 1972) and more grains may have formed as a result.

Modern New Zealand cultivars have been selected for yield and quality in the absence of irrigation and under medium soil fertility, and they may benefit from some mild nutritional or water stress during early phases of ear growth. Currently, Winchmore workers recommend that wheat growing on Lismore stony silt loams should be irrigated when soil-water levels in the top 15 cm fall to the wilting point (10%) at any time up to flowering (Drewitt & Rickard 1971). Normally this means that wheat is irrigated once between early November and mid December, a period which coincides with the booting to flowering stage. Irrigated or non-irrigated wheat crops in Canterbury will, therefore, in most years be subject to increasing soil-moisture deficits during the growth stage when the number of grains per spikelet is determined. Mild water stress appears to have no measurable effect on grain yield of field wheat, and early irrigation has no positive effect (Drewitt & Rickard 1971). Conversely, Langer & Ampong (1970) found in a pot trial that water stress drastically reduced grain number per ear in New Zealand wheats when imposed at the stage of spikelet formation, but it seems likely that the intensity of water stress far exceeded that occurring up to flowering on Lismore stony silt loams in most seasons.

We may draw some conclusions from this experiment and the one reported earlier (Scott *et al.* 1973). On moisture-retentive, potentially high-yielding soils in Canterbury grain set appears to be limited by the availability of carbohydrate before anthesis. Agronomic treatments which may lower carbohydrate levels by increasing their consumption or by decreasing their assimilation include excessive sowing rates, the use of poorly structured wheat cultivars, and the promotion of vegetative growth by water or nutrition at the expense of reproductive growth.

Controversy exists in Canterbury as to whether soils with poor or high moisture retention properties should receive priority for supplies of irrigation water. In an age when water is rapidly becoming a limited resource it is imperative that all water is used efficiently, and it seems unwise, in view of these results, to advocate the widespread use of irrigation for wheat in high-fertility soils with a high volume of stored water available to the plant.

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REFERENCES

Allan, R. E.; Vogel, O. A.; Russell, T. S.; Peterson, C. J. 1965: *Crop Science 5*: 5–8.

Bingham, J. 1966: *Annals of Applied Biology 57*: 365–77.

Bremner, P. M. 1969: *Journal of Agricultural Science 72*: 281–7.

Brouwer, R. 1962: *Netherlands Journal of Agricultural Science 10*: 361–76.

Campbell, C. A.; McBean, D. S.; Green, D. G. 1969: *Canadian Journal of Plant Science 49*: 29–37.

Dougherty, C. T. 1973a: *N.Z. Journal of Agricultural Research 16*: 12–8.

——— 1973b: *N.Z. Department of Scientific and Industrial Research Information Series No. 96*: 12–6.

Drewitt, E. G.; Rickard, D. S. 1971: *Proceedings of the First Annual Conference of the Agronomy Society of New Zealand*: 147–57.

Fisher, J. E. 1973: *Canadian Journal of Plant Science 53*: 7–15.

Frankel, O. H. 1935: *Journal of Agricultural Science 25*: 466–509.

Fuehring, H. D. 1973: *Agronomy Journal 65*: 348–51.

Hsiao, T. C. 1973: *Annual Review of Plant Physiology 24*: 519–70.

Khan, M. N.; Heyne, E. G.; Arp, L. 1973: *Crop Science 13*: 223–6.

Kramer, P. J. 1969: "Plant and Soil Water Relationships". McGraw-Hill Book Company, New York. 482 pp.

Langer, R. H. M. 1965: *N.Z. Journal of Agricultural Research 8*: 10–4.

Langer, R. H. M.; Ampong, A. 1970: *Ibid. 13*: 869–77.

Langer, R. H. M.; Hanif, M. 1973: *Annals of Botany 37*: 743–51.

Langer, R. H. M.; Khatri, M. I. 1965. *N.Z. Journal of Agricultural Research 8*: 213–22.

Langer, R. H. M.; Liew, F. K. Y. 1973: *Australian Journal of Agricultural Research 24*: 647–56.

Ludecke, T. E. 1972: *Proceedings of the 22nd Lincoln College Farmers Conference*: 85–91.

Ludecke, T. E.; Tham, K. C. 1971: *Proceedings of the First Annual Conference of the Agronomy Society of New Zealand*: 203–14.

McEwan, J. M. 1959: The wheat varieties of New Zealand. *N.Z. Department of Scientific and Industrial Research Bulletin 131.*

McEwan, J. M.; Vizer, K. J.; Douglas, J. M. 1972: *N.Z. Journal of Agriculture 125*: 50–1.

Meyer, R. F.; Boyer, J. S. 1972: *Planta 108*: 77–87.

Patrick, J. W. 1972: *Australian Journal of Biological Science 25*: 455–67.

Scott, W. R.; Dougherty, C. T.; Langer, R. H. M.; Meijer, G. 1973: *N.Z. Journal of Experimental Agriculture 1*: 369–76.

Syme, J. R. 1968: *Australian Journal of Experimental Agriculture and Animal Husbandry 8*: 578–81.

——— 1969: *Ibid. 9*: 528–31.

——— 1970: *Ibid. 10*: 350–3.

Thorne, G. N.; Blacklock, J. C. 1971: *Annals of Applied Biology 78*: 93–111.

Walker, T. W. 1956: *New Zealand Wheat Review 6*: 35–9.

Willey, R. W.; Holliday, R. 1971: *Journal of Agricultural Science 77*: 453–61.

Wright, G. M.; 1969: *N.Z. Journal of Agricultural Research 12*: 727–46.

——— 1972: *Ibid. 15*: 43–7.

Levels of water-soluble carbohydrate in the pre-anthesis ear of wheat, and grain set per spikelet

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ABSTRACT

Low levels of water-soluble carbohydrates in wheat ears before emergence were associated with poor grain set per spikelet when seeding rates were approximately twice conventional ones. Grain set and grain filling in 'Arawa' were better than in 'Aotea', and 'Arawa' also had higher levels of water-soluble carbohydrate in the pre-anthesis ears. There was no obvious relationship between nitrogen fertilisation and water-soluble carbohydrate content of ears near emergence. Irrigation tended to lower levels of water-soluble carbohydrate in pre-anthesis ears of 'Aotea' and 'Arawa' and reduce grain set. Reduction in grain set through irrigation was greater in wheat to which nitrogen fertiliser was applied. 'Karamu', a semidwarf wheat, set more grains in mid-ear spikelets when nitrogen was applied, whereas the New Zealand cultivars 'Aotea' and 'Arawa' did not.

INTRODUCTION

Many researchers have implied, on the basis of shading, defoliation, water stress, sowing rate, and other treatments, that floret growth and grain set are limited by the availability of assimilate, particularly during the period of rapid ear growth which precedes anthesis (e.g., Willey & Holliday 1971; Fischer 1973; Pendleton & Weibel 1965; Scott *et al.* 1973; Lupton *et al.* 1974; Dougherty *et al.* 1974; Dougherty & Langer 1974; Wardlaw 1970), and in a recent review Bingham (1972) wrote "Presumably the ultimate cause of floret failure in normal conditions is insufficient assimilate supply." However, little evidence has been forwarded to show that the levels of assimilate in developing ears are affected by agronomic treatments or by the crop environment. In this paper we relate differences in the levels of water-soluble carbohydrates in the pre-anthesis ears to grain set.

MATERIALS AND METHODS

The details of the factorial experiment with two blocks on which this paper is based have been presented in a previous paper (Dougherty *et al.* 1975). The four factors and their levels were as follows:

Cultivars
- C0: 'Arawa'
- C1: 'Aotea'
- C2: 'Karamu'

Irrigation
- W0: Not irrigated
- W1: Irrigated 20 November to 18 December
- W2: Irrigated 3 December to 18 December

Sowing rate
- S0: 250 viable seeds/m^2
- S1: 500 viable seeds/m^2

Nitrogen fertilisation
- N0: None
- N1: 200 kg N/ha

Sub-plots were thinned at weekly intervals from 5 October 1973, soon after the double-ridge stage of reproductive development, until near anthesis (3 December) to leave one mainstem per 1000 cm^2. Tillers developing on these mainstems were cut off near their origin at weekly intervals as they appeared. On maturation grains were removed, counted, dried to constant weight at 60°c, and weighed for each of six spikelets located at positions 7 to 12 from the base of the spike.

On several occasions between the boot stage and anthesis mainstems were severed at the soil

TABLE 1 — Effect of thinning at weekly intervals on mean grain set (grains/spikelet) and grain size of spikelets 7–12 of mainstems during pre-anthesis floret growth

Date of thinning	No. grains/ spikelet	Mean grain weight (mg)
5 November	3.49	42.3
12 November	3.43	42.2
19 November	3.36	42.5
26 November	3.32	42.7
3 December	3.27	44.1
LSD (5%)	0.20	2.5

TABLE 2 — Grain set and mean grain size in spikelets 7–12 of mainstem ears for main effects of the thinning experiment

	Grains/spikelet (no.)	Grain dry weight (mg)
Cultivar		
C0	3.43	45.8
C1	3.27	38.1
C2	3.36	44.8
LSD (5%)	0.12	1.5
Irrigation		
W0	3.54	43.5
W1	3.17	44.2
W2	3.35	42.8
LSD (5%)	0.12	1.5
Sowing rate		
S0	3.48	43.1
S1	3.24	42.7
LSD (5%)	0.10	1.2
Nitrogen		
N0	3.30	44.7
N1	3.41	41.1
LSD (5%)	0.10	1.2

surface and 10 ears per treatment were removed and inundated in liquid nitrogen in the laboratory. Samples were stored at −18°c until lyophylised and ground by hammer mill to pass a 40-mesh sieve. Sub-samples in triplicate of 200 mg were shaken in 30 ml distilled water and the filtrate analysed for water-soluble carbohydrates by the phenol–sulphuric acid method of Hodge & Hofreiter (1962). Glucose was used for standards and soluble carbohydrate levels expressed as glucose equivalents.

RESULTS

Thinning experiment

Thinning the tiller population to one mainstem per 1000 cm² during early November resulted in the formation of up to 3.5 grains per spikelet in the middle of the ear, but had no appreciable effect on mean grain weight (Table 1). In contrast, mid-ear spikelets of mainstems

TABLE 3 — Effect of nitrogen (N) and irrigation (W) on mean grain numbers per mid-ear spikelet (LSD (5%): 0.17)

	Nitrogen N0	N1
Cultivar		
C0	3.42	3.44
C1	3.28	3.27
C2	3.19	3.53
Irrigation		
W0	3.60	3.49
W1	3.06	3.29
W2	3.24	3.46

TABLE 4 — Mean dry weight, water-soluble carbohydrate levels of ears of 'Karamu' harvested on 29 November, and mean number of grains per spikelet at final harvest for mainstem ears and for all ears

	Ear dry wt. (g/ear)	Carbohydrate (mg/ear)	Grains/spikelet Mainstem ears	All ears
A Sampling time				
1200 h	0.39	102	2.36	1.64
1500 h	0.39	116	2.36	1.64
W Irrigation				
W0	0.40	117	2.31	1.65
W1	0.39	102	2.41	1.63
S Sowing rate				
S0	0.41	114	2.48	1.78
S1	0.38	105	2.24	1.49
N Nitrogen				
N0	0.38	107	2.34	1.61
N1	0.40	112	2.38	1.67
LSD (5%)	0.02	13	0.11	0.06
Significant interactions	none	A × N**	none	none

TABLE 5 — Interactions between sampling time (A) and nitrogen treatment (N) for water-soluble carbohydrate (mg/ear) in 'Karamu' ears on 29 November (LSD (5%): 18)

	Sampling time 1200 h	1500 h
N0	91	123
N1	114	110

growing within the unthinned crop averaged 2.87 grains per spikelet. Because there were no interactions between the factors and the time of thinning, the responses to thinning and to the factorial treatments for grain set and grain weight are shown separately (Table 2). Grain set per spikelet was significantly less in 'Karamu' than in 'Aotea' and 'Arawa' in the absence of nitrogen fertiliser, but it improved markedly with nitrogen fertilisation in contrast to the response of the New Zealand cultivars (Table 3). Irrigation (W1 and W2) depressed grain set in mid-ear spikelets of wheat not fertilised with nitrogen, particularly when irrigated on the early schedule (W1) (Table 3). Nitrogen fertiliser improved grain set in irrigated wheat, but depressed grain set in unirrigated wheat (Table 3). Irrigation had no significant effect on mean grain weight, but nitrogen fertiliser depressed it (Table 2). 'Aotea' grains were significantly lighter than those of the other two cultivars. Fewer grains were formed in mid-ear spikelets of wheat growing in the high sowing rate treatment, but grain weight was not significantly affected (Table 2).

TABLE 7 — Effect of sowing rate (S) on mean ear dry weight (g/ear) of 'Arawa' and 'Aotea' ears on 6 December (LSD (5%): 0.12)

	'Arawa'	'Aotea'
S0	0.35	0.17
S1	0.29	0.18

Water-soluble carbohydrate in pre-anthesis ears

When 'Karamu' ears were analysed at noon and 1500 h on 29 November about the time of their emergence, levels of water-soluble carbohydrate (mg/ear) were lowered by irrigation and high sowing rate and increased by nitrogen fertilisation (Tables 4, 5). Grain set, as indicated by mean numbers of grain per spikelet at the final harvest, was higher in mainstem ears than in all ears. Fewer grains per spikelet were formed in ears from wheat grown at the high sowing rate (Table 4). Irrigation increased grain set in 'Karamu' mainstem ears, but this trend was not apparent in ears representing the whole population (Table 4). Nitrogen fertiliser only had a slight, non-significant effect on grain set. All treatments had relatively little effect on mean ear dry weights.

'Arawa' and 'Aotea' ears were analysed for water-soluble carbohydrates soon after ear emergence at 1400 h on 6 December and at 1000 h on 12 December 1973. 'Aotea' was at an earlier stage of development (Table 6), as indicated by its mean ear dry weight. High

TABLE 6 — Water-soluble carbohydrates, dry weights of 'Arawa' (C0) and 'Aotea' (C1) ears harvested at 1400 h on 6 December and at 1000 h on 12 December, and mean numbers of grains per spikelet for mainstem and for all ears

	Ear dry wt. (g/ear) 6.12.73	12.12.73	Soluble carbohydrates (mg/ear) 6.12.73	12.12.73	Grains/spikelet (no.) Mainstem ears	All ears
Cultivar						
C0	0.32	0.36	115	68	2.43	1.52
C1	0.17	0.25	96	49	2.06	1.44
Irrigation						
W0	0.28	0.33	123	64	2.30	1.49
W1	0.22	0.29	89	53	2.18	1.47
Sowing rate						
S0	0.26	0.33	113	65	2.36	1.59
S1	0.24	0.28	99	52	2.12	1.38
Nitrogen						
N0	0.25	0.31	118	58	2.24	1.54
N1	0.25	0.30	94	59	2.24	1.42
LSD (5%)	0.02	0.01	29	6	0.09	0.06
Significant interactions	C × S*	none	none	none	none	none

sowing rate depressed the dry weight of 'Arawa' ears (Table 7). Ear dry weights were also less in irrigated wheat, but nitrogen fertiliser had no effect. Less water-soluble carbohydrate was recorded in ears from 'Aotea', from irrigated wheat, from wheat grown at the high sowing rate, and, on 6 December, in wheat fertilised with nitrogen (Table 6). On both 6 and 12 December 'Arawa' had more water-soluble carbohydrate in the ear and the same cultivar was characterised by better grain set than 'Aotea' (Table 6). Irrigation depressed water-soluble carbohydrate levels in ears and reduced grain set, particularly in mainstem ears. The high sowing rate also reduced water-soluble carbohydrate in ears and decreased grain set. Nitrogen fertiliser had little effect on the quantities of water-soluble carbohydrate in the ear or on grain set (Table 6). 'Arawa' and 'Aotea' differed from 'Karamu' only in the effect of nitrogen fertiliser on levels of water-soluble carbohydrate in the ear (Table 4, 6).

DISCUSSION

Grain set in mid-ear spikelets of ears of mainstems improved particularly when plants were thinned soon after floral initiation (Table 1). Thinning right up to ear emergence continued to result in better grain set, for in unthinned control plots the mid-ear spikelets averaged only 2.87 grains per spikelet. Probably most of the effect of the thinning treatment is attributable to a reduction in the level of competition for light. This is in line with the results of a previous experiment in which we found that net assimilation rates were lower during early reproductive growth of 'Aotea' grown at above-normal seeding rates (Scott *et al.* 1973). In that instance poor grain set was related to lower crop growth and net assimilation rates and high leaf area indices during pre-anthesis ear growth. Other data on the development of ears in this crop (Scott *et al.* 1975), and the work of Langer & Hanif (1973) on 'Aotea', indicate that mid-ear spikelets are the least plastic with respect to grain set, and hence the effect of thinning may be more marked on the spikelets at the extremities of the ear. We appreciate that the thinning treatments may have had effects other than reducing light competition, such as improved supply of soil water and nutrients, especially nitrogen, but we consider the light effect to have been the most important.

The stage of development of wheat which is the most sensitive to shading and water stress with respect to grain set has been identified as that of rapid ear growth, approximately 2 weeks before anthesis when competition for substrates, particularly from stem internodes, is likely to be intense (Patrick 1972; Fischer 1973; Bingham 1972; Lupton *et al.* 1974). Wardlaw (1970) has shown that grain set is also sensitive to assimilate supplies for 10 days after anthesis. These views conflict with those of Puckridge (1968) and Willey & Holliday (1971), who believe that the whole of the ear development period is important and that there is no particularly sensitive phase. Regrettably, the results of our thinning experiment are not entirely conclusive, for, although the earliest thinning had the most effect on grain set, the treatments involved different time intervals and they ceased too early. Two additional weekly thinning treatments would have been useful in this analysis, for then the experiment would have encompased the entire period of rapid ear growth preceding anthesis and the early sensitive part of grain growth. However, as continuing competition within the crop from 3 December resulted in the reduction from 3.27 to 2.87 of grain numbers in mid-ear spikelets, it can be assumed that what appears to be the most sensitive stage of this crop, with respect to grain set, coincided with rapid ear growth and early stages of grain formation.

Nitrogen fertiliser improved grain set in mid-ear spikelets of mainstems of the semidwarf wheat 'Karamu' but not in the New Zealand cultivars (Table 3). Syme (1970) also noted that grain set in the predecessor of 'Karamu' improved with better nitrogen nutrition. Although grain set in 'Aotea' and 'Arawa' are affected by nitrogen nutrition (Langer & Hanif 1973; Langer & Liew 1973), it is apparent that the semidwarf wheats are more responsive to higher fertility than standard wheats (Syme 1970). Comparisons of standard New Zealand cultivars with 'Karamu' are complicated by the considerable differences in stage of development arising from the early floral initiation of the semidwarf. In this spring-sown experiment 'Karamu' reached the double-ridge stage on 16 October, 'Arawa' on 23 October, and 'Aotea' on 29 October (Dougherty *et al.* 1975).

Poor grain set occurred in wheat which had lower levels of water-soluble carbohydrate in the ear during the period of rapid ear growth. In a previous experiment we noted that poor grain set was associated with low net assimilation rates and high leaf area indices during the pre-anthesis period of ear development and with supra-optimal sowing rates (Scott *et al.* 1973). Differences in grain set between cultivars and the effects of irrigation and nitrogen fertilisation may at least be partially attributable to variations in the supply of assimilate to the developing ear.

Frequently, tillers of wheat growing under stress conditions in the field appear to have as few as one functional leaf. This deficiency may limit the supply of assimilate to the ear, for, as Patrick (1972) observed, the ear is supplied from the three uppermost leaves and sheaths before ear emergence and by the flag leaf after its emergence. Until pollination the ear remains a minor sink (Lupton 1968) and, although it usually competes successfully with stem extension, the growth of the ear primordium appears limited by the availability of substrate (Patrick 1972). Lupton *et al.* (1974) found that high grain yields were correlated with rapid rates of pre-anthesis ear growth and with flag-leaf-area duration. The advantages of semidwarf wheats may lie, according to Bingham (1972), in a more favourable distribution of assimilates, as the Norin 10 genes restrict the competitiveness of the internodes of the stem during the week preceding anthesis. The level of assimilate destined for the developing ear depends on the relative strengths of the competing vegetative sinks (Wardlaw *et al.* 1965). Irrigation, which favours vegetative sinks, may reduce the amounts of assimilate reaching the developing ear and thus reduce grain set. Conversely, mild water stress may increase grain set, perhaps by encouraging the concentration of sucrose in the developing ear by osmoregulation (Hsiao 1973). In a previous field experiment we attributed a yield depression in irrigated, nitrogen-fertilised wheat to changes in sink competitiveness (Dougherty & Langer 1974).

Generally, ear dry weights were lower in ears that had less water-soluble carbohydrate (Tables 4, 6). If, as we suggest, the rate of ear development is regulated by the level of assimilate, treatments causing long-term reductions in assimilate supply should decrease ear growth rates. The nitrogen fertiliser treatment had little effect on ear dry weights, soluble-carbohydrate levels, or grain set, but under other circumstances nitrogen fertiliser may reduce (Dougherty & Langer 1974) or increase (Langer & Liew 1973) grain set. Usually, however, nitrogen fertiliser appears to delay ear development, as does irrigation (Dougherty & Langer 1974). Delayed development in itself may not lead to reduced ear yields if the period of rapid ear growth is not shortened, and it could lead to an increase in ear yield if extended, so that more functional florets develop to set grain (Bingham 1972). Generally, however, treatments do not affect the time of floral initiation, so it can be assumed that treatments which reduced carbohydrate levels and ear dry weights reduced the growth rate of the ear. Lupton *et al.* (1974) found that grain yields were positively correlated with primordium length, and in fast-growing genotypes ears developed more quickly than other parts of the canopy. Thus it appears that the size and rate of development of the pre-anthesis ear are related to the availability of assimilate.

Langer & Hanif (1973) also observed that distal florets degenerated before ear emergence, but the ones in intermediate positions, which they called potentially fertile florets, continued to develop until soon after fertilisation of lower florets. These authors also noted that potentially fertile florets needed a fast rate of development to reach the critical size for pollination, although the mechanism which triggered the degeneration of these florets was a matter for conjecture.

The results of our carbohydrate analyses, the thinning experiment, and our field experiments (Scott *et al.* 1973; Dougherty *et al.* 1974; Dougherty & Langer 1974; Dougherty *et al.* 1975) indicate that the degeneration of potentially fertile florets in the field may occur when carbohydrate levels in the developing ear fall to sub-critical levels. Bingham (1972) also concluded that the ultimate cause of floret failure in normal conditions is insufficient assimilate supply. Thus it is not unreasonable to assume that environmental and agronomic factors which alter the supply of substrate to the developing ear affect its growth rate and grain yield.

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REFERENCES

Bingham, J. 1972: Physiological objectives in breeding for grain yield in wheat. *Proceedings of the Sixth Congress of Eucarpia 1971:* 15–29.

Dougherty, C. T.; Langer, R. H. M. 1974: An analysis of a nitrogen-induced depression of yield in irrigated Kopara wheat. *N.Z. Journal of Agricultural Research 17:* 325–31.

Dougherty, C. T.; Scott, W. R.; Langer, R. H. M.; Meijer, G. 1974: Effects of irrigation and fertiliser on the yields of 'Arawa', 'Aotea', and 'Karamu' wheats. *Ibid. 17:* 241–9.

Dougherty, C. T.; Scott, W. R.; Langer, R. H. M. 1975: Effects of sowing rate, irrigation, and nitrogen on the components of yield of spring-sown semidwarf and standard New Zealand wheats. *Ibid. 18:* 197–207.

Fischer, R. A. 1973: The effect of water stress at various stages of development on yield processes in wheat. Proceedings 1970 UNESCO Symposium, Uppsala. "Plant response to climatic factors". *Ecology and Conservation 5:* 233–41.

Hodge, J. E.; Hofreiter, B. I. 1962: Determination of reducing sugars and carbohydrates. "Methods in Carbohydrate Chemistry 1". pp. 380–94. Whistler, R. L., Wolfrom, M. L., Eds., Academic Press, New York.

Hsiao, T. C. 1973: Plant responses to water stress. *Annual Review of Plant Physiology 24:* 519–70.

Langer, R. H. M.; Hanif, M. 1973: A study of floret development in wheat (*Triticum aestivum* L.) *Annals of Botany 37:* 743–51.

Langer, R. H. M.; Liew, F. K. Y. 1973: Effects of varying nitrogen supply at different stages of the reproductive phase on spikelet and grain production and on grain nitrogen in wheat. *Australian Journal of Agricultural Research 24:* 647–56.

Lupton, F. G. H. 1968: The analysis of grain yield of wheat in terms of photosynthetic ability and efficiency of translocation. *Annals of Applied Biology 61:* 109–19.

Lupton, F. G. H.; Oliver, R. H.; Ruckenbauer, P. 1974: An analysis of the factors determining yields in crosses between semidwarf and taller wheat varieties. *Journal of Agricultural Science 82:* 483–96.

Patrick, J. W. 1972: Distribution of assimilate during stem elongation in wheat. *Australian Journal of Biological Sciences 25:* 455–67.

Pendleton, J. W.; Weibel, R. L. 1965: Shading studies on winter wheat. *Agronomy Journal 57:* 292–3.

Puckridge, D. W. 1968: Competition for light and its effect on leaf and spikelet development of wheat plants. *Australian Journal of Agricultural Research 19:* 191–201.

Scott, W. R.; Dougherty, C. T.; Langer, R. H. M.; Meijer, G. 1973: Wheat yield as affected by sowing rate, irrigation, and time of white clover introduction. *N.Z. Journal of Experimental Agriculture 1:* 369–76.

Syme, J. R. 1970: A high-yielding Mexican semidwarf wheat and the relationship of yield to harvest index and other varietal characteristics. *Australian Journal of Experimental Agriculture and Animal Husbandry 10:* 350–3.

Wardlaw, I. F. 1970: The early stages of grain development in wheat: response to light and temperature in a single variety. *Australian Journal of Biological Sciences 23:* 765–74.

Wardlaw, I. F.; Carr, D. J.; Anderson, M. J. 1965: The relative supply of carbohydrate and nitrogen to wheat grains, and an assessment of the shading and defoliation techniques used for these determinations. *Australian Journal of Agricultural Research 16:* 893–901.

Willey, R. W.; Holliday, R. 1971: Plant population, shading and thinning studies in wheat. *Journal of Agricultural Science, Cambridge 77:* 453–61.

Effects of sowing rate, irrigation, and nitrogen on the components of yield of spring-sown semidwarf and standard New Zealand wheats

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ABSTRACT

'Karamu', a Mexican semidwarf wheat, outyielded 'Aotea' and 'Arawa' by an average of 20% when spring sown because of better grain set per spikelet and by the formation of more spikelets per ear. Irrigation raised grain yields in all cultivars by increasing tiller survival. Sowing at twice conventional rates depressed grain yields in all cultivars by reducing grain set. Nitrogen fertilisation lowered grain yields of all cultivars by 7% in unirrigated plots by decreasing ear populations, apparently by intensifying water stress. Nitrogen applied at the same rate to irrigated plots increased ear populations and grain yields by 10%. Responses support the hypothesis that poor grain set in wheat in the field is caused by insufficient assimilate supply to the developing ear.

INTRODUCTION

Grain yields of wheat grown on moisture-retentive soils such as Wakanui silt loam may frequently be limited by low populations of ear-bearing tillers (Scott *et al.* 1973; Dougherty *et al.* 1974). The dynamics of tiller populations of wheat crops are quite complex and considerable emphasis on the processes involved in tiller survival seems warranted, particularly as mortalities of 40% or more appear normal (Langer 1965; Scott *et al.* 1973; Dougherty & Langer 1974). Although the physiological mechanisms are not fully understood (Jewiss 1972; Langer *et al.* 1973), tiller production does not appear to be limiting in our wheat crops possibly because New Zealand cultivars are relatively freely tillering (McEwan 1959). Overproduction of tillers may, however, limit yields in certain circumstances (Dougherty *et al.* 1974).

Among the components of yield of wheat grain set per spikelet appears to be one of the most sensitive of the agronomic and environmental pressures (Scott *et al.* 1973; Dougherty *et al.* 1974; Dougherty & Langer 1974). Langer & Hanif (1973) have shown that florets which reach a certain size by the time of pollination may develop grains while the remainder degenerate. Carbohydrate supplies to the developing spikelet during the preanthesis period of ear development may regulate the rate of floret growth and thus predetermine grain set (Bingham 1972; Lupton *et al.* 1974).

When ear densities approach 800/m^2 grain yields tend to reach a plateau as more and more lower order and, therefore, lower yielding ears reach harvestable size (Dougherty *et al.* 1974). At higher densities competition between tillers also appears to intensify so that grain set is reduced. The number of grains formed in each spikelet seems to be largely determined by competition for assimilates during preanthesis floret growth (Scott *et al.* 1973; Dougherty *et al.* 1974; Dougherty & Langer 1974).

The objective of the field experiment described here was to create, by agronomic means, internal stresses which were expected to modify grain set and to analyse the effects of these treatments on the components of yield and their regulation. A second paper in this series will report on the effects of these treatments on the levels of soluble carbohydrates in the preanthesis ear and in another we will present more detailed analyses of the growth of mainstem ears.

MATERIALS AND METHODS

Experimental design

A 3 × 3 × 2 × 2 factorial experiment was laid out in two randomised blocks on Wakanui silt loams on the Lincoln College Research Farm.

Previously the site was occupied by an irrigated permanent pasture composed mainly of white clover and perennial ryegrass. The treatments and their levels were as follows:

Cultivars
- C0: 'Arawa'
- C1: 'Aotea'
- C2: 'Karamu'

Irrigation
- W0: Not irrigated
- W1: Early irrigation
- W2: Late irrigation

Sowing rate
- S0: Approximately 250 viable seeds/m²
- S1: Approximately 500 viable seeds/m²

Nitrogen fertilisation
- N0: None
- N1: 200 kg N/ha

Establishment

Initially all plots were sown on 2 and 3 July 1973 and nitrogen applied to N1 plots at 100 kg N/ha on 30–31 August 1973. Population counts on 13 September revealed that fewer than 100 plants/m² had established and that there was much variability. All plots were sprayed with a paraquat–diquat mixture on 13 September to destroy all vegetation. The poor establishment was thought to be attributable to the wet soil conditions brought about by an unusually wet period during August. On 14 September all plots were redrilled and treatments re-established, and on 18 September all plots were re-sprayed with paraquat–diquat to destroy remnants of the first planting before the emergence of the second.

Sowing rate

The plots (30 × 3 m) were sown with a combine drill in 15 cm rows with superphosphate at 300 kg/ha. Sowing rates for each cultivar were adjusted for viability and seed size to give approximately 250 viable seeds/m² at the low sowing rate (S0) and 500 viable seeds/m² for the high rate (S1) (Table 1). The lower rate, approximately 120 kg/ha for 'Arawa' and 'Karamu', is normal for spring-sown wheat in this location (Scott *et al.* 1973). Sowing rates of 'Aotea' were considerably less because of small seed size.

TABLE 1 — Characteristics of seed, rates of sowing and establishment

	Arawa	Aotea	Karamu
Seed weight (mg)	46.3	30.0	46.3
Germination (%)	92.5	93.5	95.0
Sowing rates (kg/ha)			
S0	126	83	123
S1	248	166	246
Viable seeds/m²			
S0	252	259	252
S1	495	517	504
Establishment (%)			
S0	98	70	73
S1	92	56	78

TABLE 2 — Ammonium and nitrate nitrogen (kg/ha) in various soil zones on 18 September 1973

Zone (cm)	N0 NH_4^+-N	N0 NO_3^--N	N1 NH_4^+-N	N1 NO_3^--N
0–10	3.2	2.4	65.7	76.4
10–20	3.1	4.3	18.5	56.0
20–40	2.3	7.5	12.5	39.6
40–60	2.4	17.4	4.8	29.6
60–90	4.4	42.5	7.3	42.4
Total	15.3	74.1	108.7	244.0

Cultivars

Descriptions of the three cultivars used have been published (McEwan 1959; McEwan *et al.* 1972). 'Arawa' was selected because of its tall growth habit and its lower tillering characteristic. 'Aotea' was included primarily because of its ability to tiller. 'Karamu', a semidwarf wheat, has the potential to produce more grain per spikelet (Dougherty *et al.* 1974) and is recommended as a suitable spring wheat for this area (Smith 1974).

TABLE 3 — Ammonium and nitrate nitrogen (kg/ha) in various soil zones of unfertilised treatments (N0) on 27 September 1973

Zone (cm)	NH_4^+-N	NO_3^--N	Total
0–10	3.3	7.9	11.1
10–20	4.6	12.6	17.2
20–40	4.5	27.2	31.8
40–60	4.7	28.4	33.1
60–90	14.3	34.5	48.8
Total	31.4	110.5	142.0

TABLE 4 — Mean dates of reproductive stages of development of 'Karamu', 'Arawa' and 'Aotea'

	Stages of development: Double ridge	Ear emergence	Anthesis
'Karamu'	16 Oct	24 Nov	3 Dec
'Arawa'	23 Oct	3 Dec	10 Dec
'Aotea'	29 Oct	6 Dec	13 Dec

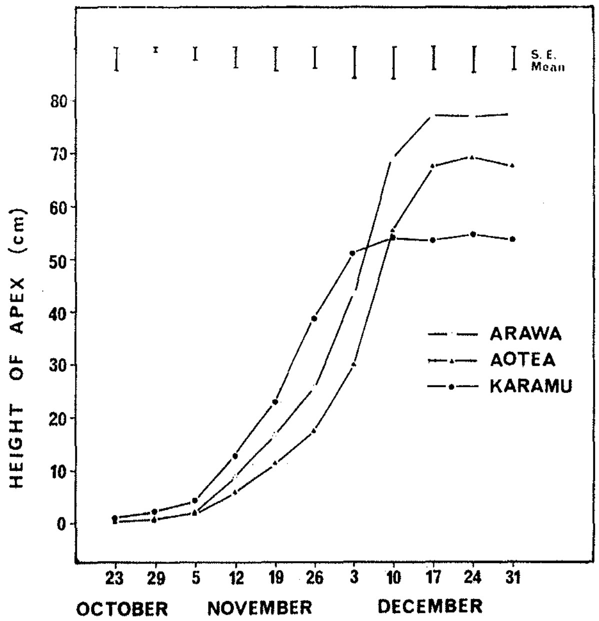

Fig. 1 — Mean height of mainstem spices of 'Arawa', 'Aotea', and 'Karamu' above roots.

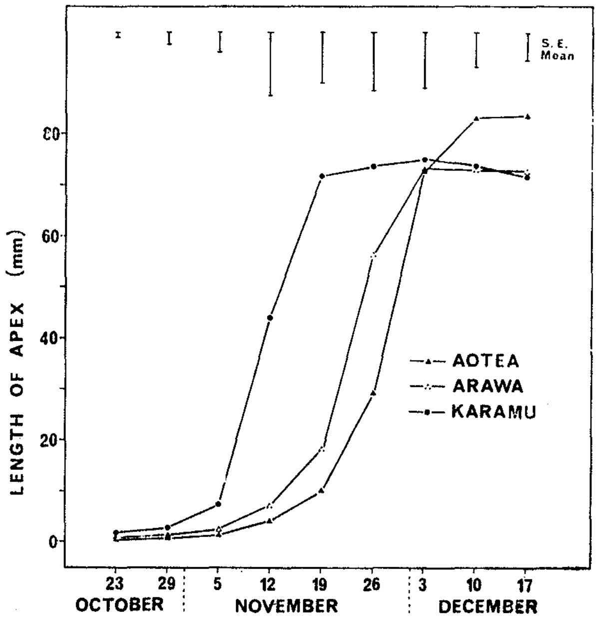

Fig. 2 — Mean lengths of 'Arawa', 'Aotea', and 'Karamu' spikes.

Irrigation

Irrigated plots were reticulated with a microtube trickle system and the irrigation schedule based on tensiometer measurements of soil water potential at 30 cm depth. Soil water levels in irrigated plots were maintained above −0.5 bars for the duration of the irrigation treatments. Control plots (W0) were not irrigated except for 3 mm applied on 25 October to carry insecticide into the root zone. The early irrigation treatment began on 20 November when 'Karamu' plots were at late boot (Feekes 10), 'Arawa' with the flag leaf fully emerged (Feekes 9), and 'Aotea' with the flag leaf emerging (Feekes 8+). The late irrigation (W2) began on 3 December for 'Karamu' (at anthesis; Feekes 10.5) and 'Arawa' (ears emerging; Feekes 10.1), and for 'Aotea' plots on 12 December when ears were emerging (Feekes 10.1). All irrigation treatments (W1 and W2) ended on 18 December.

Nitrogen fertilisation

Nitrogen as nitrolime (26:0:0) was broadcast at 100 kg N/ha on 30 and 31 August on all N1 plots. Rain (27 mm) fell in the next 24 h and considerable leaching may have resulted because of high soil water content after the 149 mm total precipitation of August. Soil samples were taken on 18 and 27 September and analysed by T. E. Ludecke, Department of Soil Science, Lincoln College, for ammonium and nitrate nitrogen (Tables 2, 3). On 30 October nitrolime was applied at 100 kg N/ha to all plots receiving the N1 treatments.

Pest and weed control

Phorate granules were applied at the rate of 225 g a.i./ha on 24 October 1973 followed by 3 mm of spray irrigation the next day to promote root uptake for the control of Argentine stem weevil (*Hyperodes bonariensis* Kusch.). On 30 October all plots were sprayed with benomyl (280 g a.i./ha) to reduce the incidence of powdery mildew (*Erysiphe graminis* D.C.) and with MCPA (630 g a.i./ha) and dicamba (105 g a.i./ha) to control weeds. On 5 December demeton-S-methyl (250 g a.i./ha) was applied by air to control cereal aphid (*Rhopalosiphum padi* L.).

Analyses of yield

At maturity 10 separate 1000 cm^2 quadrats per plot were selected at random and cut to ground level and pooled for determination of straw yield and components of grain yield. Barren and fertile spikelets were counted on a random subsample of 20 ears per quadrat. Grain from the quadrats was threshed and cleaned mechanically before weighing. Mean grain weight was established by counting and weighing a subsample of 400 grains. Straw was weighed after drying to a constant weight at 75°c. Grain and straw yields were expressed at 14% moisture content.

Reproductive development

At weekly intervals from 23 October main shoots were sampled from all plots. Until the double ridge stage was reached the apical meristems were dissected and their lengths measured. After this stage, the growth in length of the

TABLE 5 — Plant densities (10 October 1973) number of ears/plant and/m^2 at harvest

	Plant density	Ears/plant	Ears/m^2
Cultivar			
C0	354	1.51	488
C1	237	2.64	588
C2	290	2.05	530
LSD (5%)	26	0.19	37
Irrigation			
W0	299	1.71	453
W1	291	2.34	588
W2	290	2.15	565
LSD (5%)	26	0.19	37
Sowing rate			
S0	208	2.54	505
S1	379	1.59	566
LSD (5%)	21	0.15	31
Nitrogen			
N0	295	1.97	515
N1	291	2.16	556
LSD (5%)	21	0.15	31
Significant interactions	C × S**	C × W** W × N*	C × W* W × N**

developing ear was recorded weekly; concurrently the length of the mainstem from the base of the ear primordia to its insertion above the uppermost root was measured. The dates of ear emergence and anthesis were based on estimates of 50% of mainstems reaching these stages of development.

RESULTS

Cultivar

The stage of development of mainstems of all three cultivars was modified slightly by treatments, but only the mean dates of well defined events are presented in Table 4. Development was delayed by irrigation, particularly where nitrogen fertiliser was also applied. Growth in height of mainstems and length of spike for the three cultivars are presented in Figs 1 and 2.

TABLE 6 — Establishment (plants/m^2) of cultivars (C) at different sowing rates (S) (LSD (5%):33)

	S0	S1
C0	256	453
C1	181	292
C2	186	393

TABLE 7 — Interaction between nitrogen (N) and irrigation (W) treatments for ear numbers/plant (LSD (5%) = 0.26)

	W0	W1	W2
N0	1.76	2.12	2.03
N1	1.66	2.55	2.27

TABLE 8 — Effect of irrigation (W) on the mean number of ears/plant for cultivars (C) (LSD (5%): 0.33)

	W0	W1	W2
C0	1.17	1.59	1.76
C1	2.26	3.28	2.38
C2	1.71	2.14	2.30

Mean grain yields of 'Karamu' plots (C2) were approximately 20% higher and mean straw yields about 30% lower than in the taller cultivars, with the result that the harvest indices of the semidwarf plots were much higher (Table 11). 'Karamu' plant populations were not affected by the irrigation treatments and averaged about 290/m^2 (Table 5). Irrigation treatments (W1 and W2), however, generally increased ear populations including those of 'Karamu' by more than 25% (Table 9). 'Karamu' ears contained more spikelets (Table 14), but because of a slightly greater incidence of barrenness, they had on average about one more fertile spikelet than 'Aotea' and about 0.6 more than 'Arawa' (Table 18). 'Karamu' plots had about the same number of spikelets/m^2 as 'Aotea' and over 1000/m^2 more than 'Arawa' (Table 18). 'Karamu' generally averaged 23 grains per ear, 3 to 4 more than 'Aotea' and 'Arawa', most of this being attributable to better grain set per spikelet in the semidwarf wheat and to its greater mean number of spikelets per ear (Table 14). 'Karamu' grains weighed on average, 4 mg more than 'Aotea' and 4.6 mg less than 'Arawa'.

'Aotea' and 'Arawa' were not significantly different in grain yields, straw yields, or harvest index (Table 11), but on 10 October 'Arawa' plots averaged over 100 more plants per square metre (Table 6). Low ear numbers of 'Arawa' partially compensated for the higher density, so

TABLE 9 — Interaction between cultivar (C) and irrigation (W) treatments for ears/m^2 (LSD (5%): 65)

	W0	W1	W2
C0	408	512	545
C1	511	684	568
C2	439	569	582

TABLE 10 — Interaction between irrigation (W) and nitrogen (N) treatments for ears/m^2 (LSD (5%): 53)

	N0	N1
W0	466	439
W1	536	641
W2	542	587

TABLE 11 — Grain, straw, and total yields (g/m²) at harvest and harvest index (%)

	Grain	Straw	Total	Harvest index %
Cultivar				
C0	423	733	1156	37.2
C1	399	697	1111	36.6
C2	490	494	968	49.2
LSD (5%)	27	62	71	2.1
Irrigation				
W0	396	549	943	42.4
W1	474	735	1226	39.7
W2	428	640	1066	40.9
LSD (5%)	27	62	71	2.1
Sowing rate				
S0	451	639	1093	42.3
S1	414	644	1064	39.7
LSD (5%)	22	52	58	1.7
Nitrogen				
N0	435	587	1024	43.0
N1	431	696	1133	39.0
LSD (5%)	22	52	58	1.7
Significant interactions	W × N*	W × N*	C × W** C × S* W × N**	none

that at harvest the 'Arawa' plots averaged 488 ears, about 100/m² more than 'Aotea' (Table 5). Grain yields per ear of 'Arawa' were generally higher than 'Aotea' and this could be at least partially attributable to the presence of higher proportions of mainstem ears. The difference in ear yields between 'Arawa' and 'Aotea' was not closely related to the number of spikelets per ear or per square metre (Tables 18, 20). Similarly, wheat from 'Arawa' plots averaged only slightly more grains per ear and grains per spikelet than 'Aotea'. Thus the main difference between these two cultivars was the 25% greater mean grain weight of 'Arawa' (Table 14).

Irrigation and nitrogen

The distribution of ammonium and nitrate nitrogen in the soil profile for unfertilised (N0) and fertilised (N1) treatments shows that the nitrogen status of the soils was considerably changed by the application of fertiliser on 30–31 August (Table 2). The quantities of ammonium and nitrate in soils of unfertilised plots had increased from 42.5 to 93.2 kg/ha, presumably because of mineralisation (Table 3).

Nitrogen fertiliser depressed grain yield by 10% in unirrigated wheat (W0), gave a 7% increase with early irrigation, and had no effect with late irrigation (Table 12). Grain yields were raised some 10% by early irrigation of unfertilised (N0) and by 30% in fertilised wheat (N1). Nitrogen fertiliser had no effect on yield of wheat on the late irrigation schedule (Table 12). There was also no significant nitrogen effect on straw yields in unirrigated wheat, but the early irrigation treatment (W1) increased straw yields by 19% in wheat not receiving nitrogen and by 48% in those plots treated with 200 kg/ha (Table 13). The late irrigation treatment increased grain and straw yields significantly only in nitrogen-fertilised wheat (Tables 12, 13). Irrigation increased tiller survival so that ear populations were greater at harvest (Table 5). Assuming no plant mortality, the early irrigation (W1) raised the mean number of ears per plant of 'Arawa', 'Aotea', and 'Karamu' by 36%, 45%, and 25%, respectively, above W0 plants (Table 8). Thus the early irrigation (W1) had its greatest effect on ear survival on the latest developing wheat, 'Aotea', and its least effect on the earliest wheat, 'Karamu'. The late irrigation (W2) also increased the number of ears of 'Arawa' and 'Karamu', but in 'Aotea', the latest

TABLE 12 — Interaction between irrigation (W) and nitrogen (N) treatments for grain yields (g/m²) (LSD (5%) : 14)

	W0	W1	W2
N0	418	458	428
N1	374	491	428

TABLE 13 — Interaction between irrigation (W) and nitrogen (N) for straw yields (g/m²) (LSD) (5%): 88)

	W0	W1	W2
N0	532	632	597
N1	567	838	684

TABLE 14 — Components of ear yield

	Wt. grain/ear (g)	No. grains/ear	No. spikelets/ear	No. grains/spikelet	Mean grain wt. (mg)
Cultivar					
C0	0.89	19.9	13.7	1.46	44.4
C1	0.69	19.3	13.4	1.44	35.9
C2	0.91	23.1	14.5	1.58	39.8
LSD (5%)	0.05	1.2	0.3	0.08	0.7
Irrigation					
W0	0.88	21.7	14.0	1.54	41.0
W1	0.83	21.1	13.8	1.52	39.4
W2	0.77	19.4	13.8	1.41	39.7
LSD (5%)	0.05	1.2	0.3	0.08	0.7
Sowing rate					
S0	0.91	22.7	14.1	1.61	40.2
S1	0.74	18.8	13.7	1.37	39.9
LSD (5%)	0.04	0.9	0.2	0.06	0.6
Nitrogen					
N0	0.86	20.9	13.7	1.53	41.3
N1	0.79	20.6	14.1	1.46	38.8
LSD (5%)	0.04	0.9	0.2	0.06	0.6
Significant interactions	S × N*	None	S × N*	None	C × W**

developing wheat, it only resulted in a 5% increase above plants from W0 plots. These changes were reflected in the numbers of ears per square metre at harvest (Table 9).

The early irrigation treatments (W1) decreased grain yield per ear by 4% in unfertilised wheat (N0) and by 8% in wheat fertilised with nitrogen (N1). This treatment (W1) had little effect on the mean number of fertile spikelets per ear or on the mean number of grains per spikelet (Tables 14, 18). Thus the decrease in ear yield is mainly attributable to smaller mean grain weights (Tables 14, 17). The late irrigation (W2) resulted in substantially lower grain yields per ear, 14% in unfertilised wheat (N0) and 15% in wheat treated with 100 kg N/ha. The late irrigation reduced grain set per spikelet by 10% and also resulted in slightly reduced grain size. Overall the early irrigation (W1) increased grain yields by ensuring that more tillers produced harvestable ears. The late irrigation was delayed sufficiently to reduce both grain set and tiller

TABLE 15 — Influence of sowing rate (S) and nitrogen (N) on grain yield/ear (g) of wheat (LSD (5%) : 0.05)

	S0	S1
N0	0.96	0.76
N1	0.86	0.73

TABLE 16 — Interaction between fertiliser (N) and sowing rate (S) treatments for mean number of spikelets/ear (LSD (5%) : 0.3)

	S0	S1
N0	14.0	13.4
N1	14.2	14.0

TABLE 17 — Interaction between cultivar (C) and irrigation treatments (W) for mean grain weight (mg) (LSD (5%) : 1.2)

	W0	W1	W2
C0 'Arawa'	45.7	43.8	43.7
C1 'Aotea'	37.6	35.2	34.9
C2 'Karamu'	39.7	39.3	40.3

TABLE 18 — Mean number of barren and fertile spikelets/ear and the mean number of spikelets/m²

	Fertile spikelets/ ear	Barren spikelets/ ear	spikelets/m²
Cultivar			
C0	12.13	1.54	6649
C1	11.69	1.73	7888
C2	12.69	1.86	7708
LSD (5%)	0.40	0.22	523
Irrigation			
W0	12.24	1.80	6348
W1	12.23	1.53	8100
W2	12.04	1.80	7797
LSD (5%)	0.40	0.22	523
Sowing rate			
S0	12.44	1.65	7088
S1	11.90	1.77	7741
LSD (5%)	0.32	0.18	426
Nitrogen			
N0	12.00	1.70	7035
N1	12.34	1.72	7794
LSD (5%)	0.32	0.18	426
Significant interactions	none	C × N*	C × W* W × N**

TABLE 19 — Interaction between cultivar (C) and nitrogen (N) treatments for mean number of barren spikelets/ear (LSD (5%) : 0.31)

	C0 'Arawa'	C1 'Aotea'	C2 'Karamu'
N0	1.48	1.61	2.01
N1	1.60	1.85	1.70

TABLE 20 — Interaction between cultivar (C) and irrigation (W) treatments for mean number of spikelets/m² (LSD (5%) : 905)

	W0	W1	W2
C0 'Arawa'	5594	6914	7439
C1 'Aotea'	6960	9164	7539
C2 'Karamu	6489	8221	8414

survival. Data on mean numbers of all spikelets/m² (Tables 18, 20, 21) largely reflect changes in ear populations (Tables 5, 9, 10).

Sowing rate

The low sowing rate (S0) gave an establishment of 208 plants/m² and the high sowing rate 379 plants/m² by 10 October 1973 (Table 5). 'Arawa' populations were much higher on that date than those of the other two cultivars because of superior establishment (Table 6). About 70% of the viable seeds of 'Aotea' produced living plants when sown at the lower rate, but only 56% were successful at the higher seeding rate (Table 1). The poor establishment of 'Aotea' at the higher seeding rate may, perhaps, reflect low vigour of the seed, possibly related to its small mean weight (Table 1). About 73% of viable seeds in S0 plots and 78% in S1 plots produced living 'Karamu' plants by 10 October (Table 1).

Grain yields were depressed significantly (8%) by the high sowing rate treatment (S1) (Table 11). Although higher plant density ensured nearly 60 more ears per square metre at harvest (Table 5), it had no effect on mean straw or total above-ground dry matter yields, but slightly reduced mean harvest indices (Table 11).

Grain yields per ear averaged 0.91 g at the low sowing rate (S0) and 0.74 g at the higher rate (S1) (Table 14). However, the depression attributable to high sowing rate was 30% in wheat which did not receive nitrogen fertiliser (N0), and 15% in nitrogen-fertilised wheat (N1). The high sowing rate (S1) resulted in a highly significant reduction in the mean number of spikelets per ear in ears of wheat when fertiliser was not applied (Table 16).

Grain numbers per spikelet calculated for the low sowing rate plots (S0) averaged 1.61 compared with 1.37 for S1 plots. Thus the reduction in grain yield per ear caused by high sowing rate is largely accounted for by the 15% decrease in grain set. Ears from low sowing rate treatments (S0) averaged, as a result, 22.7 grains per ear but only 18.8 from high sowing rate (S1) plots (Table 14). Sowing rates had no significant effect on mean grain weight.

Relationships between components of yield

Simple linear correlations between grain yield and its components for all data revealed that mean grain weight accounted for the smallest amount of the variation in grain yield and the other three components had similar and higher correlation coefficients (Table 22). When fitted against grain yield by stepwise linear regression spikelets/ear, ears/m², grains/spikelets, and mean grain weight were ranked in this decreasing order.

DISCUSSION

'Karamu' outyielded the New Zealand cultivars (Table 11) primarily because it had more spikelets per ear and more grains per spikelet (Table 14). Clements *et al.* (1974) also concluded that 'Karamu's' superiority was largely due to higher mean ear yields. The basis for the advantages of semidwarf wheats are not well defined. Fisher (1973) and Holmes (1973) suggested that it lies in delayed development of double ridges in the apical meristem. Lupton *et al.* (1974) put forward the idea that the ears of semidwarf wheats develop earlier and faster than those of standard cultivars. These authors also concluded that the size and rate of development of the ear and ear primordia are among the

TABLE 21 — Interaction between irrigation (W) and nitrogen (N) treatments for mean number of spikelets/m² (LSD (5%) : 739)

	W0	W1	W2
N0	6436	7267	7402
N1	6259	8933	8192

TABLE 22 — Simple correlation matrix for $\log_e$ transformation of components of yield

Component	1	2	3	4
1. Ears/m²	1.00			
2. Spikelets/ear	− 0.10	1.00		
3. Grain/ spikelet	− 0.50	+ 0.27	1.00	
4. Grain weight	− 0.49	+ 0.07	+ 0.10	1.00
5. Grain yield	+ 0.40	+0.44	+ 0.41	+ 0.10

most important characters to be considered in breeding for yield in wheat.

'Karamu' ears had more spikelets than 'Aotea' or 'Arawa' ears when sown in spring, but all three cultivars had more and similar numbers of spikelets per ear when sown in winter (Dougherty *et al.* 1974). When planted in the winter 'Karamu's' advantage in spikelets per ear was considerably reduced. The vernalisation and photoperiodic responses of these wheats probably accounts for the differences (Rawson 1971).

During the period of rapid ear growth the main competing sinks are the elongating stem internodes (Patrick 1972). Bingham (1972) observed that lower growth rate of the stem of a dwarf wheat was not apparent until a week before anthesis, and he surmised that floret growth rates and grain set were likely to be affected by assimilate supply about 2 weeks before anthesis. Lupton *et al.* (1974) noted that the later stages of preanthesis ear development were critical in yield determination. Thus the yield advantage of semidwarf wheats may arise from a more favourable distribution of assimilate in the direction of the developing ear.

Another advantage of 'Karamu' may lie in its early conversion to a reproductive state (Table 4) and, consequently, reduced tiller production, since this process ceases or slows to a low rate at or about internode elongation (Langer *et al.* 1973). 'Karamu' produced fewer tillers per plant and had lower rates of tiller mortality as a consequence. Thorne & Blacklock (1971) also noted that tiller survival of semidwarf wheats was superior to that of standard British wheats, and Bingham (1972) attributes the high-yielding ability of new British wheats to restricted tillering capacity and improved tiller survival. In contrast, Clements *et al.* (1974) noted that 'Karamu' had similar tillering patterns to other cultivars and that there was no evidence that semidwarf wheats could support higher tiller populations. It is our current view, based on earlier work (Scott *et al.* 1973), that tillers which do not survive to produce a harvestable ear reduce grain set in the remaining ears, probably because of decreased supply of assimilate to the pre-anthesis ear. These responses of 'Karamu', in comparison with those of 'Arawa' and 'Aotea', reinforce our view that a major limitation of New Zealand wheats is their restricted ability to form grains from the eight or so florets available in each spikelet (Dougherty & Langer 1974).

Both irrigation treatments (W1 and W2) increased grain yields by ensuring that more tillers produced a harvestable ear (Table 9). Differences in ear population at harvest normally account for most of the variation in wheat yields in Canterbury (Scott *et al.* 1973; Drewitt *et al.* 1973; Dougherty *et al.* 1974). Water stress, or irrigation (W1), had more impact on the latest developing 'Aotea', probably because of its longer duration of tillering, for, as Langer *et al.* (1973) note, tillering virtually ceases about the time of internode elongation.

Tiller mortality was high in the period between 20 November and 3 December, especially in plots which received nitrogen fertiliser (Table 10). Although rainfall records show water stress intensified after the critical phase of 2 weeks before anthesis (Fischer 1973), it seems probable that grain set is less sensitive to water stress than tiller survival. Lower order tillers are more likely to succumb to water stress, as their root systems are usually less well developed. Later developing cultivars should have proportionately more lower order tillers and, consequently, may be more susceptible to water stress. Thorne & Blacklock (1971) also observed that semidwarf wheats have better tiller survival and are also generally earlier maturing.

Water potentials of ears and leaves of the wheat were measured during December and related to various environmental parameters in a separate study (Martin & Dougherty 1975). Water potentials of wheat ears from irrigated plots were frequently below -10 bars. In 'Arawa' wheat from both irrigated and unirrigated plots, water potentials of leaves were frequently less than -20 bars during typical December days. Values for leaves and ears were similar at sunrise, but as the day progressed they declined at a slower rate in ears so that they were as much as 10 bars higher than flag leaves during much of the day. It is difficult to translate water potential data into a quantitative measure of plant water stress, but it appears likely that these values do not represent stress with respect to tiller mortality. Fischer (1973) used similar methods and found that vegetative structures such as leaves were more sensitive to water stress than reproductive processes such as grain set. This reaction of wheat is also reflected in the greater response of straw yield to irrigation (Tables 12, 13). The developing ear of wheat may be protected from water stress by its physical properties and by a mechanism known as osmoregulation (Hsiao 1973).

Although early irrigation (W1) increased ears/m^2 at harvest, it did not have much effect on the other components of yield (Table 14). Normally spikelet initiation occurs at a time when water stress is unlikely in Canterbury and when competition for assimilates is less intense than during later stages of ear development (Patrick 1972). Grain set per spikelet, however, may be modified by the water relations of a crop (Fischer 1973; Dougherty *et al.* 1974; Dougherty & Langer 1974), but in this instance (W1) grain set was not affected (Table 14). Grain set is determined over a relatively long period of the life cycle, approximately from the double ridge stage until after anthesis, a period of about 48 days in this example. Fischer (1973) noted that grain set was particularly sensitive to water stress 5 to 15 days before ear emergence when the ear, anthers, and carpels are elongating rapidly. Water stress at this stage causes abnormal anthers and considerable male sterility in wheat florets. Thus the most sensitive stage of wheat florets to water stress may coincide with their critical stage for assimilate supply.

Grain set per spikelet was poorer in wheat irrigated late (W2) than in the wheat from control plots (W0) and ear yields were lower as a consequence (Table 14). In another situation involving the same three wheats we attributed an irrigation-induced depression in grain set to the diversion of assimilates away from the ear (Dougherty *et al.* 1974). Fischer (1973) also suggested that the effects of irrigation on grain set may operate through assimilate supplies and distribution.

The yield responses to irrigation under nitrogen fertilisation were approximately 24% for wheat on the early schedule (W1) and 14% on the late schedule (W2) (Table 12). Irrigation of autumn-sown wheat on Wakanui silt loam has, however, given variable responses from depressions (Dougherty *et al.* 1974) to increases (Scott *et al.* 1973). Irrigation responses, however, tend to increase as planting of wheat is delayed on Lismore stony silt loam from late May to late July (Drewitt 1974). Wilson (1974) noted that wheat on Templeton silt loam was more responsive to irrigation when sown in the spring than autumn.

Grain yields of wheat grown at the high seeding rate (S1) were depressed by 8% primarily because grain set was reduced by 15%, and this was not wholly compensated by higher ear populations (Tables 5, 11). In a similar experiment in a higher yielding situation, we found that poor grain set in wheat at high sowing rates was associated with high leaf area indices and low net assimilation rates during preanthesis floret development (Scott *et al.* 1973). Fischer (1973) noted that grain set in wheat was depressed by shading between 22 days before and 5 days after ear emergence. He also concluded that carbohydrate supply to the developing florets was critical. Wardlaw (1970) also found that shading for 10 days after anthesis reduced grain set.

Clements *et al.* (1974) raised the sowing rate of spring wheat from 77 to 284 kg/ha and found that the increase in ear populations was partially offset by a reduction in the number of grains per ear. They also noted that at conventional sowing rates more than 95% of the total grain yield was produced by the mainstem and two earliest tillers. Thus it would seem likely that the reduction in mean number of grains per spikelet observed at the higher sowing rate was an indication of reduced grain set and not related to changes in the structure of the ear population (Bremner 1969).

Nitrogen fertiliser depressed grain yields in unirrigated wheat by decreasing the mean ear populations at harvest (Table 10). Generally this effect has been attributed to the intensification of water stress by the accelerated use of soil water by wheat crops in which evapotranspiration rates are increased. This response, known as "haying off", has already been observed in nitrogen-fertilised wheats on Wakanui silt loam (Dougherty 1973). Nitrogen fertiliser increased yields of wheat on the early irrigation schedule primarily by increasing ear populations at harvest (Table 10).

Nitrogen fertiliser also increased grain yields per ear, particularly in wheat growing at the lower sowing rate (Table 15). The origin of this response appears to be partially attributable to the nitrogen–sowing rate interaction for mean number of spikelets per ear (Table 16). Langer & Liew (1973) found that spikelet numbers depended on nitrogen status between the double ridge stage and floret initiation. Thus the reduction in mean numbers of spikelets per ear observed in wheat grown at the higher population density (S1), in the absence of nitrogen fertiliser, may indicate that spikelet numbers were limited by nitrogen nutrition (Table 16).

Nitrogen fertiliser also reduced grain set per spikelet and mean grain weight (Table 14). In a previous experiment with 'Kopara' wheat we attributed poor grain set associated with nitrogen fertilisation to decreased supply of assimilate to the developing ears (Dougherty & Langer 1974). Thus, the response may have been, perhaps as in the 'Kopara' experiment, a consequence of nitrogen-induced competition for assimilates between vegetative and reproductive organs, for nitrogen fertiliser increased straw yields by 32% and grain yield by only 9% in wheat subjected to the early irrigation treatment (Tables 12, 13). Langer & Liew (1973) noted that better nitrogen nutrition increased grain set in 'Arawa', and

Langer & Hanif (1973) found that the rate of floret development in 'Hilgendorf' was accelerated under improved nitrogen nutrition.

In this experiment, however, nitrogen fertilisation at high sowing rates increased spikelet numbers and decreased grain set. Our results may be explained by a declining availability of nitrogen during the time of floret growth so that growth rates of florets fell and fewer reached the critical size for pollination. Rapid changes in the availability of plant-available soil nitrogen are likely in the soils of the Canterbury plains under wheat (Ludecke 1974).

It is also possible that nitrogen fertilisation depressed overall mean numbers of grains per spikelet (Bremner 1969) by increasing the proportion of lower order tillers which have generally poorer grain set. Thus the production in grain set in the ear caused by nitrogen fertiliser could have been attributable to changes in the structure of the tiller population and to the reduced availability of metabolites in the ear.

According to Ludecke (1974), yield responses of autumn-sown wheat to nitrogen fertiliser may be correlated to soil nitrate nitrogen levels in the 0–60 cm depth. When this relationship is used in association with the levels of nitrate nitrogen in this zone on 27 September 1974 (Table 3) a yield response of 7.7% would be predicted for recommended rates of nitrogen fertilisation. Nitrogen fertilisation depressed yields by 11% in unirrigated plots, increased them by 7% in wheat irrigated early, and had no effect at all on wheat on the late schedule (Table 12). Thus Ludecke's relationship appears to hold for this spring wheat situation providing water was not limiting. From the results of this experiment and others concerned with the nitrogen fertiliser–soil water interaction (Dougherty 1973; Dougherty *et al.* 1974; Dougherty & Langer 1974) it seems likely that the yield response relationship developed by Ludecke (1974) will be highly dependent on soil water status and, therefore, soil type, season, and irrigation practice.

CONCLUSIONS

1. 'Karamu' appears to have an advantage over 'Aotea' and 'Arawa' when spring-sown in that it produces more spikelets per ear and sets more grain per spikelet. These advantages are less marked in winter-sown 'Karamu'.
2. Wheat yields in Canterbury are not often limited by sowing rates but are quite dependent on tiller survival. Ear populations of spring-sown wheats cannot be established and maintained at densities which are high enough to produce yields as high as wheat sown in winter. Restricted tiller production and increased tiller survival would appear, on the basis of our work, desirable traits for new cultivars.
3. The responses to irrigation confirm our previous results that its major effect is on tiller survival and indicate that spring-sown crops are generally more responsive to irrigation and more susceptible to water stress.
4. On Wakanui silt loam responses of wheat to nitrogen fertiliser depend on the level of plant-available soil nitrogen and soil water. There was no evidence that the responses of spring wheat differed from those of wheat planted in the winter or that the nitrogen–water interactions were different.

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REFERENCES

Bingham, J. 1972: *Proceedings of the Sixth Congress of Eucarpia, Cambridge 1971:* 15–29.

Bremner, P. M. 1969: *Journal of Agricultural Science 72:* 281–7.

Clements, R. J.; Cross, R. J.; Sanders, P. 1974: *N.Z. Journal of Experimental Agriculture 2:* 139–44.

Dougherty, C. T. 1973: *N.Z. Journal of Agricultural Research 16:* 12–8.

Dougherty, C. T.; Langer, R. H. M. 1974: *Ibid. 17:* 325–31.

Dougherty, C. T.; Scott, W. R.; Langer, R. H .M.; Meijer, G. 1974: *Ibid. 17:* 241–9.

Drewitt, E. G.; Rickard, D. S. 1973: *Proceedings of the Agronomy Society of New Zealand 3:* 73–80.

Drewitt, E. G. 1974: *Ibid. 4:* In press.

Fischer, R. A. 1973: "Plant response to climatic factors". Proceedings Uppsala Symposium, 1970. *Ecology and conservation. 5:* 233–41.

Fisher, J .E. 1973: *Canadian Journal of Plant Science 53:* 7–15.

Holmes, D. P. 1973: *Canadian Journal of Botany 51:* 941–56.

Hsiao, T. C. 1973: *Annual Review of Plant Physiology 24:* 519–70.

Jewiss, O. R. 1972: *Journal of British Grasslands Society 27:* 65–82.

Langer, R. H. M. 1965: *N.Z. Journal of Agricultural Research 8:* 10–4.

Langer, R. H. M.; Hanif, M. 1973: *Annals of Botany 37:* 743–51.

Langer, R. H. M.; Liew, F. K. Y. 1973: *Australian Journal of Agricultural Research 24:* 647–56.

Langer, R. H. M.; Prasad, P. C.; Laude, H. M. 1973: *Annals of Botany 37:* 565–71.

Ludecke, T. E. 1974: *Proceedings of Agronomy Society of N.Z. 4:* In press.

Lupton, F. G. H.; Oliver, R. H.; Ruckenbauer, P. 1974: *Journal of Agricultural Science 82:* 483–96.

Martin, R. J.; Dougherty, C. T. 1975: *N.Z. Journal of Agricultural Research 18:* In press.

McEwan, J. M. 1959: The wheat varieties of New Zealand. *N.Z. Department of Scientific and Industrial Research Bulletin 131.*

McEwan, J. M.; Vizer, K .J.; Douglas, J. M. 1972: *N.Z. Journal of Agriculture 125:* 50–1.

Patrick, J. W. 1972: *Australian Journal of Biological Sciences 25:* 455–67.

Rawson, H. M. 1971: *Australian Journal of Agricultural Research 22:* 537–46.

Scott, W. R.; Dougherty, C. T.; Langer, R. H. M.; Meijer, G. 1973: *N.Z. Journal of Experimental Agriculture 1:* 369–76.

Smith, H. C. 1974: *N.Z. Journal of Agriculture 128:* 50–5.

Syme, J. R. 1974: *Australian Journal of Agricultural Research 25:* 1–7.

Thorne, G. N.; Blacklock, J. C. 1971: *Annals of Applied Biology 78:* 93–111.

Wardlaw, I. F. 1970: *Australian Journal of Biological Sciences 23:* 765–74.

Wilson, D. R. 1974: *Proceedings of Agronomy Society of New Zealand 4:* 34–7.