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Differences in grain growth, crop photosynthesis and distribution of assimilates between a semi-dwarf and a standard cultivar of winter wheat

J. H. J. Spiertz* and H. van de Haar

Department of Field Crops and Grassland Husbandry,
Agricultural University, Wageningen, the Netherlands

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Summary

The crop performance of a semi-dwarf cultivar (Maris Hobbit) was compared with a standard-height cultivar (Lely), at various levels of nitrogen supply. The grain yields of Maris Hobbit were considerably higher due to a higher number of grains and a heavier grain weight. Owing to the higher grain yield and a lower stem weight, the harvest index of Maris Hobbit was higher than that of Lely: 0.47 and 0.40, respectively. The content of water-soluble carbohydrates in the stems of both cultivars appeared to be very high until 3 weeks after anthesis, despite the occurrence of low light intensities. Lely used more assimilates for structural stem material than did Maris Hobbit.

Quantity and time of nitrogen application greatly affected grain number, but affected grain weight to a lesser extent. Thus within each cultivar grain number per m^2 was the main determinant of grain yield. Late nitrogen dressings promoted photosynthetic production, grain weight and protein content of the grains. The low protein percentages of the grains were attributed to the low temperatures during grain-filling period. The distribution of nitrogen within the wheat plant was only slightly influenced by nitrogen dressings and cultivar differences. Nitrogen harvest index ranged from 0.74 to 0.79. Grain nitrogen was derived from the vegetative organs (63-94%) and from uptake after anthesis (6-37%). The importance of carbohydrate and nitrogen economy for grain yield are discussed.

* Present address: Centre for Agrobiological Research (CABO), P. O. Box 14, 6700 AA Wageningen, the Netherlands.

Introduction

Variations in grain yield between cultivars are often attributed to differences in disease resistance. However, under disease-free conditions grain yields between cultivars have also been found to vary (Spiertz, 1973). The harvest index of cereal cultivars has tended to rise progressively, with little change in biological yield (Van Dobben, 1962; Fischer, 1975; Kramer, 1978).

Based on theoretical considerations, Donald (1968) has outlined a wheat ideotype that should be most efficient in grain production. The main features of his ideotype are: single culm, strong stem, dwarf stature and large spike. Such a plant should be a poor competitor in a crop stand. It should also provide an improved harvest index. Austin & Jones (1976) contended that there is no single ideal model plant or ideotype for wheat. They gave a list of desirable attributes, but concluded that many of these attributes are mutually exclusive. In fact the response of the wheat plant to various growing conditions (drought, nitrogen stress, etc) is still imperfectly understood.

To study the magnitude of cultivar differences in crop response to prevailing weather conditions and to a varying nitrogen supply, observations were made on the cultivars Lely and Maris Hobbit. The former is a Dutch standard cultivar for fertile soils; which has shown a high-yielding capacity under favourable growing conditions (Spiertz & Ellen, 1978); the latter was chosen because of its attributes of superior grain set and dry matter distribution (Anonymous, 1977). Maris Hobbit is one of the semi-dwarf winter wheat cultivars that are well adapted to growing conditions in the Netherlands.

The aim of the experiment was to study cultivar differences in grain yield and grain growth pattern at various levels of nitrogen supply.

Materials and methods

The experiment was carried out in 1977 on the experimental farm of the Department of Field Crops and Grassland Husbandry, Agricultural University, Wageningen. The experiment was laid down on a fine-textured clay soil. The nitrate-nitrogen content of the top 1 m of the soil layer was found to be approximately 50 kg N per ha at the end of February 1977. The preceding crop was potatoes.

The wheat was sown on 15 October 1976 at a rate of 350 kernels per m^2 and a row distance of 0.25 m. The basic fertilizer dressing consisted of 500 kg N-P-K mixture (0-15-30) per ha on 15 March.

Nitrogen was applied as a split-dressing in the following treatments:

	March (F_3)*	*May (F_8 to F_9*)*	*Total*
N_1	50	0	50 kg N ha^{-1}
N_2	0	50	50 kg N ha^{-1}
N_{1+2}	50	50	100 kg N ha^{-1}

* According to developmental stages of the Feekes scale.

Control plots without nitrogen dressing were only present with the cultivar Lely.

The fungicide applications were sequential according to the following scheme:
11 May: 4 kg Bavistin M + 5 kg sulphur per ha
6 June: 4 kg Bavistin M + 5 kg sulphur per ha
24 June: 5 kg sulphur per ha
30 June: 0.5 kg Bayleton per ha

The complete experimental field was protected against insect damage by an application of 0.5 kg Pyrimor and 0.5 kg Dimethoaat per ha on 24 June and 6 July, respectively.

The experiment consisted of a split-split-plot design with cultivars and fungicide treatment in the splits. Nitrogen treatments were completely randomized and there were 6 replicates. The individual plots were 9 m long and 3 m wide. During the growing season the plots protected against diseases were sampled. The samples were taken from 2 rows of 0.50 m length. At the final harvest, 24 August, the complete plots, except for two border rows, were harvested.

The sampling procedure at the intermediate harvests and the chemical analyses were carried out as described by Spiertz & Ellen (1978).

Crop photosynthesis was measured from anthesis onwards by enclosing an area of 1 m^2 in a perspex chamber about 1.20 m high. CO_2 content was maintained at about 320 mg/kg during daytime; during the dark much higher values occurred. Air temperature was generally kept at 20 °C, but under high radiation conditions cooling capacity was insufficient and this resulted in the temperature rising to a maximum of 25 °C. CO_2 exchange rate was measured with an URAS infrared gas analyser by sampling ingoing and outgoing air. To prevent gas exchange at soil level the chamber was kept constantly at an overflow pressure, which varied between 0.5 and 2.0 cm H_2O. Solar radiation, air temperature and CO_2 content of air were monitored on recorders and cassette tape. These data were processed by a computer; calculations of net photosynthesis were based on at least four sampling runs.

Growing conditions

Weather

The growing season was characterized by a mild winter followed by exceptionally high temperatures during the first half of March (Fig. 1). During the tillering phase weather was unfavourable: cold, wet and overcast sky. Poor light conditions also occurred during flowering and after mid-kernel filling. High radiation and temperature occurred during the last 10 days of May and the first week of July. Much rain fell during ripening and grain harvest.

Diseases

Although yellow rust was prevalent in wheat crops in the Netherlands in the 1977 growing season, the cultivars in our experiment were only slightly infected.

Early mildew infections were controlled with fungicides. At the end of the kernel-filling period there was a late infection of brown rust *(Puccinia recondita)*.

Fungicide applications caused the leaf tips of Maris Hobbit to turn yellow.

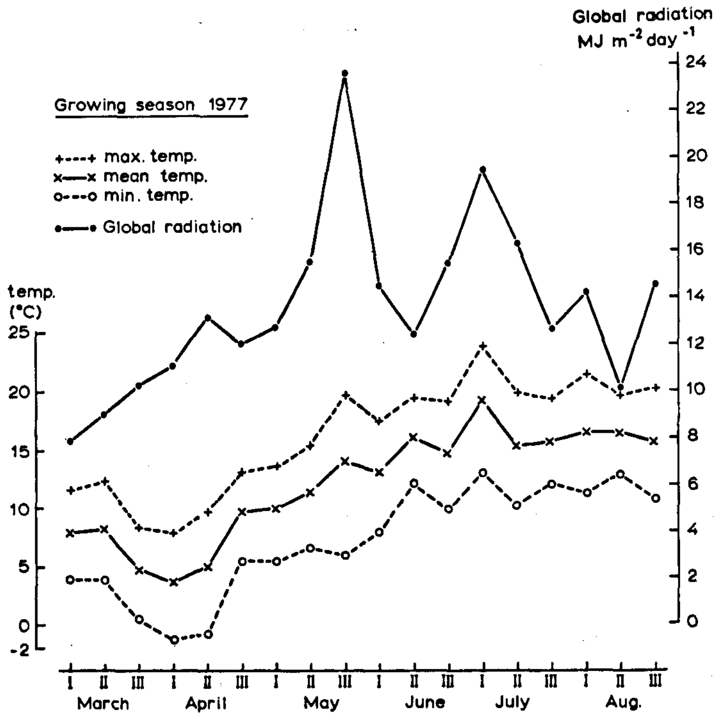


Fig. 1. Average values per decade of solar radiation and air temperature during the 1977 growing season.

Results

Grain yield and yield components

Grain yields of Maris Hobbit were considerably higher than those of Lely, although the above-ground biological yields showed hardly any difference at the highest nitrogen dressing (Table 1). Thus Maris Hobbit had a more favourable dry matter distribution than Lely as shown by the harvest index: 0.47 and 0.40, respectively. The higher grain yield of Maris Hobbit was caused by a higher grain number per ear and per m^2 as well as by a considerably larger grain weight. Estimates of the maximum level of grain yield are derived from the harvest of 10 August, because subsequently losses occurred due to pre-harvest sprouting. At the highest nitrogen dressing, 50 + 50 kg N ha^{-1}, Maris Hobbit and Lely yielded 813 and 635 g grain m^{-2}, respectively. The corresponding numbers of grains per m^2 were 16 400 and 14 900, whilst the grain weight ranged from 50.8 to 46.0 mg $kernel^{-1}$.

The cultivars responded similarly to the various nitrogen dressings. A single late nitrogen dressing of 50 kg N ha^{-1} decreased grain number considerably more than an early dressing. This reduction was partly compensated for by an increased grain weight. A late nitrogen dressing, reduced straw yield more than grain yield, resulting in a higher harvest index. The combination of an early plus a late nitrogen gift increased grain number as well as grain weight. Thus grain yield was consider-

Table 1. Yield and yield components of the cultivars Lely and Maris Hobbit with various nitrogen treatments.

Parameter[1]		Lely				Maris Hobbit			Mean		c.v.	Fisher-test[2,3]		
		0	50+0	0+50	50+50	50+0	0+50	50+50	Lely	Hobbit	(%)	C	N	C×N
Grain yield	a (g m^{-2})	458	581	557	657	681	577	759	599	674	9.5	**	***	**
Grain yield	b (g m^{-2})	398	546	603	678	729	697	813	609	746	9.6	***	****	n.s.
Total dry weight	b (g m^{-2})	1018	1454	1464	1682	1620	1468	1683	1533	1590	9.4	n.s.	***	n.s.
Harvest-index	b (%)	39.1	37.6	41.2	40.3	45.0	47.5	48.3	39.7	46.9	3.2	****	****	n.s.
Grain weight	b (mg kernel^{-1})	41.7	43.1	46.2	46.0	48.9	53.5	50.8	45.1	51.1	3.5	****	****	n.s.
Grains per ear	c (n)	29.1	32.3	28.1	34.8	33.6	31.0	35.5	31.7	33.4	6.9	**	***	n.s.
Number of ears	d (per m^2)	361	410	425	429	438	427	462	421	442	9.2	*	n.s.	n.s.
Number of kernels	e (per m^2) × 10^3	10.5	13.2	11.9	14.9	14.7	13.2	16.4	13.4	14.8	—	—	—	—

[1] a = combine harvest at 24 August; b = intermediate harvest at 10 August; c = average of 5 sampling dates; d = average of 7 sampling dates; e = c × d.
[2] C = cultivar; N = nitrogen (without Lely-0).
[3] n.s. = $P \geq 0.10$; *$0.10 > P \geq 0.05$; ** $0.05 > P \geq 0.01$; *** $0.041 > P \geq 0.001$; **** $P > 0.001$.

Table 2. Yield and distribution of nitrogen after anthesis in the cultivars Lely and Maris Hobbit with various nitrogen dressings

Parameter	Lely				Maris Hobbit			Mean		c.v.	Fisher-test[2,3]		
	0	50+0	0+50	50+50	50+0	0+50	50+50	Lely	Hobbit	(%)	C	N	C×N
% N of grain	1.46	1.42	1.72	1.73	1.31	1.52	1.52	1.62	1.44	5.9	***	****	n.s.
mg N per grain (× 10^{-3})	609	612	795	796	641	813	772	731	736	—	—	—	—
nitrogen yield grains (g m^{-2})	5.8	7.8	10.4	11.7	9.3	10.6	12.4	10.0	10.7	13.1	n.s.	****	n.s.
nitrogen yield crop (g m^{-2})	7.6	10.6	13.1	15.7	12.4	13.4	16.1	13.1	14.0	—	—	—	—
nitrogen harvestindex %	77.3	73.8	79.2	74.5	74.3	78.8	76.9	75.8	76.7	2.5	***	****	n.s.
Nitrogen loss after anthesis (g m^{-2})													
- leaves	2.2	3.7	3.0	4.8	3.9	3.3	5.5	3.8	4.2	—	—	—	—
- stem (and sheath)	1.3	2.2	2.4	3.8	2.1	2.8	3.1	2.8	2.7	—	—	—	—
- chaff	0.8	1.1	1.2	1.2	1.4	1.2	1.4	1.2	1.3	—	—	—	—
- total	4.2	7.0	6.6	9.8	7.3	7.2	10.0	7.8	8.2	—	—	—	—
Contribution to grain nitrogen (%)	73	94	63	78	87	71	82	77	80	—	—	—	—
Nitrogen uptake after anthesis													
- g m^{-2}	1.6	0.4	3.9	2.9	1.1	2.9	2.3	2.4	2.1	—	—	—	—
- % of grain nitrogen	27	6	37	22	13	29	18	23	20	—	—	—	—

[2], [3] See Table 1.

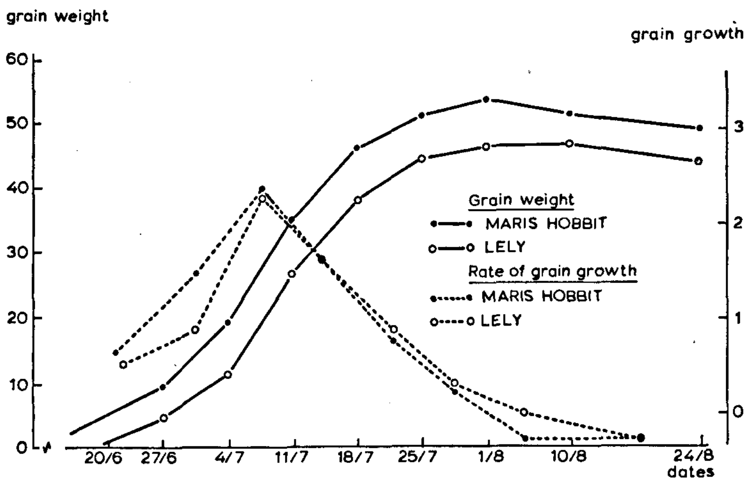


Fig. 2. Course of grain weight (10^{-3} g) and rate of grain growth (10^{-3} g day^{-1}) per kernel in the cultivars Lely and Maris Hobbit at a nitrogen dressing of 50 + 50 N ha^{-1}.

ably increased by the additional nitrogen dressing. This marked response to nitrogen was quite unexpected in the growing season of 1977. Nitrogen mineralization during the growing season was obviously below normal.

Fungicide application increased grain yield by 420 kg ha^{-1} in Lely, but had a slightly negative effect on the grain yield of Maris Hobbit. Harvest index and individual grain weight were not affected. These small effects of the frequent fungicide treatments show that diseases were unimportant in this experiment.

Rate and duration of grain growth

Grain growth started about four days earlier in Maris Hobbit than in Lely: 13 and 17 June, respectively. Both cultivars had a grain growth pattern characterized by a slow initial growth rate followed by a two-week period of 'linear' growth and a simultaneous decline until maximum kernel weight was reached (Fig. 2).

The lower grain weight of Lely was mainly caused by a slower rate of grain growth during the first half of the grain-filling period. Both cultivars showed the highest rate of grain growth in the period from 4 to 11 July, when a rate of about 2.25 mg day^{-1} kernel^{-1} was reached. From the point of maximum grain weight until final harvest on 24 August, Maris Hobbit lost 9.7% and Lely 6.4% of the grain weight. These losses must have been caused by respiration.

The effective grain-filling period lasted 42 and 48 days in Maris Hobbit and Lely, respectively. Late nitrogen dressings barely affected the duration of grain growth, but delayed a decline in the rate of grain growth after the mid-kernel filling stage. Grain growth per m^2 depended more on number of grains than on grain weight. The small differences in the course of grain growth per m^2 between an early and a late nitrogen dressing of 50 kg N ha^{-1} were striking (Fig. 3). Mutual compensation occurred between grain number and grain weight. During the effective grain-filling period the level of nitrogen supply caused mean grain growth rates to vary from

14.7 to 18.4 g m^{-2} day^{-1} and from 17.9 to 21.0 g m^{-2} day^{-1} with Lely and Maris Hobbit, respectively. Actual growth rates during the lineair phase were considerably higher: from 22.8 to 30.7 and from 28.6 to 32.1 g m^{-2} day^{-1} with Lely and Maris Hobbit, respectively. The unfertilized treatment had much lower growth rates: 11.8 and 17.1 g m^{-2} day^{-1} during the effective and linear phase of grain-filling, respectively.

Leaf area, solar radiation and crop photosynthesis

Generally, tillering and leaf growth were favoured in 1977 by a mild winter and a warm spell during the first half of March. An early nitrogen dressing increased the leaf area considerably (Fig. 4). Maximum leaf area index had already been attained at the boot stage. A late nitrogen dressing delayed the decline of the leaf area during the post-floral period. Leaf-area index and duration were slightly higher for Maris Hobbit. But average stem length was about 15 cm longer in Lely than in Maris Hobbit.

Photosynthetic production of the crop depends on the activity of the green tissues and the amount of photosynthetic active radiation. Radiation was low for a fortnight after anthesis and at the end of the grain-filling period. During the period of linear grain growth there was a spell of bright sunshine.

From anthesis onwards crop photosynthesis and dark respiration were measured weekly in the 50 and 50 + 50 kg N ha^{-1} plots of Maris Hobbit. Due to bad weather conditions and technical restrictions, most of the measurements in the Lely plots had to be cancelled. The available data on Lely showed only minor deviations from the net photosynthesis of Maris Hobbit. This finding is confirmed by the total dry matter yields of the two cultivars.

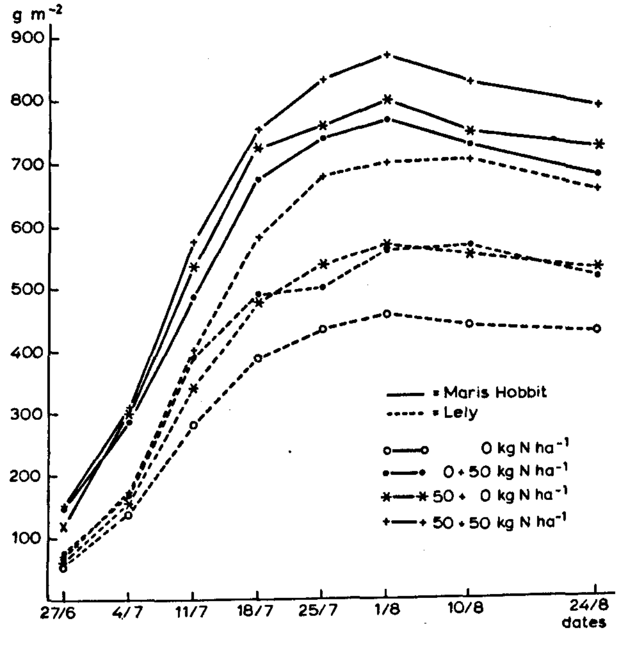


Fig. 3. Course of the grain growth calculated from grain weight, average grain number and average number of ears of the cultivars Lely and Maris Hobbit at various nitrogen dressings.

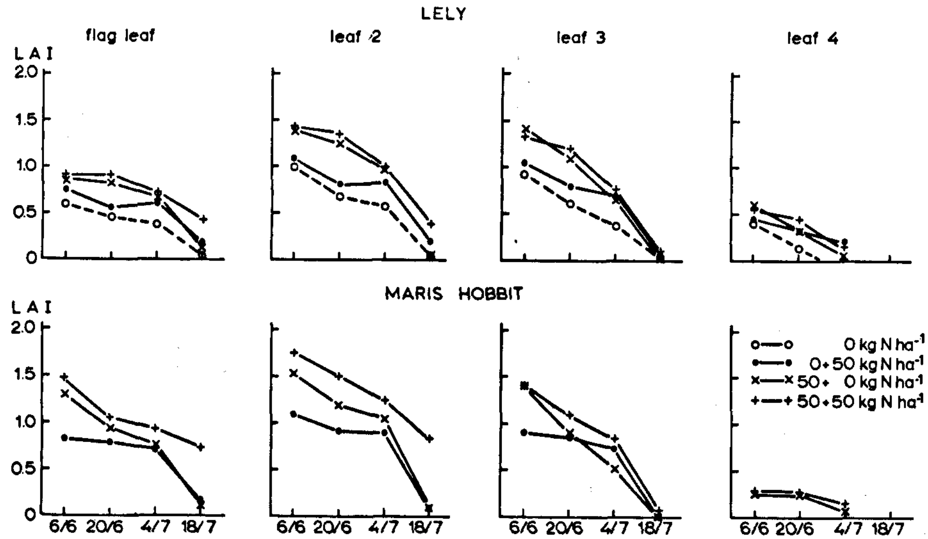


Fig. 4. Leaf area index (LAI) of the individual leaf layers of the cultivars Lely and Maris Hobbit at various nitrogen dressings.

Nitrogen had a very positive effect on crop photosynthesis. An additional 50 kg N ha^{-1} at the booting stage slightly increased P_{max} at anthesis, but had a considerable effect on net photosynthesis from 3 weeks after anthesis onwards (Fig. 6A and B).

Estimates were derived for the daily course of net photosynthesis from the photo-

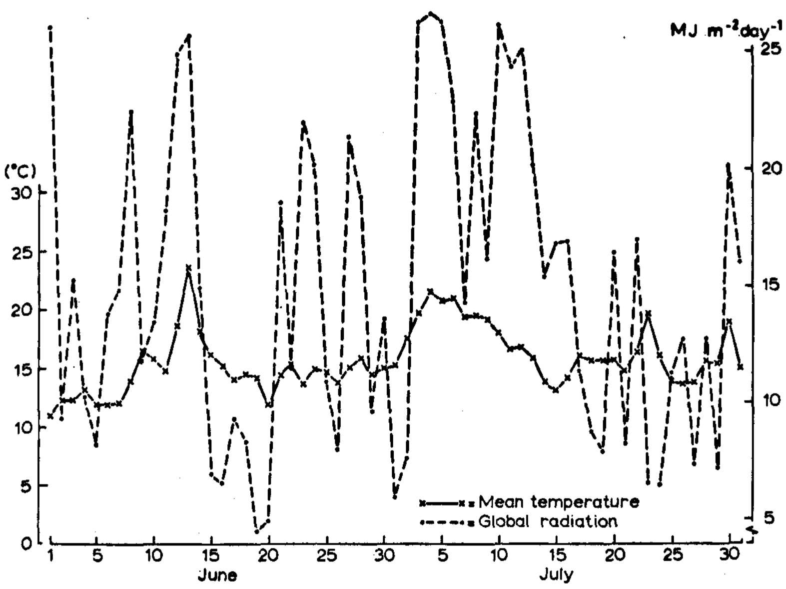


Fig. 5. Daily values of solar radiation and mean air temperature during the grain-filling period.

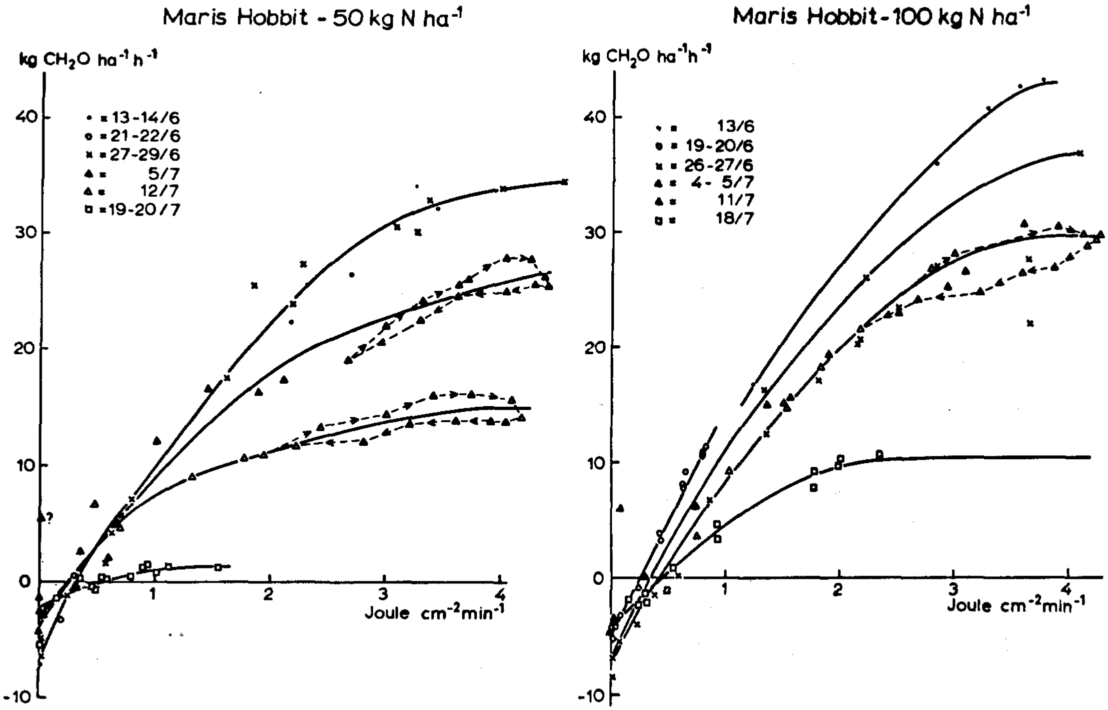


Fig. 6. Photosynthesis-light response curves for the Maris Hobbit crop. A (left): nitrogen dressing of 50 kg N ha^{-1}; B (right): nitrogen dressing of 50 + 50 N ha^{-1}.

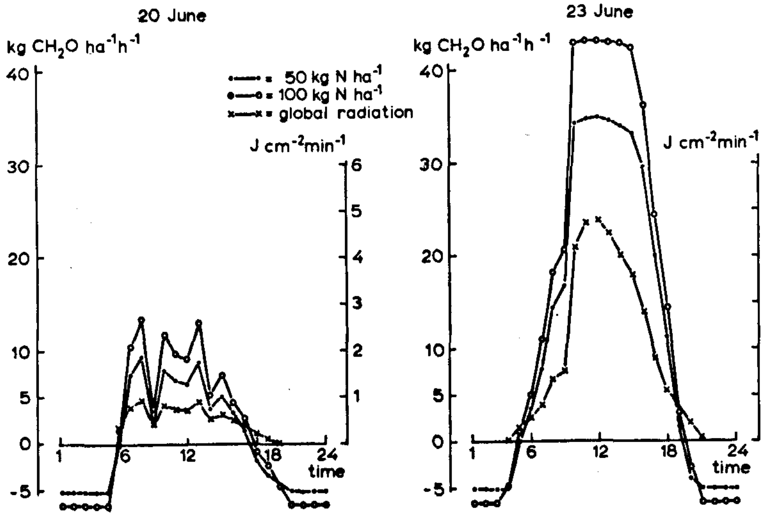
synthesis-light curves and the diurnal course of radiation. The data presented in Fig. 7A, B and C are examples of the daily variation in the course of net photosynthesis. These data also clearly show that the magnitude of the positive effect of additional nitrogen on net photosynthesis depend on light intensity. Under low light conditions the effect of additional nitrogen seemed to be small. The net photosynthesis curves of 23 June and 12 July also show that light saturation occurred during the midday period. On 12 July the maximum photosynthetic rate had already dropped from about 42 to 30 kg CH_2O ha^{-1} h^{-1}, whilst the light saturation period was longer than on 28 June.

The daily amounts of net photosynthesis are the main source of assimilates for the grains. Therefore the estimates of daily net photosynthesis were compared to the growth rate of the grains (Fig. 8). It appeared that during the first weeks after anthesis there was a surplus of assimilates, whilst at the end of the kernel filling there was a deficit.

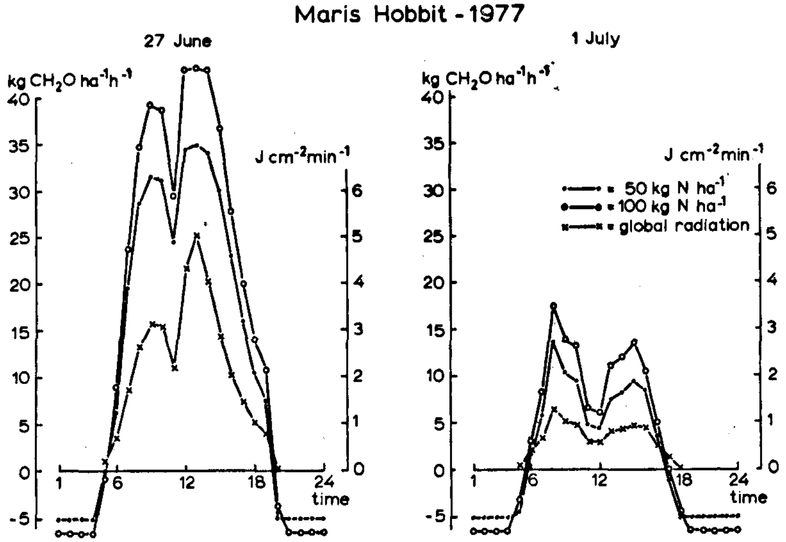
Carbohydrate reserves and distribution of dry matter

The balance of production of assimilates and utilization by the grains is reflected in the accumulation of reserves, mainly carbohydrates, in the stem. The content of carbohydrate reserves in the stem proved to be quite high, 30-40%, from ear emer-

Maris Hobbit - 1977



Maris Hobbit - 1977



Maris Hobbit - 1977

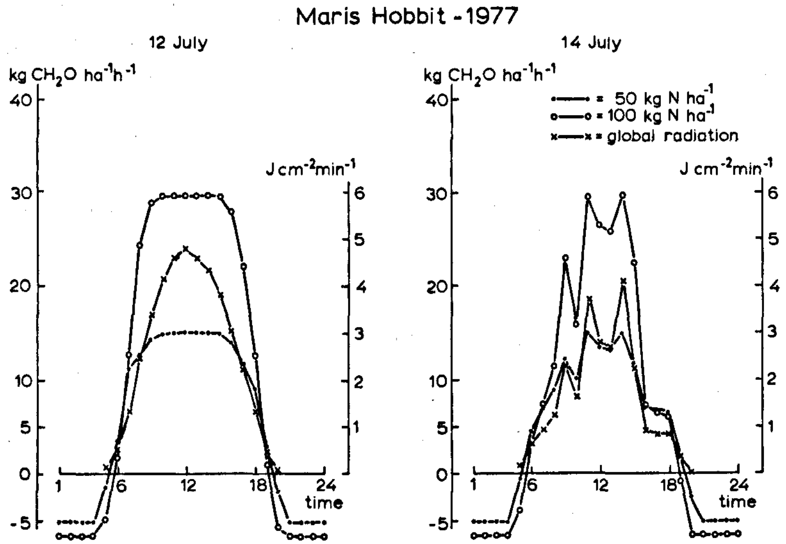


Fig. 7. Daily pattern of solar radiation and net photosynthesis at two nitrogen levels. A (top) 20 and 23 June 1977; B (middle) 27 June and 1 July 1977; C (bottom) 12 and 14 July 1977.

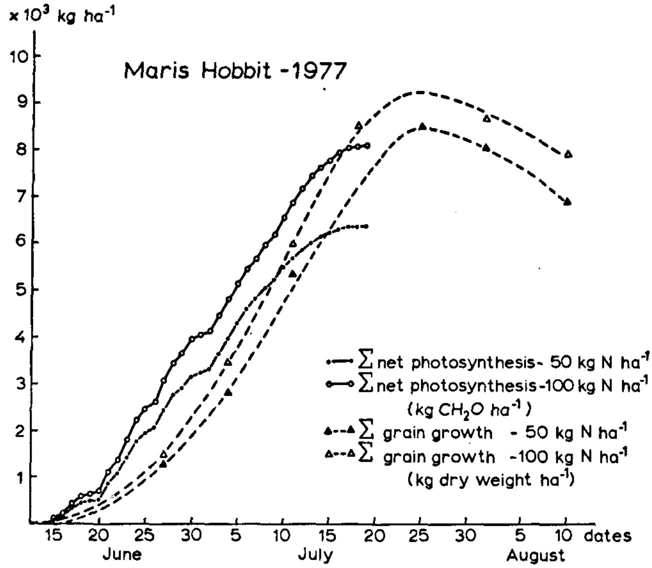


Fig. 8. Cumulative amount of net photosynthesis after anthesis and actual grain growth of the cultivar Maris Hobbit at 50 + 50 kg N ha^{-1}.

gence until 3 weeks after anthesis (Fig. 9). On average, the water-soluble carbohydrates (w.s.c.) reached a higher content in the stem of Maris Hobbit than of Lely, especially during the period of poor light conditions after anthesis. A late nitrogen dressing raised the w.s.c. content of the stem in Lely during the first weeks of grain-filling. Thus carbohydrate supply cannot have limited grain growth until 3 weeks after flowering. The sharp decline in the w.s.c. content of the stem coincides with the beginning of the linear phase of grain growth and with a drop in the photosynthetic rate of the crop.

The w.s.c. content in the top leaves varied around the 5 % level, with lower values during the period of bad weather one week after anthesis, and the highest values about 3 or 4 weeks after anthesis (Fig. 9). Generally, w.s.c. contents turned out to be somewhat lower with late nitrogen applications.

Kernels and chaff were only analysed for w.s.c. at the 50 + 50 nitrogen level. The small differences between the cultivars were striking; although the grain growth of Maris Hobbit started earlier, w.s.c. contents of the grains of Lely were only higher in first 3 weeks. On average, the w.s.c. content of the grains decreased from about 45 % to 7.5 % during the second to fourth week of grain-filling and levelled off to about 5 % during the following weeks. The w.s.c. content of the chaff decreased during the grain-filling period from about 10 % to 2 %.

In contrast to the small differences in w.s.c. contents between the cultivars, clear

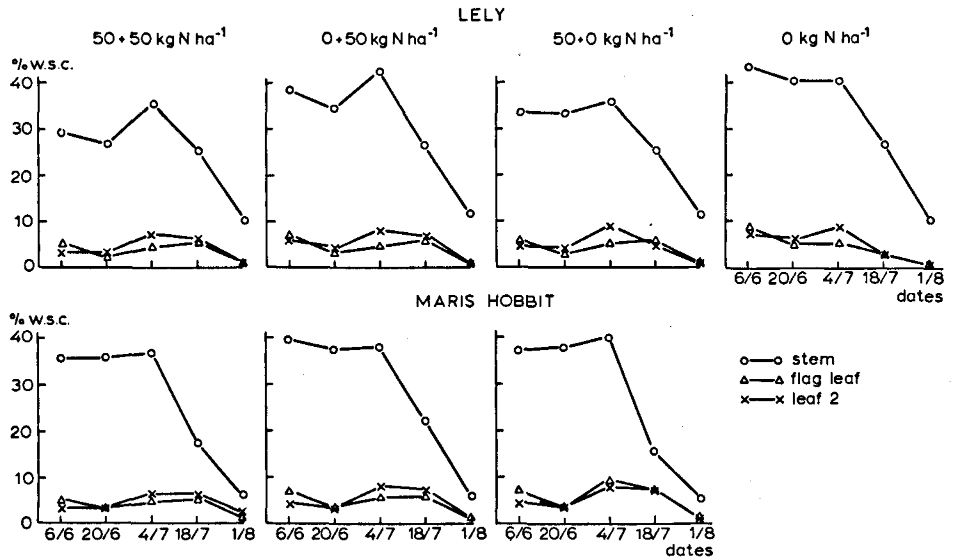


Fig. 9. Water-soluble carbohydrate content (%) in the stem of the cultivars Lely and Maris Hobbit at various nitrogen dressings.

differences in dry weight distribution existed after ear emergence. The most important contrast was the increase in stem weight in Lely, from ear emergence 4 weeks onwards, compared with a practically constant stem weight in Maris Hobbit (Fig. 10). Conversely, the ear weight of Maris Hobbit increased faster during this period than

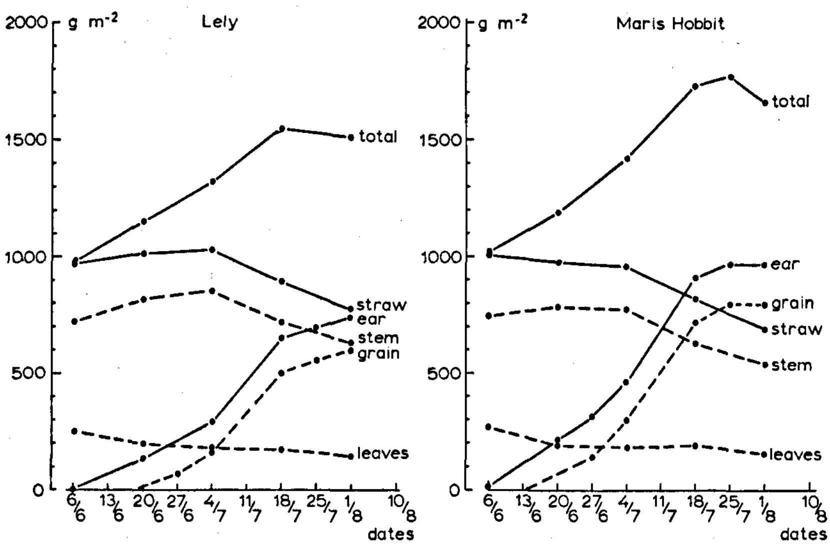


Fig. 10. Dry weight distribution after anthesis in the above-ground part of the cultivars Lely and Maris Hobbit, averaged for the nitrogen treatments.

that of Lely. This indicates competition between stem and ear growth in Lely for several weeks after emergence. However, this competition for assimilates was not reflected in the w.s.c. content.

Another consequence of the longer stem of Lely was that more assimilates were needed for the structural material of the stem. Consequently, stem weight stayed higher in Lely than in Maris Hobbit during grain growth. The dry matter weights of the leaves and the chaff were slightly higher for Maris Hobbit than for Lely (Fig. 10). It was also shown that Maris Hobbit had a higher biological yield than Lely at the end of July, but part of this difference disappeared owing to a greater loss of dry weight in grains and straw due to bad weather conditions during ripening.

Nitrogen uptake and distribution

The pattern of nitrogen uptake was characterized by

- a high nitrogen content at the first sampling date, 12 April; the amount of nitrogen in the shoots in Lely and Maris Hobbit ranged from 42 to 62 kg ha^{-1} and from 57 to 70 kg ha^{-1}, respectively;
- a very low nitrogen uptake in the plots without N dressing during May and June; obviously, nitrogen mineralization in the soil was very low during this period;
- the nitrogen dressing at the boot stage favoured nitrogen uptake by the grains.

Compared with the dry matter yields, the nitrogen yields of the aerial parts were low; the nitrogen yield of the wheat crop in Lely and Maris Hobbit varied from 106 to 157 kg ha^{-1} and from 124 to 161 kg ha^{-1}, respectively. The control plots of Lely yielded only 76 kg N ha^{-1} (Table 2). Although Maris Hobbit had a slightly higher nitrogen harvest index (76.7% compared to 75.8%) nitrogen content in the grains was extremely low. The lowest value corresponded with a protein content of 7.5% and the highest with 8.8%. The nitrogen content of the grains of Lely were considerably higher: from 8.2% to 10% protein. Nevertheless these values are still below the long-term average level.

Nitrogen supply to the grains could be accounted for partly by nitrogen loss from the vegetative organs (leaves, stem, chaff) and partly by uptake after anthesis. The relative contribution by the two sources depended greatly on the timing and amount of nitrogen dressing (Table 2). On average, 80% of the nitrogen amount in the grains was contributed by the nitrogen reserves of the vegetative parts and 20% was nitrogen uptake after anthesis.

The residual amounts of nitrogen in the vegetative parts did not vary significantly; nitrogen residues in the leaves, stem and chaff ranged from 5 - 10, from 10 - 20 and from 4- 6 kg N ha^{-1}, respectively.

Discussion

Grain yield response to nitrogen was very positive in this experiment, contrary to many other field experiments in the growing season of 1977 which showed a lack of positive response at higher nitrogen levels. This lack of positive response could be due to an abnormally high level of soil nitrogen after the dry season of 1976, to the occurrence of diseases, and to low levels of solar radiation during the tillering, flowering and ripening phases in 1977. The high nitrogen response in this experiment was the consequence of an unexpectedly poor nitrogen mineralization. This might have been caused by the irrigation of the previous potato crop, which lowered the amount of residual soil nitrogen and damaged the structure of the fine-textures heavy clay soil. On the other hand the minor influence of diseases in this field experiment also promoted crop response to nitrogen. Probably the nitrogen dressing of 50 + 50 kg N ha^{-1} was nearly sufficient to allow both cultivar to achieve their full potential grain production. The low nitrogen dressings, 50 kg N ha^{-1} and the control plot without fertilization would have occasionally suffered from nitrogen stress. This enabled us to compare Lely and Maris Hobbit under conditions of sub-optimal nitrogen supply.

Grain yield differed considerably between Lely and Maris Hobbit with all nitrogen dressings. The higher grain yield of Hobbit, on average about 135 g m^{-2}, was caused by a greater number of grains per m^2 and a heavier individual grain weight. The increase in both components may have a similar cause, namely, a distribution of assimilates so that more goes to the developing ear and less to the stem. Obviously the balance between stem growth and ear growth is regulated by plant hormones. In some high-yielding cultivars it has been found that the improved ear/stem ratio is already evident by the time the first node of the stem is visible when the ear weighs less than 0.01 g (Lupton et al., 1974). Makunga et al. (1978) found that the ear of Maris Hobbit incorporated more ^{14}C supplied to the flag leaf before anthesis than other cultivars. This favoured ear formation was reflected in the dry matter distribution (Fig. 10) and also in a higher number of kernels per ear in our experiment. The upper leaves of Maris Hobbit had a larger leaf area and a greater dry weight than those of Lely. By contrast, the lower leaves of Maris Hobbit were smaller and weighed less. Differences in leaf and chaff weight were of minor importance; the lower straw yield of Maris Hobbit was mainly caused by a reduced stem weight. This pattern of dry matter distribution contributed largely to the increased harvest index of Maris Hobbit. Thorne et al. (1969) found higher harvest indices and grain yield/leaf area durations ratios for semi-dwarf compared to standard-height cultivars. The latter parameter suggests an improvement in the efficiency of photosynthesis by the crop in the use of assimilates for grain filling. Light response curves and maximum level of net photosynthesis of the 50 + 50 kg N treatment resembled the data presented by de Vos (1977) for the first weeks after anthesis. Contrary to his finding, we found that nitrogen had a considerable effect on the level of maximum rate of net photosynthesis and on the decline in photosynthesis from 3 weeks after anthesis onwards. These effects of nitrogen supply on the rate of photosynthesis were mainly but not exclusively associated with differences in leaf area index. Dark respiration was also increased by additional nitrogen; this may have been mainly caused by more rapid grain growth per m^2. De Vos (1977) also found no differences in crop photosynthesis between two winter wheat cultivars approximately 15 days after flowering.

In our experiment the number of measurements of photosynthesis and respiration in the Lely crop were too small to justify reliable conclusions to be drawn on differences between cultivars. However, large differences in the use of photosynthetic assimilates were inferred from the growth pattern of the ear and the stem after emergence. A higher stem weight in Lely was not caused by a higher water-soluble carbohydrate content. Thus assimilates were used to a greater extent for structural stem material. Both cultivars showed very high levels of w.s.c. reserves in the stem up to 3 weeks after anthesis. The explanation for these high w.s.c. contents, up to 40% under relatively poor light conditions, might be that grain growth and respiration were more restricted by the prevailing daily temperatures (about 14 °C) than was photosynthesis.

The predominant effect of temperature on grain growth and w.s.c. content in the stem has also been established in phytotron experiments (Spiertz, 1977). In the present experiment there was no evidence of a difference between the cultivars in the utilization of the stem reserves for subsequent grain growth. This finding is confirmed by the results obtained by Rawson & Evans (1971).

Differences in the growth of the individual grains due to nitrogen treatments occurred mainly during the second half of the kernel-filling period. Obviously assimilate supply was not limiting in the early phases of grain growth. Nitrogen effects on grain weight were of minor importance for grain yield, compared with the effects on number of grains to be filled. An additional nitrogen application at the booting stage increased number of grains as well as photosynthetic production. Thus nitrogen affected sink and source capacity in a balanced way, which was reflected in the small effects on the harvest index. The small effect of nitrogen on the distribution of assimilates was also found by Makunga et al. (1978) with C^{14} treatments.

The higher yield potential of new cultivars is almost entirely due to an improvement in the carbohydrate economy of the plant. There have been only a small increase in capacity to take up nitrogen from the soil and to produce grain protein. Consequently, grain protein percentage has tended to fall as yielding ability has been increased (Bingham, 1976). Pushman & Bingham (1976) stated that this effect can be compensated by later nitrogen application. In our experiment this compensation was only partial.

However, there is no simple relation between yield and percentage nitrogen in the grain. In cultivars or under conditions where senescence of leaves and mobilization of nitrogen from the leaves is slow, higher grain yields may be associated with lower percentage nitrogen in the grain (e.g. 1.44% for Maris Hobbit in 1977). On the other hand, where leaf senescence is rapid, starch storage may be more adversely affected than protein storage and lower yields may be associated with higher percentage nitrogen in the grain (McNeal et al., 1972). This balance is strongly governed by temperature; high temperatures favour protein storage more than the accumulation of starch in the grain (Campbell & Read, 1968; Spiertz, 1977). Thus the low temperatures in the growing season of 1977 would have reduced protein percentage of the grain.

More than half of the grain protein may be derived from nitrogen uptake by the wheat plant after anthesis (Hucklesby et al., 1971; Spiertz & Ellen, 1978), if soil nitrogen supply and root activity are adequate. In these circumstances the nitrogen content of the grain may remain high or even rise as grain filling proceeds (Johnson et al., 1967). In our experiment only 23% and 20% of the grain nitrogen in Lely and Maris Hobbit, respectively, was derived from uptake after anthesis. This indicates either poor root activity or depletion of soil nitrogen after anthesis. With little further uptake during grain filling, most of grain nitrogen will be derived by remobilization from leaves, stem and chaff (Austin et al., 1977). The differences in efficiency of translocation of nitrogen from the vegetative parts to the developing grains between cultivars and nitrogen treatments were very small. The overall mean for the nitrogen harvest index amounted to 76.3% within a range from 73.8 to 79.2% for all treatments (Table 2).

At high yield levels a low nitrogen content of the grains need not result from a lower grain nitrogen yield, but can be caused by enhanced starch storage per unit available nitrogen. Despite large differences between Maris Hobbit and Lely in nitrogen content of the grains (1.44 and 1.62%, respectively) nitrogen yield per grain amounted to 0.73 mg for both cultivars. Late nitrogen dressing raised the nitrogen contents of the grains considerably in both cultivars.

In a study on the importance of nitrate reductase activity for grain protein Rao et al. (1977) concluded that no single identifiable factor can be used as a physiological criterion in selecting wheat genotypes for better nitrogen utilization. Selection must consider two or more factors simultaneously, including long-term capacity for nitrogen assimilation (uptake and reduction of nitrate) and efficiency of translocation of vegetative nitrogen to the developing grains.

Considering the patterns of grain growth and yield differences we may conclude that carbohydrate supply to the grains was not yield-limiting. However, this supply corresponded to the number of grains that had to be filled. Thus grain yield depended mainly on number of grains per m^2. Nitrogen dressing affected grain number and photosynthetic production to the same extent. An early nitrogen dressing favoured grain number more than a late dressing; the latter increased the protein yield of the grains.

The results of this experiment confirm the great importance of ear formation for the final grain yield. It has already been shown that under various environmental conditions the formation of a larger ear with a high number of grains per ear favours a high grain yield (Ledent, 1977 Evans, 1978).

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