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An Assessment of the Production and Performance of F_1 Hybrid Wheats Based on *Triticum timopheevi* Cytoplasm

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Summary. This work reports on the production and yield assessment of F_1 wheat hybrids from crosses between cytoplasmic male sterile lines, with *Triticum timopheevi* cytoplasm, and cultivars with fertility restoring genes.

In four years of trials conducted between 1974 and 1977, only three F_1 hybrids out of a total of 168 yielded significantly more than the control variety 'Maris Huntsman', which currently occupies a substantial proportion of the area planted with winter wheat in the UK. Because of the rapid increase in yield of conventional wheat varieties, which has already led to varieties which outyielded 'Maris Huntsman', the yield advantage of these F_1 hybrids is insufficient for them to be developed as commercial varieties.

The efficient production of uncontaminated male sterile and F_1 seed presents problems of isolation and a difficult biological problem in increasing the cross breeding potential of maintainer and restorer lines. These together with selection for other parental characters such as restoration, short straw and resistance to sprouting make the development of F_1 hybrids more difficult and expensive than that of conventional varieties.

Key words: F_1 hybrid wheat – Yield – Restoration – Seed production – Sprouting

Introduction

Early reports of heterosis in wheat, surveyed by Briggle (1963), showed that positive heterosis for yield ranged to well over 100 per cent. However, much of the earlier work was carried out using F_1 seed produced by hand pollination of emasculated ears. The plants were either grown in the glasshouse or in the field as rows of F_1 plants with few if any replications, and were therefore of doubtful value in the assessment of the yield potential of commercial F_1 hybrids (Rajki and Rajki 1966; Johnson and Schmidt 1968). Nevertheless, the promise of high levels of yield advantage from such work provided the impetus for attempting to increase the yield of wheat by developing F_1 hybrids when a suitable breeding method for doing this, based on cytoplasmic male sterility, became available in the early 1960's.

The first evidence of cytoplasmic male sterility in wheat was provided when the *Triticum vulgare* genome was transferred into the cytoplasm of *Aegilops caudata* (Kihara 1951). This cytoplasm caused pistillody and in combination with the *T. durum* genome it also decreased female fertility (Kihara and Tsunewaki 1961). Later it was shown that the female fertility of *T. aestivum* was also reduced by *Ae. caudata* cytoplasm, which in addition exerted other deleterious effects such as the formation of germless grains, haploids and twin seedlings and reduction of plant vigour (Kihara and Tsunewaki 1966).

In 1953, Fukasawa reported cytoplasmic male sterility when the genome of *Triticum durum* was backcrossed into the cytoplasm of *Aegilops ovata*. Female fertility was not impaired but flowering was delayed. With hexaploid wheat, *ovata* cytoplasm delayed ear emergence and reduced plant height (Hori and Tsunewaki 1969). Both *Ae. caudata* and *ovata* cytoplasms therefore had undesirable side effects making them unsuitable for use in developing F_1 hybrid wheats.

In 1962, Wilson and Ross reported cytoplasmic male sterility and high female fertility when the genome of *T. aestivum* (Bison) was transferred by backcrossing into the cytoplasm of *T. timopheevi*. In general, no differences appeared to exist between the *T. timopheevi* male steriles (A-lines) and their normal (B-line) counterparts in both *T. aestivum* and *T. durum* wheats, although occasionally under field conditions the A-line might be slightly later in heading than the B-line (Wilson 1968).

Cytoplasmic male sterility, based on *T. timopheevi* cytoplasm, thus provided a method for producing male

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sterile lines of *T. aestivum* cultivars by successive backcrosses to *T. timopheevi* cytoplasm. Male sterile seed of these cultivars could then be produced in large amounts by wind pollination.

The production of a fertile F_1 hybrid requires that an A-line is crossed with a cultivar which carries a nuclear gene(s) (*R* gene(s)) which restores male fertility to the F_1 generation. In 1962, Wilson showed that restorer genes could be transferred to the genome of *T. aestivum* from *T. timopheevi* when he recovered male fertile as well as male sterile plants whilst transferring the genome of the variety 'Marquis' into *T. timopheevi* cytoplasm. Also in 1962, Schmidt, Johnson and Maan reported fertility restoration by a *T. timopheevi* derived hexaploid wheat. These discoveries stimulated the search for genes restoring male fertility to *T. timopheevi* cytoplasm. Apltauerová (1967) and Zeven (1968) reported *T. aestivum* varieties which had restorer genes. Reports of the transfer of restorer genes from *T. timopheevi*, and of restorer genes found in other *Triticum* and *Aegilops* species, have been reviewed by Maan (1973), Gotsov, Popov and Panayotov (1975) and Sage (1976).

If F_1 hybrid wheats are to be grown as commercial varieties, they must show a yield advantage relative to the highest yielding commercially grown inbred line, and a satisfactory breeding method capable of producing seed in large enough quantities for commercial use has to be available. Furthermore, farmers will only grow an F_1 hybrid provided its yield is sufficiently high to give extra profit having taken into account the higher cost of seed production and the need to purchase new seed for each crop.

Whilst screening parental combinations for heterotic increases in yield, the most realistic assessment will be achieved by evaluating F_1 hybrids under husbandry conditions similar to those likely to be used commercially. This means conducting adequately replicated trials under such conditions, preferably using F_1 seed produced by a method which can be used commercially, so that this can also be assessed.

This paper reports on work carried out at the Plant Breeding Institute in the production of F_1 hybrids based on *T. timopheevi* cytoplasmic male sterility, and their assessment in autumn drilled replicated yield trials in the years 1973-1977, using seeding rates approximating to those used commercially.

Materials and Methods

Work on hybrid wheat using Bison[10] A-line (Livers and Heyne 1962) as a source of *T. timopheevi* cytoplasmic male sterility began at the Institute with the production of male sterile lines of spring wheat cultivars. Because of the larger winter wheat area in Britain, with a higher yield level and probably better restoration, the emphasis was later changed to producing A-lines of winter wheat cultivars.

Following the initial stages of backcrossing in the glasshouse, each A-line was multiplied in a field plot isolated by at least 50 metres from other wheats. Both A and B-lines were maintained as pure stocks, drilled plots of each being derived from ear or plant rows from the previous year (Hanson 1973), and sown in an approximate ratio of one A-line to two B-lines.

When sufficient seed of the A-lines had been produced, usually after at least five backcrosses to the alien cytoplasm, it was drilled in isolated field plots as three rowed strips alternating with strips of a restorer line, in an approximate 1:1 ratio. Harvesting was done using a Hege plot combine, which was carefully cleaned using a portable air compressor before the F_1 seed set on each male sterile line was harvested.

An assessment of the effectiveness of cross pollination of A-lines by their respective B-lines was obtained by comparing the seed yield and 1,000 seed weights obtained from A and B-line

Table 1. Cultivars developed as male sterile lines with *T. timopheevi* cytoplasm, and restorer lines, used in the production of F_1 hybrids

Male sterile lines		Restorer lines	
Spring	Winter	Spring	Winter
Caesar	Cama	53 sp 17 [(Bison A-line X Marquis restorer) X Maris Ensign^2] X Maris Beacon	Argent (TJB 364/636)
Cardinal	Joss Cambier	TW 74 (Minister X E.L.S.)	Bléd'or
Clarion	Maris Envoy		Hesbignon
Janus	Maris Freeman		Maris Beacon
Kloka	Maris Hobbit		Maris Huntsman
Kolibri	Maris Ploughman		Minister
Maris Ensign	Maris Templar		Primépi
Maris Dove	Maris Ranger		TJB 147/1281 (Maris Beacon X Maris Ranger)
Sirius	Viking		TJB 259/41 'Mardler sib' (Maris Huntsman) X (Maris Ranger X Maris Fundin sib))
TB 306 (Svenno X Jufy I)			TL 459 ((*T. carthlicum* X Hybrid 46) X Maris Fundin sib)
TB 435/119 (Jufy I X Stella)			
Toro			
Troll			
TW 161/2/7/10 [(Jufy I X E.L.S.) X Jufy I^3] X (Norin 10 X Koga I)			

plots of equal areas. A comparison of crossed seed set obtained on different male sterile lines by various restorer lines was obtained by counts of the number of seed, total number of spikelets and number of spikelets with seed, on a sample of ten ears.

In 1972, the proportion of non-viable F_1 seed harvested from three male sterile lines, 'Maris Ranger,' 'TB 306' and 'TB 435/119,' was assessed from six sub-samples of 100 F_1 seed. Counts were based on the number of sprouted seed and the number of seed failing to germinate after five days on moist filter paper in petri dishes.

In the four years 1974-1977, 168 F_1 hybrids were assessed in drilled yield trials using lattice experimental designs. These involved fourteen spring and nine winter wheat male sterile parents, and two spring and ten winter wheat cultivars capable of restoring male sterility induced by *T. timopheevi* cytoplasm (Table 1). A seeding rate of 138 kg/ha of dressed seed was used for all trials, the plot size and number of replications being determined by the amount of F_1 seed available.

In 1974, 49 F_1 hybrids were tested using 3.02 m^2 plots, in a trial consisting of five replicates. In 1975, 91 F_1 hybrids were grown in two trials each with 6.04 m^2 plots and four replicates, whilst for 1976 43 F_1 hybrids were grown in 5.81 m^2 plots with five replicates. Finally, in 1977, 46 F_1 hybrids were grown in a trial using 6.04 m^2 plots with six replicates. The trials were harvested with a Hege or Wintersteiger combine depending on plot size.

For 1976 and 1977 an assessment of male fertility restoration in the F_1 hybrids relative to their B-lines was obtained from the percentage of spikelets with seed, on a random sample of ten ears in one replicate, which were bagged before flowering. In 1977, a sample of ten non-bagged ears were also assessed in the same way for 64 hybrids grown in trial.

Results

Production of Male Sterile and Hybrid Grain

The yield of male sterile seed obtained on four A-lines by cross pollination with their respective B-lines ranged from 43 to 63 per cent, with no large difference in weight between the corresponding A and B-line seed. These male sterile lines were amongst those which gave the highest seed sets by cross pollination.

Data for seed set on three male sterile (ms) lines pollinated by 'Minister' and 'Primépi' in 1972 is presented in Table 2. Crossed seed set was less on ms 'Maris Ranger' than on ms 'TB 306' and ms 'TB 435/199' when pollinated by both 'Primépi' and 'Minister'. The viability of the F_1 seed, particularly that from ms 'TB 306', was reduced by premature germination.

In 1974 when seven restorer lines were used for producing F_1 seed, the variety 'Minister' gave the highest crossed seed set over a range of thirteen male sterile lines (Table 3). Satisfactory seed set was obtained with most other pollinators, but much lower seed sets were obtained from crosses involving 'Maris Beacon' and 'Hesbignon'. Some male sterile lines, notably ms 'TB 435/119', ms 'Kloka' and ms 'Maris Ranger', gave a high set of crossed seed with all seven pollinators.

Table 2. Set of hybrid seed and percentage non-viable seed in three male sterile lines, wind pollinated by 'Primépi' and 'Minister' (1972)

	Percent spikelets with seed	Mean seed no. per spikelet	Per cent non-viable seeds
(a) Restorer parents			
Primépi	93.9	2.0	8.2
Minister	97.4	2.4	5.0
(b) Pollinated by Primépi			
ms Maris Ranger^4	65.8	1.0	14.8
ms TB 306^7	78.0	1.3	35.3
ms TB 435/119^6	81.0	1.6	12.4
(c) Pollinated by Minister			
ms Maris Ranger^4	62.1	1.0	20.5
ms TB 306^7	92.3	2.0	29.5
ms TB 435/119^6	87.6	2.0	9.6

In this and subsequent tables and figures superscripts denote the number of crosses to *T. timopheevi* cytoplasm

Yield of F_1 Hybrids

Yield data for 49 F_1 hybrids grown in 1974 are presented in Figure 1. Only one F_1 hybrid, ms 'Toro' × '53 sp 17' yielded significantly ($P < 0.05$) more than 'Maris Huntsman', which had a yield of 6.48 tonnes/ha. At this level of significance, 24 F_1 's were not distinguishable from 'Maris Huntsman'.

The yields of the 91 F_1 hybrids grown in two trials in 1975 are shown in Figure 2. In Trial 1, 'Maris Huntsman' yielding 5.05 tonnes/ha was the highest yielding cultivar, with five F_1 hybrids not differing significantly ($P < 0.05$) from this. In Trial 2, although seventeen F_1 hybrids did not differ significantly ($P < 0.05$) from 'Maris Huntsman' yielding 4.63 tonnes/ha, none significantly outyielded this control.

In 1976, four F_1 hybrids, ms 'Maris Hobbit' × 'Maris Huntsman', ms 'Maris Hobbit' × '53 sp 17', ms 'Cardinal' × 'Maris Huntsman' and ms 'Maris Ranger' × 'Maris Huntsman', did not differ significantly ($P < 0.05$) in yield from 'Maris Huntsman', which yielded 5.21 tonnes/ha, but no hybrid outyielded this control (Fig. 3). With the exception of the F_1 hybrid ms 'Cardinal' × 'Maris Huntsman', restoration in these F_1 hybrids, measured as the percentage of spikelets with grain set, was high (Fig. 4).

The yield of 46 F_1 hybrids grown in 1977 are shown in Figure 5. Two F_1 hybrids, ms 'Maris Hobbit' × 'Maris Huntsman' and ms 'Maris Hobbit' × 'TJB 147/1281', significantly ($P < 0.01$) outyielded 'Maris Huntsman'. The former outyielded both its parents and the yield of a further 36 F_1 hybrids did not differ significantly ($P < 0.05$) from that of 'Maris Huntsman'.

Restoration levels, for all the F_1 hybrids grown in 1977, are presented in Figure 6. Restoration was generally lower than in 1976, F_1 's based on some male sterile lines such as ms 'Cama' and ms 'Maris Dove' being poorly restored by all the restorers, whilst F_1 hybrids with 'Maris Hobbit' and 'Maris Ranger' as male sterile parents had higher levels of restoration with these restorers. Grain set on non-bagged ears of F_1 hybrids was higher than on bagged ears.

Discussion

When conditions for field multiplication were satisfactory as in the case of 'Maris Freeman' in 1975 and 'Maris Fundin' in 1976, the yield of the A-line averaged 60 per cent that of the B-line. However, in the development of A-lines, only those cultivars which had reasonably good anther extrusion and provided high crossed seed sets were retained. The multiplication of a few cultivars was discon-

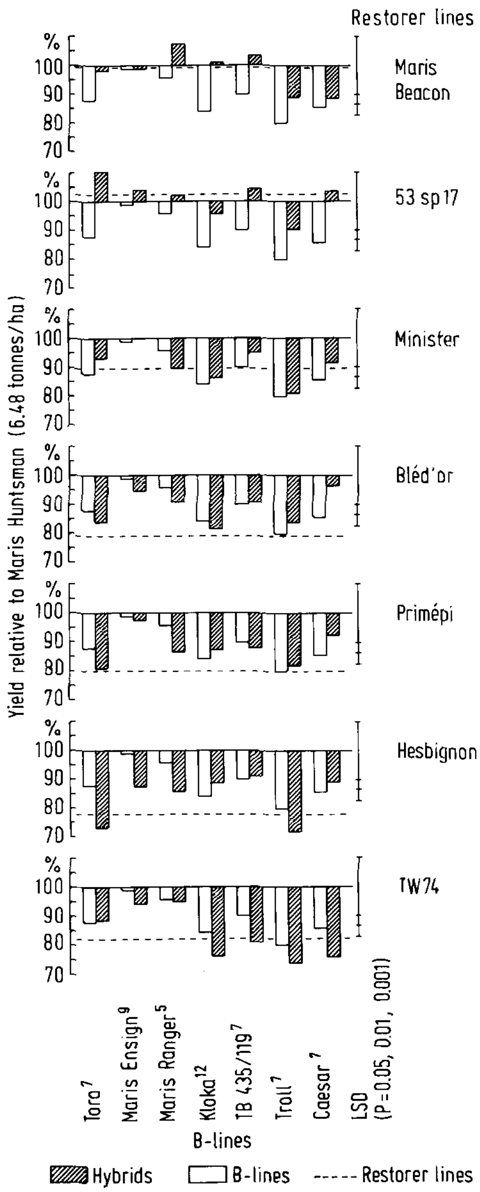

Fig. 1. Yield of 49 F_1 hybrids, B-lines and restorer lines relative to 'Maris Huntsman', 1974

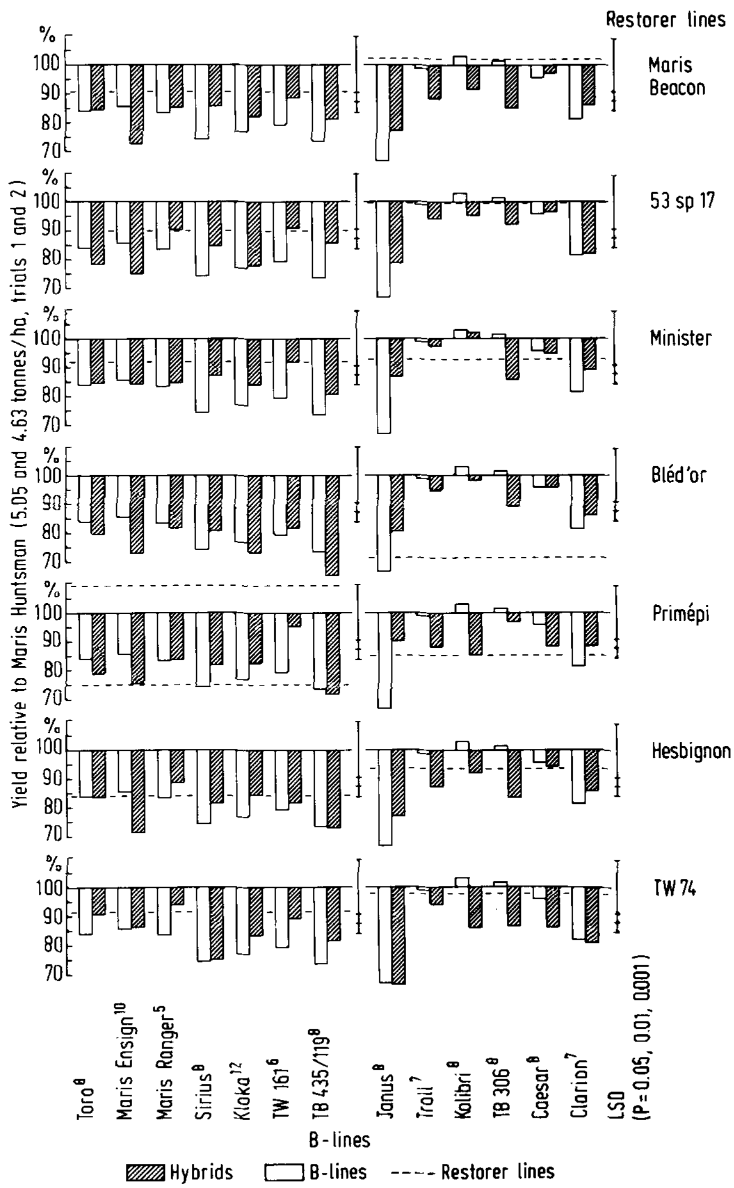

Fig. 2. Yield of 91 F_1 hybrids, B-lines and restorer lines relative to 'Maris Huntsman', 1975

Table 3. Set of hybrid seed in thirteen male sterile lines, wind pollinated by seven restorer lines (1974)

Female parent	Restorer parents Maris Beacon 100	53 sp 17 99	Minister 100	Primépi 100	TW 74/34/3 100	Hesbignon 100	Blédʼor 100	Mean
(a) Percentage spikelets with seed								
TB 306[8]	57	55	91	73	87	62	85	72.9
Maris Ranger[5]	43	82	92	73	90	65	93	76.9
Kloka[12]	53	95	90	86	91	57	98	81.4
TB 435/119[8]	96	94	95	93	98	85	95	93.7
Troll[8]	61	55	93	57	89	38	81	67.7
Maris Ensign[10]	36	57	96	85	48	59	85	66.6
Clarion[7]	47	41	85	34	37	55	43	48.9
Toro[8]	79	38	92	76	43	64	73	66.4
Caesar[8]	51	22	76	41	13	29	18	35.7
Kolibri[8]	45	53	90	75	77	26	67	61.9
Janus[8]	74	71	93	76	87	35	73	72.7
Sirius[8]	48	81	81	65	85	29	88	68.1
TW 161/2/7/10/1/8[6]	13	93	58	73	55	15	75	54.6
Mean	54.1	64.4	87.1	69.8	69.2	47.6	74.9	
(b) Seed set per spikelet (total per ear)								
	3.0	2.1	2.8	2.1	2.2	2.7	2.3	
TB 306[8]	0.8	0.7	1.8	1.1	1.4	0.9	1.5	1.17
Maris Ranger[5]	0.6	1.4	1.8	1.0	1.7	0.9	1.9	1.33
Kloka[12]	0.7	2.0	1.9	1.4	1.6	1.0	2.2	1.54
TB 435/119[8]	2.2	1.9	2.4	1.7	0.5	1.5	2.2	1.77
Troll[7]	0.8	0.8	1.7	0.7	1.3	0.5	1.2	1.00
Maris Ensign[10]	0.4	0.8	1.7	1.3	0.6	0.8	1.4	1.00
Clarion[7]	0.7	0.6	1.5	0.4	0.4	0.7	1.8	0.87
Toro[8]	1.3	0.5	1.7	1.1	0.5	0.9	1.1	1.01
Caesar[8]	0.6	0.3	1.3	0.5	0.3	0.3	0.2	0.50
Kolibri[8]	0.5	0.7	1.5	1.0	1.3	0.3	0.9	0.89
Janus[8]	1.1	1.1	1.7	1.3	1.4	0.4	1.3	1.19
Sirius[8]	0.6	1.3	1.4	0.9	1.4	0.3	1.5	1.06
TW 161/2/7/10/1/8[6]	0.1	1.8	0.9	1.2	0.7	0.2	1.2	0.87
Mean	0.80	1.07	1.64	1.05	1.01	0.67	1.42	

tinued because their male sterility was environmentally unstable, partially fertile plants appearing amongst the male steriles, probably due to the presence of latent restoring genes (Wilson 1968; Sage 1976). Fertile plants amongst the sterile plants in two other lines arose because of pollen contamination by restorers the previous year. These stocks were cleaned by careful roguing.

In the production of F_1 seed in 1974 (Table 3) the three male steriles ms 'TB 435/119', ms 'Kloka' and ms 'Maris Ranger' produced a high set of crossed seed with all seven pollinators; these were among the shortest strawed male sterile lines and were generally shorter than the pollinators. The concept of using shorter strawed male steriles as a means of improving cross pollination can be extended to the development of extreme dwarf varieties (Johnson and Schmidt 1968; Zeven 1969), based on the (semi-dominant) Rht_3 dwarfing gene found in 'Minister Dwarf', 'Tom Thumb' and 'Tom Pouce' (Gale and Law 1977). Such lines can be used in combination with taller cultivars to produce F_1 's of below mid-parent height, thus avoiding the undesirable increases in height which can occur in hybrid combinations. A programme to improve the agronomic performance of extreme dwarfs was incorporated into the hybrid wheat breeding programme at the Institute in 1972; improvements have been made but the yield potential of F_1 hybrids based on selected cultivars from this programme has not been tested.

Poor matching of flowering time between the A-line and restorer line may result in low crossed grain set, additionally the production of pollen by the restorer lines is often poor. This occurred in 1976 when three out of the five high yielding *T. aestivum* cultivars used as restorer

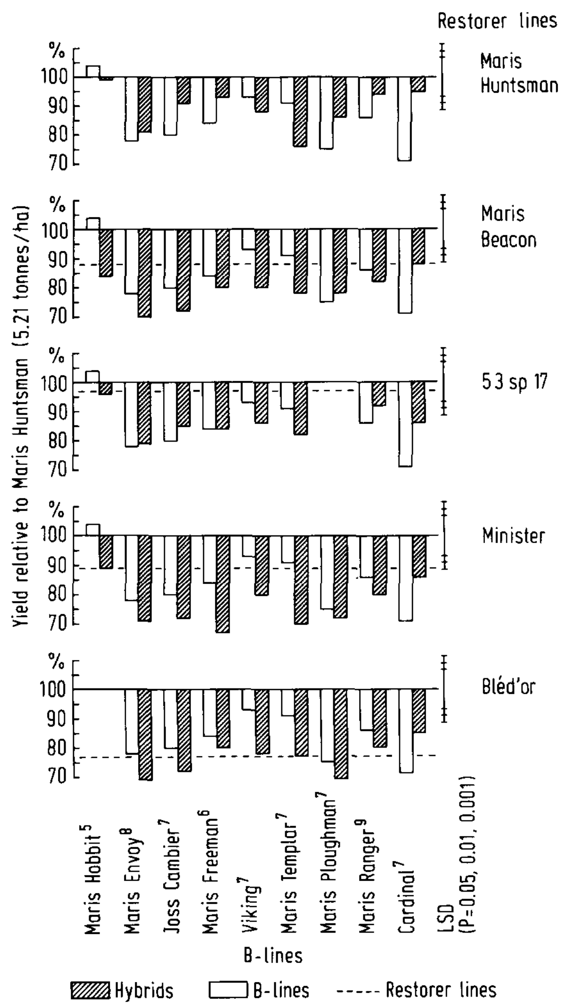

Fig. 3. Yield of 43 F_1 hybrids, B-lines and restorer lines relative to 'Maris Huntsman', 1976

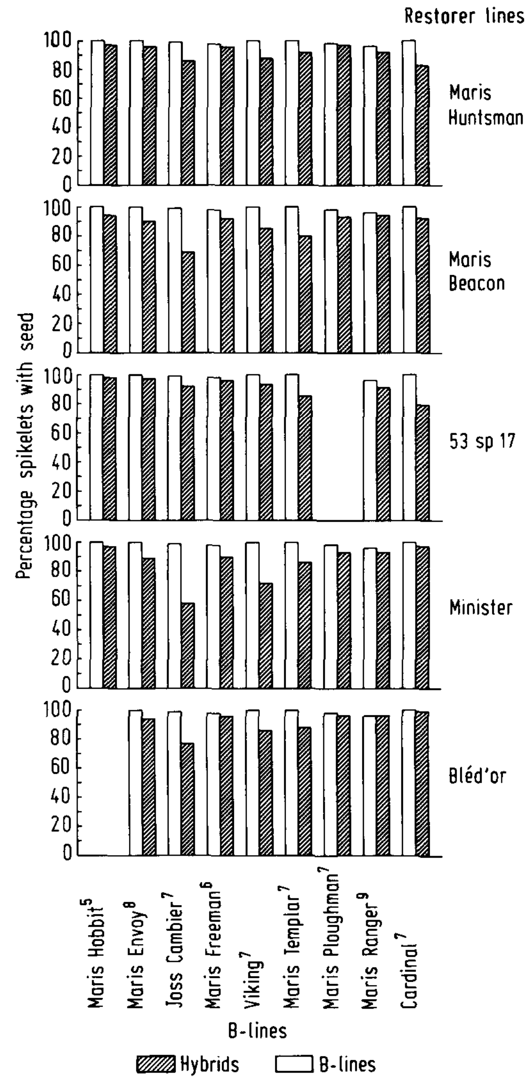

Fig. 4. Fertility in bagged ears of 43 F_1 hybrids and their B-lines in trial 1976

lines gave low seed sets on the male sterile lines; 'TJB 259/41' especially showed very poor anther extrusion. Thus, not all crosses using these restorers produced sufficient seed for the F_1 hybrids to be incorporated into yield trials, and others could only be assessed using fewer replications. This emphasises the need to develop restorer lines with improved cross-pollination potential.

Difficulty in finding suitable isolation, and in producing male sterile and F_1 seed for experimental purposes using small isolation plots, indicates the problems which will be encountered if F_1 seed production is attempted on a large scale. We have no experience in this matter but some doubt has been expressed as to the adequacy of the alternate strip method for the commercial production of F_1 seed. Lelley (1966) concluded that strips of the male sterile should not exceed 4 metres in width. De Vries (1974), using strips up to 4 metres in width, found that the highest seed yield for a given area was obtained with the lowest tested ratio of 1:2 pollinator to male sterile, above which the increase in cross pollination was insufficient to compensate for the loss in yield resulting from the reduction in land sown to the male sterile. Miller and Lucken (1976) concluded that successful hybrid seed production depended on using high yielding adapted parents grown in high yielding environments. A high yielding restorer line would also maximise the income obtained when the surplus is sold in order to reduce the cost of F_1 seed production.

An alternative to the strip method is to grow a mixture of pollinator and male sterile, so that pollen movement is

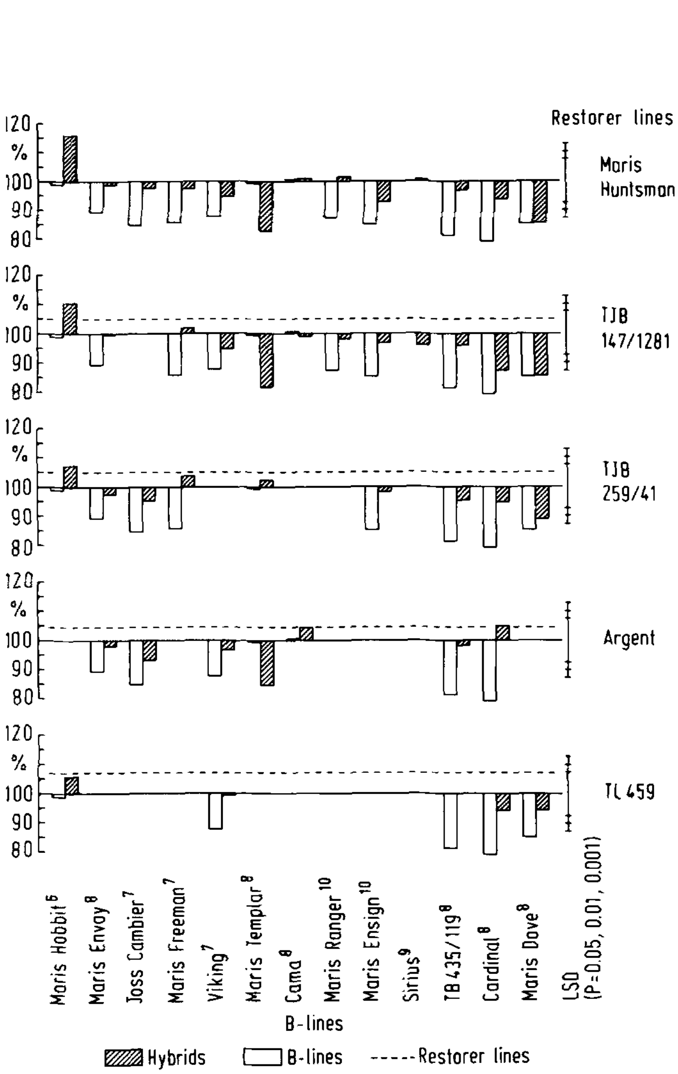

Fig. 5. Yield of 46 F_1 hybrids, B-lines and restorer lines relative to 'Maris Huntsman', 1977

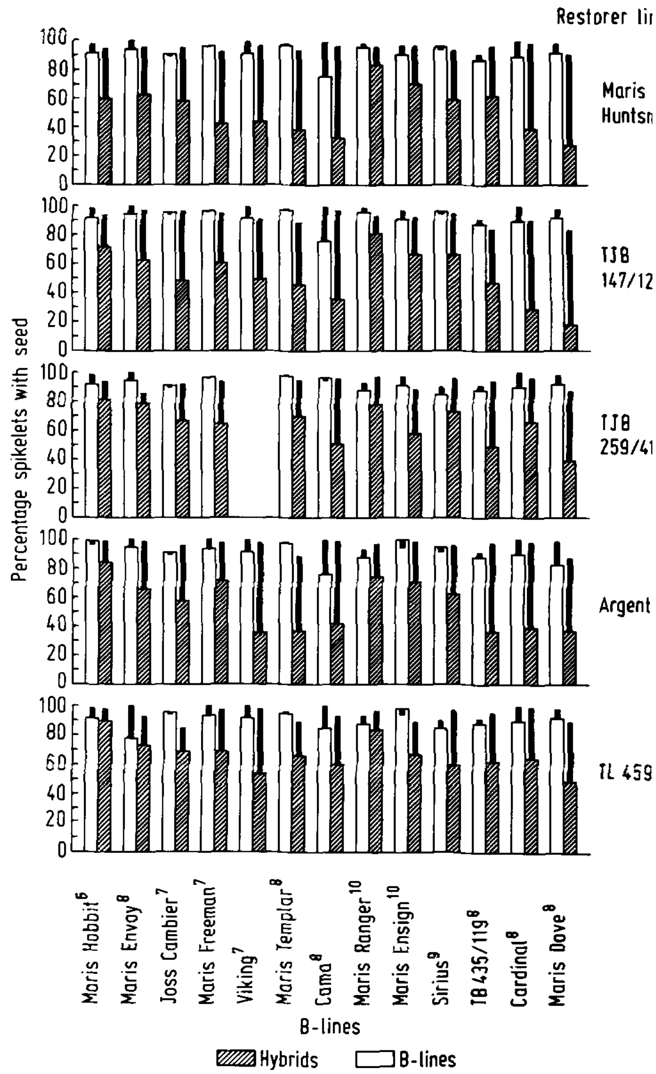

Fig. 6. Fertility of bagged ears in 64 F_1 hybrids and their B-lines in 1977. The fertility of non-bagged ears is indicated by the narrower solid line on each column

over shorter distances. It is then necessary to incorporate a marker gene into the pollinator so that the selfed seed can be sorted from the F_1 seed. Barabás, Sági and Kertész (1973) suggest the use of a seed colour gene which can be sorted by machines activated by colour sensitive photoelectric cells. The use of such a method will inevitably add to the seed production costs in comparison with the strip method. The increased costs may be offset by increased seed set on the male sterile parent by cross-pollination and/or a lower ratio of pollinator to sterile.

For commercial production it is important that seed set by wind pollination is high, as this will govern the price of seed. It is also important that wind pollination is reliable so that the price remains relatively stable. Low seed set may also reduce the quality of the seed (Miller, Rogers and Lucken 1975). Late ripening may induce sprouting in immature ears or unpollinated florets may become infected by floral diseases such as ergot.

Susceptibility to pre-harvest sprouting, which increases α-amylase activity in the grain (Bingham and Whitmore 1966), commonly occurs when wet weather delays harvesting and results in a reduction of grain quality. The problem is of more concern in maritime climates of higher latitudes such as north-western Europe where the more sprouting resistant red-grained wheats are used, and in areas of the United States and Australia where the more sprouting susceptible white-grained wheats are grown, (MacKey 1976). Weather conditions at Cambridge in 1972 were not especially conducive to sprouting, the white grained variety Minister having only 5%, but high levels of sprouting were seen on some male sterile lines (Table 2). The higher levels of sprouting in seed set on male sterile lines has been shown to be associated with the interaction between the *T. timopheevi* cytoplasm and the nucleus of *T. aestivum* (Doig, Done and Rogers 1975). The susceptibility of A-lines varies and is determined by the genotype of the male sterile (Doig et al. 1975; Ellis and Clayton 1976). Similarly the α-amylase activity of A-lines varies according to the genome (Jönsson 1976).

Delayed pollination of the A-lines does not apparently increase sprouting but efficient cross pollination, resulting in high seed sets on male sterile ears by B or restorer lines, is important, as this reduces sprouting (Ellis and Clayton 1976) and α-amylase levels (Jöhnsson 1976). High levels of restoration are also important, as incomplete restoration in F_1's is associated with high levels of α-amylase (Jönsson 1976).

In *T. aestivum*, varieties differ in the α-amylase activity of grain which has no visible indication of germination (Bingham and Whitmore 1966; Moss, Derera and Balaam 1972), but these differences are genetically independent of those due to sprouting in the ear (Bingham 1968). Therefore, to avoid the problem of pre-harvest sprouting, tests have to be carried out, which in the case of an F_1 programme would be on male sterile lines which had received sufficient backcrosses to the *T. timopheevi* cytoplasm. This imposes an extra selection criterion which can only be applied following the initial development of an A-line.

In the yield results presented, only three F_1 hybrids from a total of 168 hybrids tested over the four year period yielded significantly more than the control variety 'Maris Huntsman'. In 1974 ms 'Toro' × '53 sp 17' significantly ($P > 0.05$) (Fig. 1) outyielded 'Maris Huntsman' but yielded significantly ($P > 0.001$) less than 'Maris Huntsman' in 1975. The other two hybrids were ms 'Maris Hobbit' × 'Maris Huntsman' and ms 'Maris Hobbit' × 'TJB 147/1281', which significantly ($P < 0.01$) outyielded 'Maris Huntsman' by 16% and 10% respectively in 1977 (Fig. 5). In the previous year however, ms 'Maris Hobbit' × 'Maris Huntsman' did not differ significantly ($P > 0.001$) in yield from 'Maris Huntsman' (Fig. 3). The yield advantage of these F_1's was seen in years when the yield of 'Maris Huntsman' was high, 6.48 and 5.51 tonnes/ha in 1974 and 1977 compared with 5.05 and 5.21 tonnes/ha in 1975 and 1976 respectively. This suggests that these hybrids may do better in high yielding environments. Even so, a yield advantage of 16% over 'Maris Huntsman' is insufficient for an F_1 hybrid to be economically viable, even if it could be repeated. This is because it would take a few years before the hybrid could be produced in commercial quantities and already the yield of 'Maris Huntsman' has been surpassed by varieties such as 'Mardler' and 'Hustler' (NIAB 1978).

Partial restoration of male fertility is normally expressed as self-fertility in the basal part of the ear (Done 1973) so that the percentage of spikelets setting grain in bagged ears gives a reasonable measure of restoration. A more complete graphical method of presenting restoration which includes seed number per fertile spikelet, as used by Hughes and Bodden (1977), is impractical for the number of hybrids considered here. The level of restoration in the F_1 hybrids was lower in 1977 (Fig. 6) than in the previous year (Fig. 4). F_1's based on some male sterile lines such as ms 'Cama' and ms 'Maris Dove' were poorly restored with all restorers whilst all the F_1 hybrids involving 'Maris Hobbit' and 'Maris Ranger' as male sterile lines had higher levels of restoration. It is disappointing that the high levels of restoration obtained with selections from the pure line breeding programme in combination with ms 'Maris Hobbit' and ms 'Maris Ranger' (Hughes and Bodden 1977) do not apply over a range of male sterile lines. Unfortunately our restorer screening programme for 1978 involving 90 F_1 restorer selections is based on these two male sterile lines in addition to ms 'Maris Templar' which appears more difficult to restore.

The seed set on non-bagged ears of F_1 hybrids was higher than in bagged ears in 1977 (Fig. 6). This possibly reflects some reduction in seed set due to bagging, as observed on some inbred lines, but arises mainly because of high levels of seed set by cross pollination on non-bagged ears. This suggests that the yield data reflect more accurately the yield potential of these hybrids than is indicated by the level of restoration in bagged ears. It may also imply that incomplete restoration in an F_1 crop may not be a major disadvantage provided that the cross pollination potential of the crop is high.

Having high yielding cultivars with restorer potential in the pure line breeding programme at the Institute is an advantage because they can be used as parents of F_1 hybrids; however those which become commercial varieties pose a threat to the production of pure male sterile seed, when grown in the same area. Fertile contaminants resulting from cross pollination would have a selective advantage in a male sterile population, and would increase in each subsequent generation rendering the male sterile line progressively less pure. This possibility was recognised by Johnson and Schmidt (1968). At present in the UK, 'Maris Huntsman' a restorer, occupies about a third of the winter wheat seed sales (HGCA 1977), and 'Hustler' recently included on the NIAB provisionally recommended list (NIAB 1978) has restorer genes. Other cultivars with 'Maris Huntsman' as a common parent, such as 'Vantage', 'Marksman' and 'Brigand', which are in National List Trials have also given restoration. In addition, varieties recently released by other breeders, such as 'Armada' and 'Conway' have restoration possibly derived from Hybrid 46. For the present, therefore, varieties with restorer potential are likely to occupy a proportion of the UK winter wheat area. Because breeders are likely to include current high yielding varieties as parents in their breeding programmes, it is possible that this would remain a problem for the production of hybrid varieties. The problem would increase if F_1 hybrid varieties were grown commercially and the area they occupied increased, as they would be releasing pollen which carried restorer genes necessary for restoration of male fertility in the F_1 hybrid (Johnson and Schmidt 1968). Male sterile lines with low seed set by cross-pollination with their B-lines, would be particularly prone to contamination in this way.

The efficient production of uncontaminated male sterile and F_1 seed presents problems of isolation from commercial varieties such as 'Maris Huntsman' which carry restorer genes, and the difficult biological problem of increasing the cross breeding potential of maintainer and restorer lines. In addition, A-lines would have to be screened for resistance to sprouting in the ear and for ease of restoration, whilst restorer lines capable of adequately restoring A-lines over a range of environments would have to be developed. These characters are additional to those normally selected in wheat breeding, so that the development of parents for F_1 hybrids is considerably more complex than that of conventional inbred varieties. To maintain an F_1 hybrid programme, it is still necessary to have a pure line breeding programme to provide improved parents (Hayward 1975). This extra work, however, can only be justified if F_1's provide sufficient yield advantage to compensate for the increased cost of F_1 seed, as well as providing an incentive for the farmer to grow an F_1 in preference to the highest yielding inbred variety. In addition, F_1 varieties would only become established if the frequency of obtaining crosses with such an advantage is sufficiently high for this to be maintained over new varieties produced by conventional methods. At present in the UK the reverse is the case, with a rapid rate of yield increase in conventional varieties, so that in practise the advantage of an F_1 variety if released commercially would probably be of short duration.

In the USA F_1 hybrids are being developed for the hard red winter wheat region, where 15-16 M hectares are grown within an extensive area so that isolation for the multiplication of male sterile and F_1 seed is a less serious problem than in the UK where the 1-1.2 M hectares of winter wheat are intensively grown. American seed companies apparently remain optimistic about the future of F_1 hybrid varieties, and some companies are already marketing them on a limited scale. However, on the basis of a regional trial conducted at nine sites in 1976, Johnson (1978) could not establish superiority of F_1 hybrids produced by both state and private breeders over commercial inbred lines grown as controls.

The results reported in this paper are based on a limited number of F_1 hybrids involving cultivars not ideally suited as parents. But they suggest that the yield advantage and the frequency of its occurence are insufficient for F_1 hybrids to provide an alternative method of producing commercial varieties in present day UK agriculture.

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Literature

Apltauerová, M.: *Wheat Newsletter* **14**, 29-31 (1967)

Barabás, Z.; Sági, F.; Kertész, Z.: Special ways for hybrid wheat breeding. Proc. 4th Intern. Wheat Genetics Symp., Columbia, Missouri, USA, 323-328 . 1973

Bingham, J.: Zur genetischen und pflanzenzüchterischen Betrachtung der Weizenqualität. Getreide und Mehl 7, 61-66 (1968)

Bingham, J.; Whitmore, E.T.: Varietal differences in wheat in resistance to germination in the ear and α-amylase content of the grain. J. Agricult. Sci. **66**. 197-201 (1966)

Briggle, L.W.: Heterosis in wheat – a review. Crop Sci. **3**, 407-412 (1963)

Doig, R.I.; Done, A.A.; Rogers, D.F.: Pre-harvest sprouting in bread wheat (*Triticum aestivum*) as influenced by cytoplasmic male sterility derived from *T. timopheevi*. Euphytica **24**, 229-232 (1975)

Done, A.A.: A mass selection technique for breeding restorer lines for hybrid wheat. Proc. 4th Intern. Wheat Genetics Symp., Columbia, Missouri, USA, 1-6. 1973

Ellis, J.R.S.; Clayton, P.B.: The influence of cross-pollination on pre-harvest sprouting in F_1 hybrid wheat seed. Proc. First Intern. Symp. Pre-Harvest Sprouting Damage in Cereals, Sweden, 1975, 127-132. 1976

Fukasawa, H.: Studies on restoration and substitution of nucleus in *Aegilotricum*. I. Appearance of male-sterile durum in substitution crosses. Cytologia **18**, 167-175 (1953)

Gale, M.D.; Law, C.N.: The identification and exploitation of Norin 10 semi-dwarfing genes. Plant Breeding Institute Ann. Rep. 1976, 21-35. 1977

Gotsov, K.; Popov, P.; Panayotov, I.: Nuclear-cytoplasmic relations in the subtribe *Triticinae*. Proc. 2nd Intern. Winter Wheat Conf., Zagreb, Yugoslavia, 170-175. 1975

Hanson, P.: The production of pure stocks of self-pollinating cereal varieties. Ann. Appl. Biol., **73**, 11-117 (1973)

Hayward, C.F.: The status of and prospects for hybrid winter wheat. Proc. 2nd Intern. Winter Wheat Conf., Zagreb, Yugoslavia, 84-104. 1975

Home Grown Cereals Authority. Cereal seed sales. Marketing Note. Supplement to Weekly Bulletin **12** No. 13 (1977)

Hori, T.; Tsunewaki, K.: Basic studies on hybrid wheat breeding. II. Effects of three alien cytoplasms on main quantitative characters of hexaploid wheats. Jap. J. Breed. **19**, 19-24 (1969)

Hughes, W.G.; Bodden, J.J.: Single gene restoration of cytoplasmic male sterility in wheat and its implications in the breeding of restorer lines. Theor. Appl. Genet. **50**, 129-135 (1977)

Johnson, V.A.: Breeding for yield and protein content in hard winter wheat. Cereal Foods World **23**, 84-86 (1968)

Johnson, V.A.; Schmidt, J.W.: Hybrid Wheat. Adv. Agron. **20**, 199-233 (1968)

Jönsson, J.Ö.: Pre-harvest sprouting problems in hybrid wheat breeding. Proc. First Intern. Symp. Pre-Harvest Sprouting Damage in Cereals, Sweden 1975, 115-119. 1976

Kihara, H.: Substitution of nucleus and its effects on genome manifestations. Cytologia **16**, 177-193 (1951)

Kihara, H.; Tsunewaki, K.: Pistillody of *Triticum durum* induced by an alien cytoplasm. Seiken Zihô **12**, 1-10 (1961)

Kihara, H.; Tsunewaki, K.: Basic studies on hybrid wheat breeding, carried out at the National Institute of Genetics. Seiken Zihô **18**, 55-63 (1966)

Lelley, J.: Befruchtungsbiologische Beobachtungen im Zusammenhang mit der Saatguterzeugung von Hybridweizen. Züchter **36**, 314-317 (1966)

Livers, R.; Heyne, E.G.: Wheat Newsletter **9** 10-13 (1962)

Maan, S.S.: Cytoplasmic male-sterility and male-fertility restoration systems in wheat. Proc. Symp. Genetics and Breeding of durum Wheat, Bari, Italy, 117-138. 1973

MacKey, J.: Seed dormancy in nature and agriculture. Proc. First Intern. Symp. Pre-Harvest Sprouting Damage in Cereals, Sweden, 1975, 83-91. 1976

Miller, J.F.; Lucken, K.A.: Hybrid wheat seed production methods for North Dakota. Crop Sci. **16**, 217-221 (1976)

Miller, J.F.; Rogers, K.J.; Lucken, K.A.: Effects of field production techniques on hybrid wheat seed quality. Crop Sci. **15**, 329-332 (1975)

Moss, H.J.; Derera, N.F.; Balaam, L.N.: Effect of pre-harvest rain on germination in the ear and α-amylase activity of Australian wheat. Austr. J. Agricult. Res. **23**, 769-777 (1972)

National Institute of Agricultural Botany. Farmers Leaflet No. 8, Recommended Varieties of Cereals 1978

Rajki, E.; Rajki, S.: Research work on hybrid wheat at Martonvasar. Acta Agronomica Acad. Scient. Hung. **15**, 199-214 (1966)

Sage, G.C.M.: Nucleo-cytoplasmic relationships in wheat. Adv. Agron. **28**, 265-298 (1976)

Schmidt, J.W.; Johnson, V.A.; Maan, S.S.: Hybrid wheat. Nebraska Exper. Sta. Quarterly **9**, (1962)

Vries, A.Ph.De.: Some aspects of cross-pollination in wheat (*Triticum aestivum* L.). 4. Seed set on male sterile plants as influenced by distance from the pollen source, pollinator: male sterile ratio and width of the male sterile strip. Euphytica **23**, 601-622 (1974)

Wilson, J.A.: Wheat Newsletter **9**, 28-29 (1962)

Wilson, J.A.: Problems in hybrid wheat breeding. Euphytica **17**, Supplement No. 1, 13-33 (1968)

Wilson, J.A.; Ross, W.M.: Male sterility interaction of the *Triticum aestivum* nucleus and *Triticum timopheevi* cytoplasm. Wheat Information Service **14**, 29-30 (1962)

Zeven, A.C.: Cross pollination and sources of restorer genes in wheat and a semi-hybrid variety. Euphytica **17**, Supplement No. 1, 75-81 (1968)

Zeven, A.C.: Tom Pouce Blanc and Tom Pouce Barbu Rouge, two *Triticum aestivum* sources of very short straw. Wheat Information Service **29**, 8-9 (1969)

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