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ADOPTION OF NEW TECHNIQUES IN WHEAT BREEDING

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ABSTRACT

Three areas of breeding are described: breeding hybrid wheat, breeding for protein quality, and resistance to eyespot *Pseudocercosporella herpotrichoides*. Evaluation of plant material and analyses used are covered. The rationale for the breeding approach is given and results of breeding programmes are described.

KEYWORDS

Hybrid wheat, protein quality, eyespot, *Pseudocercosporella herpotrichoides*.

INTRODUCTION

The purpose of this paper is to give some examples of the decisions taken in a breeding programme to meet, or preferably lead, changes in agronomic practice and use of the wheat crop. At the Plant Breeding Institute (PBI) the breeding of new varieties is carried out alongside research investigations at all stages in the chain of development of new parental material and more efficient breeding methods. The applied breeding programme pinpoints limitations in breeding methods and in source material and provides a test bed for new ideas. These functions can be fulfilled only if the standard of the varieties produced is competitive with other programmes in NW Europe. It follows that there are often critical decisions to be made in recognising which new line of work may provide a varietal character of value in the market place, or may improve the efficiency of breeding methods.

The driving force in the applied breeding work is to breed varieties which the farmer will grow because they enable him to increase production per acre, or reduce costs per tonne, and give grain of similar or greater unit value by meeting the preferences of the buyer. However, the farmers' requirements are not static, and at this time there are conflicting views in the UK on the changes in agronomy and varieties which may be needed to take into account cereal surpluses, reduction in support measures, and opportunities for exports. The problems arise from remarkable production achievements. For the five years 1971-75 the average yield in the UK was 4.5 tonnes per hectare and total annual production was 5.04 million tonnes from 1.12 million hectares. In 1984, when the weather was very favourable, the average yield reached 7.7 tonnes per hectare from 1.94 million hectares, giving a total crop of 15 million tonnes. Although production fell in 1985 to an estimated 12.5 million tonnes it is abundantly clear that UK farmers now have the ability to produce more wheat in total than the national requirement, at present some 10 million tonnes for all purposes. The content of home-grown wheat in bread grists has also risen greatly, to an average of more than 70% in 1984 and frequently much more than 90% for the standard white loaf. The milling and baking industry, however, still imports about 0.7 million tonnes of Canadian wheat for bread making, and this figure will be greater following the wet 1985 harvest.

The increase in yield per hectare is a measure of the ability of varieties and advances in agronomic practices to exploit the UK climate. Between 1971 and 1985 nitrogen fertiliser applications rose from an average of 80 kg N/ha to 180 kg N/ha or more. Fungicide use on wheat has also come into vogue, from practically nil in 1971, when suitable chemicals were not available, to the two or even three applications commonly made in 1985. As a consequence, some organisations are of the opinion that production should be cut by reducing inputs, for example by a tax on nitrogen, and that this would also have environmental benefits. However, the use of high inputs has greatly increased the advantage of the UK grower in average yield, which the large exporting countries cannot follow due to their continental climates. For example, in the early 1970's average yields in the UK exceeded those in the USA by 2 t/ha, this differential increased to 5 t/ha in 1984 (Bingham *et al.*, 1985).

In the UK, the total variable costs of seed, fertilisers, herbicides and protectant chemicals amount to not more than 30% of the value of an average wheat crop. We expect that the UK grower will need to obtain even higher average yields in a freer market and high inputs will continue to be necessary to reduce the cost per tonne. Further improvements in bread-making quality will be essential for home use and for export. It should also be possible to reduce the number of fungicide applications, though there can be little prospect of breeding varieties with such good disease resistance that they will not respond to a single application at ear emergence. For these reasons I will take, as examples, new developments in hybrid varieties, breeding for protein quality, and resistance to eyespot *Pseudocercosporella herpotrichoides*.

HYBRID WHEAT

The Institute first experimented with hybrid wheat in the 1970's. The work was based initially on the cytoplasmic system and later used ethrel, as a primitive male gametocide, and a spontaneous recessive mutant for male sterility. The mutant was identical to that in Cornerston (Laabassi, 1979; Bingham, 1983). The experiments gave levels of hybrid vigour for yield up to 15% above the higher yielding parent. In the event, work with cytoplasmic male sterility was discontinued, mainly because of time scale difficulties in developing parents, and with the nuclear gene for male sterility because it could not be applied commercially.

In the 1980's the situation has changed dramatically with the development of chemical hybridising agents (CHA) by several companies. These have led to the submission to UK National List Trials of the first wheat hybrids and it seems very probable that hybrid wheats will be introduced commercially in the UK within the next few years. The Institute does not have a gametocide of its own, so the work now reported has in the main resulted from collaboration with Shell UK, and with Rohm and Haas. It involves 140 F_1 hybrids grown in yield trials at Cambridge in 1985 from seed produced by the companies, and F_1 seed production plots of 460 new hybrids at the Institute, also grown in 1985.

Table 1. Use of chemical hybridising agent to produce F_1 grain. Date of ear emergence and weight of grain harvested from plots 10.5 x 1.2 m.

Female parent	Ear emergence	Male parent Rendezvous 18 June 9.4 kg	Male parent 4697/6 15 June 8.7 kg
Rendezvous	19 June	-	3.9
Norman	18 June	6.0	2.3
Brimstone	18 June	6.9	3.5
Virtue	17 June	8.7	4.3
4471/38	16 June	8.9	6.7
4909/13	13 June	9.0	6.1

The F_1 seed production plots in 1985 used a Rohm and Haas CHA with the female plots each 10.5 x 1.25 m in a 1:1 ratio with the male. The weather around anthesis was the wettest and coldest for many years yet the seed set in many crosses was remarkable, reaching 85% or more of the yield of the male in some combinations (Table 1). As expected these production plots confirmed large differences between lines in suitability for use as male, clearly related to the degree of anther extrusion, anther size, and the overall length of the flowering period. There were also surprisingly large differences between lines in female receptivity which were not dependent on date of flowering and could not be related to any difference which had been noticed in floral morphology. The hybrid seed was of good appearance and electrophoresis of the glutenin proteins showed that the level of hybridity was generally more than 95%, except for two or three very late flowering females. The results of this one year's experience indicate that the technical problems in producing hybrid seed can be overcome even in the UK climate. However, there are serious limitations in the range of hybrids that can be made due to varietal differences in pollen release and female receptivity as well as in time of flowering. For these reasons many of the highest yielding varieties in NW Europe cannot be used as either male or female parent for F_1 hybrids.

The yield trials of F_1 hybrids in 1985 were grown with the husbandry treatments normally used for trials of advanced breeding lines. The plots were 4.5 x 1.25 m, drilled at 110 kg seed/ha, N top-dressed at 125 kg/ha, and received either a comprehensive or nil fungicide treatment. The F_1 yields were commonly 10-12% greater than the higher yielding parent with fungicide treatment, and there was little indication from distribution of yield that these figures might be easily exceeded. Without fungicide treatment the effect of heterosis was relatively greater, probably due to the dominance of resistance to some foliar diseases (Tables 2 and 3).

Table 2a. Grain yield of F_1 hybrids and parents, fungicide treated.

♂ Aquila 8.6 t/ha	Yield % Aquila		Heterosis % mid-parent
♀	♀	F_1	
Norman	97.4	111.5	+ 12.8
Rendezvous	95.9	111.0	+ 13.1
Gawain	104.6	116.9	+ 14.6
3615/9	103.2	110.2	+ 8.6
3547/46	103.1	112.6	+ 11.1
3489/24	98.6	111.7	+ 12.4
LSD 0.05	6.8	6.8	

Table 2b. Grain yield of F_1 hybrids and parents, without fungicide treatment.

♂ Aquila 5.7 t/ha	Yield % Aquila		Heterosis % mid-parent
♀	♀	F_1	
Norman	85.4	112.8	+ 20.1
Rendezvous	111.2	122.8	+ 17.2
Gawain	107.7	120.2	+ 16.4
3615/9	93.0	109.1	+ 12.6
3547/46	96.8	102.4	+ 4.0
3489/24	98.1	102.6	+ 3.6
LSD 0.05	12.0	12.0	

If the price of F_1 hybrid seed was double that for first generation multiplication seed (EEC certified C1), the increase in yield needed to cover the extra cost of seed for an average wheat crop in the UK would be about 5% (Table

Table 3a. Grain yield of F_1 hybrids and parents, fungicide treated.

♂ Voyage 9.4 t/ha	Yield % Voyage		Heterosis % mid-parent
♀	♀	F_1	
Mercia	91.5	105.3	+ 9.6
3615/9	93.7	102.1	+ 5.3
3547/46	93.6	102.5	+ 5.7
3489/24	89.4	108.6	+ 13.6
LSD 0.05	6.8	6.8	

Table 3b. Grain yield of F_1 hybrids and parents, without fungicide.

♂ Voyage 6.3 t/ha	Yield % Voyage		Heterosis % mid-parent
♀	♀	F_1	
Mercia	92.0	112.3	+ 16.3
3615/9	85.4	103.4	+ 10.7
3547/46	88.8	114.6	+ 20.2
3489/24	90.1	121.3	+ 26.3
LSD 0.05	12.0	12.0	

Table 4. Increase in yield required to cover seed cost of hybrid wheat.

Conventional variety seed at	£ 280/t
Hybrid variety seed at	£ 560/t
Value of crop grain	£ 108/t

Seed cost £/ha at 150kg/ha		Equivalent crop increase		
Conventional	Hybrid	t grain	% 7.5t crop	% 10t crop
42	84	0.39	5.2	3.9

4). Farmers on more productive soils would grow hybrids on this basis. F_1 hybrids would, however, be less attractive in comparison with second generation (C2) or with farm-saved seed. We are, therefore, giving consideration to F_2 as the farm crop. Seed costs might then be little greater than the C2 of a conventional variety and hybrids would be sown much more widely.

There would be an additional hidden benefit in an F_2 hybrid. The seed yield of the line treated with the CHA to produce the F_1 would be less critical, so a wider range of both male and female lines could be used. Limited evidence indicates that the loss of heterosis for yield in F_2 might in practice be less than half, especially where there are gains in disease resistance due to dominance and mixture effects.

Farmers already have experience with variety mixtures, so uneveness in crop appearance would not be a handicap. Authenticity of seed could be controlled by certification of the F_1 seed production stocks. Farmer acceptance of F_2 hybrids would depend on performance in yield and in grain quality. To meet these objectives some additional breeding input would be needed to limit segregation for important performance characters. For example, parental lines could be matched for the major genes which control semi-dwarfness and glutenin proteins.

Table 5. Twenty F_1 wheat hybrids. Harvest components of yield, field trial, fungicide treated, Cambridge 1985.

Yield component	% Mid-parent	% Higher yielding parent
Grain yield	+ 10.8	+ 8.1
1 000 grain wt	+ 11.1	+ 9.4
Ears/m²	− 0.8	+ 1.4
Grains/ear	− 0.2	+ 0.1
Straw yield	+ 6.5	+ 10.1
Biomass	+ 8.5	+ 9.0
Harvest index	+ 2.6	− 0.2
Height	+ 6.2	+ 7.9

Data from Austin, R.B., Ford, M.A., Morgan, C.L. and Chowdhury, S. (unpublished).

The hybrid investigations in 1985 included a yield component analysis for a sample of the F_1 hybrids grown with fungicide treatment (Austin, R.B., Ford, M.A., Morgan, C.L. and Chowdhury, S., unpublished). Heterosis for yield was almost entirely due to increases in 1000 grain weight (Table 5). These results are also in accordance with the earlier experiments of Laabassi (1979) and with the results of a further set of hybrids grown in 1985 (Table 6) to evaluate the effect of the very strong semi-dwarfing gene *Rht*$_3$ when heterozygous (Gale, Salter, Curtis, and Angus, 1986). In this experiment a line homozygous for *Rht*$_3$ and near isogenic to Maris Huntsman (six backcrosses) was

Table 6a. Effects of RHt_3 and heterosis in F_1 hybrids. Fungicide treated trial, control yield 7.7t/ha.

Control	Yield % control	No. ears /m²	No. grains /ear	1000 grain wt g
Huntsman (rht_3 rht_3)	89.8	473	41.0	57.8
Huntsman (Rht_3 Rht_3)	64.3	403	52.5	46.9
Huntsman (Rht_3 rht_3)	93.1	470	58.9	47.5
7 varieties (rh_3 rht_3)	87.2	524	45.8	47.6
F_1 Huntsman x 7 varieties (Rht_3 rht_3)	106.7	467	58.9	50.2
LSD 0.05	8.6	76	2.6	1.1

Table 6b. Heterosis in F_1 hybrids calculated as $F_1/((\text{Huntsman} + \sigma \text{ parent})/2)\%$. Fungicide treated trial, control yield 7.7 t/ha.

♂ (rht_3 rht_3)	Effect measured	♀ Huntsman Rht_3 Rht_3 Yield	No. ears /m²	No. grains /ear	1 000 grain wt g
Huntsman	Rht_3 rht_3	+ 3.7	− 0.4	+ 43.7	− 17.7
7 varieties	Rht_3 rht_3 + background	+ 20.7	− 8.4	+ 36.3	− 4.8

crossed as female to Maris Huntsman and to seven varieties without a semi-dwarfing gene. The gene *Rht_3* is too extreme when homozygous for use in pure line varieties and gave low yields in 1985. The hybrid with Maris Huntsman showed that the main effects of *Rht_3* when heterozygous, were to greatly increase grain number per ear but to reduce 1000 grain weight so that there was little or no effect on yield. Hybrids with the other parents showed high heterosis for yield mainly due to 1000 grain weight. Thus, *Rht_3* increased grain number and heterosis enabled the hybrids to fill the grain more adequately.

On first examination, the results of these experiments might be considered to conflict with biometrical theory and experience in breeding varieties. It is widely accepted that heterosis for yield in wheat is mainly due to dispersion of additive dominant genes between parents, so that heterosis can be fixed in pure lines. The results of the hybrid trials might therefore indicate that increased yield in pure lines would be expressed only in 1000 grain weight. In practice, varietal improvements can be seed in any one or in combinations of the harvest components of yield. The explanation seeds to be that breeders deliberately or inadvertently use a range of genes which determine grain number per square metre by affecting number of ears, spikelets per ear, and grain number per spikelet. Such genes are common and large in effect but they do not directly increase yield, or have only a minor effect when breeding lines are seriously deficient in grain number per square metre. On this basis breeding for increased yield is dependent mainly on fixing heterosis for those physiological characters which determine ability to fill the grain. This explanation is in agreement with the observation that heterosis for grain yield was found mainly in 1000 grain weight.

Even if F_1 hybrids are not commercially viable, hybrid trials will enable breeders to predict which crosses would be the most promising for line breeding. Chemical hybridising agents could also be used to produce partial or fully outbreeding populations and thereby increase the rate of recombination. Such populations could perhaps be improved by bulk selection methods and used at any stage in their development for the selection of pure line varieties. However, we have serious reservations about the efficiency of this system for our breeding situation. For this purpose the use of a CHA would not differ in principle from the use of a gene for male sterility. When we used such a gene, none of the pure lines selected after two or more generations of outbreeding in a mixture of 25 hybrids were equal in performance to the best lines from a parallel pedigree selection programme. We believe populations have an overriding defect in lack of control of the material they contain. To be explicit, a large pedigree programme is in effect a closely controlled population with the advantage that whole crosses can be readily eliminated whenever they are found to be of general poor performance or have a major fault. With outbreeding populations we found that genetic weaknesses were much more difficult to identify and reject, and the time scale for producing a potential variety was unacceptably extended.

PROTEIN QUALITY

The most serious genetic limitation in breeding for bread-making quality in the UK lies in the inverse relationship between grain yield and protein content. When environmental factors have been taken into account, new varieties produce slightly more protein in the grain per hectare but this is not sufficient to offset increases in yield, so the genetic component of protein content has fallen (Bingham, *et al.*, 1985). There appears to be little scope to arrest this decline in an environment that is so favourable for nitrogen uptake that the soil reserve of available nitrogen is very low. The farmer has to use high rates of nitrogen fertiliser, commonly 180-200 N/ha, to obtain the protein content required by the miller, 11% at 14% moisture. For these reasons we have, for many years, been aware of the importance of protein quality in compensating for low protein content, and in reducing the need for the farmer to apply nitrogen fertiliser at rates above the optimum for grain yield alone (Pushman and Bingham, 1976).

During the last 10 years three developments of major value in testing methods and in the genetic analysis of bread-making quality have become available to breeders, namely near infrared reflectance (NIR) analysis, the sodium dodecyl sulphate (SDS) sedimentation test, and electrophoresis of glutenin proteins. These advances were adopted immediately and made it possible for breeding work to change into a much higher gear (Bingham, 1983). Now it seems likely that the first applications of molecular transformation to wheat breeding will be with genes for glutenin proteins (Flavell, *et al.*, 1984).

NIR gives rapid and accurate assessments of protein content, milling texture, and grinding resistance. It is non-destructive so the wholemeal sample can be used again for the SDS sedimentation test and for α-amylase determination. In our experience, the SDS sedimentation test is superior to the Pelshenke and Zeleny tests in detecting protein qualiy and uses a simply prepared wholemeal, whereas the Zeleny needs a white flour prepared to an exacting specification. We use the SDS sedimentation test from F_2, and for samples prepared previously we can do 1500 tests a day.

High molecular weight (HMW) subunits of glutenin play a central role in determination of the structural properties of gluten and hence dough strength and loaf volume (Payne, 1986). It has been shown by SDS polyacrylamide gel electrophoresis (SDS PAGE) that all varieties of wheat contain between three and five subunits whose structural genes are located on the long arm of homoeologous Group 1 chromosomes. The locus on Chromosome 1D codes for two subunits, the locus on 1B for one or two subunits, and that on 1A either for one subunit or none. There is also considerable allelic variation, more than 20 subunits have been detected in many different combinations.

SDS sedimentation tests of random lines of crosses segregating for these genes show that the HMW glutenin subunits differ in their effect on protein quality. Varieties of good bread-making quality may differ in the good subunits they possess, especially when they come from different breeding stables. Identification of these subunits and their genetic analysis has paved the way for systematic improvement of protein quality. For example, all varieties of good bread-making quality marketed from the PBI programme between 1935 and 1983 (including Holdfast, Maris Widgeon, Maris Freeman, Bounty, and Avalon) possess only one good glutenin protein, known as Subunit 1 (Chromosome 1A). By good fortune rather than design Moulin (1984) has inherited the good Subunits 17-18 (Chromosome 1B) from a Mexican line Yecora x CIANO 67, and Mercia (1985) has 5-10 (Chromosomes 1D) from the French variety Flanders. Moulin and Mercia were selected by the SDS sedimentation test before the glutenins had been characterised. The next step is to combine the good subunits of all three varieties on the expectation that protein quality will be improved. Single grains can be selected rapidly and precisely using the apex of the grain for the analyses. This leaves ample endosperm to grow on the embryo through a single seed descent generation.

The glutenin work is being extended to include several new subunits discovered in genetic resource collections. These include a Subunit, 2.2 Chromosome 1D, of unusually large molecular weight found in several old Japanese varieties (Payne, 1986). Another allele of the 1D locus has been detected in landraces from Iran and neighbouring countries. Apart from the hexaploid landraces, much greater variation in storage proteins has been found in diploid *Triticum* and *Aegilops* species. Amongst the *Aegilops* species alone there are numerous HMW glutenin subunits not found in bread wheat. A selection of these subunits is being transferred into wheat, using, where appropriate, lines deficient for Chromosome 5B and hence the *Ph* locus to induce pairing. The work has not yet reached the stage of testing for the effect of these new subunits on protein quality.

Recent studies have shown that a little over one third of the variation in the bread-making quality of both German and British varieties can be accounted for by variation in HMW glutenin subunits. This proportion rises to more than one half if varieties containing the rye 1B/1R translocation are excluded (Paye, 1986). The evidence for this conclusion is in correlations between a subunit score and National List gradings for bread-making quality. Part of the remaining variation will be due to variation in characters other than protein quality, including protein content, milling texture, and amylase activity. Some will undoubtedly be due to variation in other endosperm proteins. Comparable work with gliadins has now reached the stage where breeders can begin to apply it. For example the rye 1B/1R translocation now widely incorporated in varieties for its positive effects on disease resistance and yield has serious adverse effects on bread-making quality due to modifications in gliadin composition. The presence of the 1B/1R translocation is being identified in breeding lines by isoelectric focussing of the glucose phosphate isomerase of wheat and rye isozymes. (Chojeci and Gale, 1982).

RESISTANCE TO EYESPOT *(Pseudocercosporella herpotrichoides)*

Resistance to eyespot was first discovered in Cappelle-Desprez and was one of the most important characteristics of that variety, leading to its use as a parent of most new varieties grown in the UK. The resistance of Cappelle-Desprez is not, however, sufficient to overcome the need for fungicide treatment when climatic factors favour the disease. Improvement in resistance to eyespot has become urgent since the discovery of isolates tolerant to MBC fungicides in 1981. Varieties are becoming available with a much higher degree of resistance derived from *Aegilops ventricosa* via the French line VPM 1. The first of these in the UK, Rendezvous, combines resistance from the two sources Cappelle-Desprez and VPM 1.

Resistance to eyespot in VPM 1 is mainly due to a translocation from *A., ventricosa* into Chromosome 7D (Law and Worland, 1986), but may also be conditioned by *A. ventricosa* cytoplasm (C.A. Bowman, pers. comm.). This finding has implications for the further development of varieties with resistance to eyespot and for hybrid wheats.

Firstly, although Rendezvous has given good grain yields, we have not yet obtained a line which combines this resistance with yields equal to the highest yielding feed wheats. We are therefore producing reciprocal lines to investigate effects of the *A. ventricosa* cytoplasm on yield. Secondly, Rendezvous is an exceptionally good male for the production of hybrids, so we also need to know about

Table 7. Seedling eyespot test 1985. Score based on penetration of leaf sheaths. Low score indicates resistance.

Cultivar	Score		
VPM 1	4.46		
Rendezvous	4.91		
Mercia	5.00		
Renard	7.18		
Cappelle	5.71		
Holdfast	7.96		
♀ ♂ Rendezvous x Renard	5.13	)	
		)	mean 4.85
Renard x Rendezvous	4.58	)	
Rendezvous x Mercia	4.92	)	
		)	mean 4.58
Mercia x Rendezvous	4.25	)	
LSD 0.05	0.54		

dominance fo the nuclear component of the resistance. Preliminary indications based on seedling tests for resistance to eyespot (Table 7) are that the resistance is highly dominant and that the cytoplasmic component is small. These results need to be confirmed in field trials.

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SYMPOSIUM DISCUSSION

Dr A. Rathjen, University of Adelaide

Commenting on the speed of breeding techniques. We grow two generations a year, so the difference in speed between the single seed descent, the haploid system, and the pedigree and F2 progeny systems, is very little.

Dr K.M. McWhirter, University of Sydney

The general expectation of cereal growing is negative heterosis for protein content. In hybrids this has been observed in wheat in Canada, and in maize and sorghum. Is that what you are observing with these F1 hybrids?

Bingham

I expect so — I have not yet seen the protein results which are probably being done at present. I do not think there would be any other possibility because there is normally an inverse relationship between protein content and yield, which means that if the hybrids are high-yielding they will have low protein and then you have to put on more nitrogen.

McWhirter

Do you use parents for elevated protein?

Bingham

We have been unable to breed for protein content in the UK. We've used Lancota 66 and other derivatives, but they do not work in our situation where conditions are so good for nitrogen uptake. Though we are applying high nitrogen we are in fact using the nitrogen that is available very efficiently.

Dr W. Bushuk, University of Manitoba

Is the relationship you showed between high molecular weight glutenin sub-units and baking quality a functional relationship, or because of pedigree and other linkages with other glutenin protein components.

Bingham

I am sure it is a functional relationship. All the varieties produced at PBI since Biffen's time which have good bread making qualities all have that band one and none of the feed wheats have it. Also, I'm convinced by the relationships that Peter Payne has shown with the S.D.S. result.

However, I am not suggesting that these high molecular weight glutenins are the only thing — they are not. Payne has done an analysis of German and UK wheats on the national list, and related a score for presence of different glutenin sub-units to the national list classification for breadmaking. He has found that

about one third of the difference is accounted for. If varieties which have the 1B 1R translocation are demanded, the 1B 1R translocation accounts for half. We think it is very important but by no means the whole story. There is obviously more in the low molecular weight glutenins, the gliadins, α amylase activity and many other things.

Mr L.W.M. Suijs, Geertsema Zaden B.V.

You mentioned the gametocide use of Rohm and Haas. Have you any experience with other gametocides?

Bingham

We have experience with several, but the only one we have had made hybrids with on a very large scale is with Rohm and Haas.