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The Inheritance of Anther Extrusion in Two Spring Wheat Varieties

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Summary. Anther extrusion was observed on two occasions under glasshouse conditions in two spring wheat varieties which showed different levels of expression of this character, and on F_1 and F_2 generations of reciprocal crosses between them. The results indicated that anther extrusion was controlled by few, possibly only two, genes with additive effects but had a low heritability. The association of pronounced anther extrusion and particular patterns of extrusion in the ear are suggested as the basis for rapid selection in glasshouse conditions for anther extrusion.

Introduction

The use of cytoplasmic male sterility in the production of F_1 hybrid wheat necessitates efficient wind-pollination at two stages in the seed production process: in the multiplication of the male-sterile lines to be used as female parents and in the production of the F_1 seed.

The effectiveness of wind-pollination will obviously depend to a very great extent on climatic factors but must also depend on the quantity of pollen that is released into the air by the male parent at the critical time. In a review of the flowering biology of wheat, de Vries (1971) shows that pollen release can be affected by a large number of factors and Joppa, McNeal and Berg (1968) found that the most significant of these was the extent of anther extrusion.

A number of semi-dwarf wheat varieties, which would otherwise be useful in the development of hybrid wheat, are difficult to use because they extrude only a very small proportion of their anthers from their florets. The object of the present study was to investigate the inheritance of differences in anther extrusion and the possibility of introducing pronounced extrusion into material having poor extrusion.

Materials and Methods

The observation of the number of anthers extruded is difficult in the field as the constant movement of the crop in the wind causes the anthers to drop off the ear shortly after extrusion. The work reported here was, therefore, carried out with plants grown in the still air of a glasshouse. Under these conditions extruded anthers stayed in position on the ear indefinitely if the plants were left undisturbed so that it was possible to obtain accurate counts of the numbers of anthers extruded.

Previous observation had shown that the German spring wheat variety Sirius always extruded a large proportion of its anthers while the Indian semi-dwarf variety Sona 227 appeared never to extrude any anthers. Reciprocal crosses were made between these two varieties and the parents, F_1 and F_2 generations were grown together on two occasions. The material was first grown under artificial lights during the winter and reached anthesis at the end of February and the beginning of March. The material was then sown again in March and reached anthesis in July. In the winter sowing the parental populations consisted of 15 plants each, the F_1 populations of ten plants each and the F_2 populations of 100 plants each. In the summer sowing the corresponding figures were 30, 15 and 100 plants respectively.

From each sowing observations were confined to the first three ears to emerge on each plant. Approximately ten days after ear emergence the number and position on the ear of all fully extruded anthers were noted and the data were checked on successive days to ensure that all extruded anthers were recorded.

At harvest the number of grains set on each ear was recorded. For each ear the number of anthers extruded was expressed as a percentage of the total number of anthers in the ear which was taken to be three times the number of grains set. The data were then converted to angles for further analysis.

Results

Parental and F_1 populations

The mean transformed anther extrusion rates per ear for first, second and third ears of the parental and F_1 populations (Table 1) differed, in some cases significantly, both within and between each population. In the winter sowing the first and second ears of F_1 Sirius × Sona 227 showed significantly higher anther extrusion than corresponding ears in the reciprocal F_1. This F_1 population was grown on a different glasshouse bench from the other material and ear emergence was earlier (Table 2). In the summer sowing all the material was grown on the same glasshouse bench, ear emergence times were comparable in the two F_1 populations and the significant differences in anther extrusion between ears of the F_1 populations were not repeated. Since the relative ear emergence times of F_1 Sona 227 × Sirius and the parental lines was roughly similar in both sowings it is likely that the high anther extrusion of ears of F_1 Sirius × Sona 227 in the winter sowing was

Table 1. *Mean percentage anther extrusion per ear (angular transformation)*

Sowing	Ear	Sirius	F_1 Sirius × Sona 227	Mid parent point	F_1 Sona 227 × Sirius	Sona 227
Winter	1st.	46.5 ± 11.1 ab	38.4 ± 4.6 bc	24.8	21.5 ± 7.7 ef	3.0 ± 3.9 g
	2nd.	45.2 ± 16.1 abc	33.0 ± 3.5 cd	22.8	19.4 ± 12.1 ef	0.3 ± 1.2 gh
	3rd.	42.5 ± 14.5 abc	27.1 ± 8.4 de	21.9	20.3 ± 13.8 ef	1.2 ± 2.9 gh
Summer	1st.	37.7 ± 6.5 c	17.8 ± 5.2 f	19.4	16.8 ± 4.7 f	1.0 ± 2.2 h
	2nd.	49.5 ± 8.8 a	27.0 ± 10.0 def	23.4	27.6 ± 13.9 def	0.3 ± 1.6 h
	3rd.	53.8 ± 8.9 a	23.6 ± 11.6 def	27.3	25.9 ± 18.3 def	0.8 ± 2.4 h
Average		45.9 ± 5.56 x	22.8 ± 4.65* y	23.3 ± 2.67 y	21.9 ± 4.09 y	1.1 ± 1.00 z

Means and averages having the same letter suffix are not significantly different ($P = 0.05$).
* Average of Summer sowing only.

Table 2. *Mean number of days to ear emergence from 1st February or 1st June*

Sowing	Ear	Sirius	F_1 Sirius × Sona 227	F_1 Sona 227 × Sirius	Sona 227
Winter	1st.	28.8	11.3	21.1	25.8
	2nd.	35.8	19.3	27.5	28.5
	3rd.	38.2	20.6	28.1	28.8
Summer	1st.	29.7	20.5	20.1	23.9
	2nd.	33.8	25.5	25.9	27.1
	3rd.	36.5	26.9	26.6	29.1

due to their being grown on a different glasshouse bench and may have been associated with the more rapid development of the plants. The data from winter sown F_1 Sirius × Sona 227 were thus not strictly comparable with the rest of the data and were excluded from further analyses.

In the summer sowing, in the Sirius and both F_1 populations the anther extrusion of first ears was clearly lower than that of second ears although the ears of the F_1 population emerged earlier than those of Sirius (Table 2). The environmental effect which produced this depression of anther extrusion must have occurred, therefore, before ear emergence during the development of the ears. These large influences of the environment on the expression of anther extrusion suggest that anther extrusion can only have a moderate or low heritability and that in terms of percentage anther extrusion each ear on a plant develops in a different environment. The mean percentage anther extrusion of first, second and third ears from each sowing is thus the average extrusion over six different environments and, although this range of environments will not necessarily be the same for genotypes with differing maturities this average is likely to be the best overall estimate of the expression of anther extrusion within any one genotype. These averages (Table 1) show that the parental types behaved very differently and that the two F_1 populations, while not significantly different from each other or the mid-parent, were significantly different from either of the parental types.

Rajki (1960, 1962) found that in two varieties the number of anthers extruded was in direct proportion to the number of open flowering florets, which she defined as those extruding at least one anther. She also found that the degree of open flowering was higher in the basal florets of each spikelet. The number of basal and central florets from which at least one anther had been extruded was calculated from the observations of anther extrusion for each ear of the Sirius and F_1 populations. The percentage of open flowering florets was then calculated by expressing this number as a proportion of the total number of florets in which grain had set. The correlation between the percentage anther extrusion and the percentage of open flowering florets of each ear of the three populations was 0.951 ($P < 0.001$) for the winter sowing and 0.971 ($P < 0.001$) for the summer sowing. 88 per cent of the total number of open florets were basal in the Sirius populations and 72 per cent in the F_1 populations. Thus the material which extruded appreciable numbers of anthers behaved in the same way as that observed by Rajki.

This analysis of the pattern of anther extrusion in the parental and F_1 populations was taken further by counting the numbers of basal and central florets that extruded one, two or all three anthers (Table 3). For basal florets these counts show that Sona 227 extruded almost exclusively only one anther per floret

Table 3. *Mean number of basal and central florets extruding one, two or three anthers expressed as a percentage of the number of florets extruding any anthers*

Florets	Anther Number	Sirius	F_1 Sirius × Sona 227	F_1 Sona 227 × Sirius	Sona 227
Basal	1	33.33 c	65.00 d	65.73 d	96.00 e
	2	31.27 c	26.80 c	23.72 c	4.00 ab
	3	35.40 c	8.18 b	10.57 b	0.00 a
Central	1	40.28 cd	59.45 d	64.68 d	100.00 e
	2	40.76 cd	31.02 c	25.77 bc	0.00 a
	3	18.96 bc	9.53 b	9.52 b	0.00 a

Within either the basal or central florets figures having the same letter are not significantly different as shown by t-tests on data transformed to angles.

while the F_1 populations extruded predominantly one anther per floret with a smaller proportion of florets extruding two and three anthers. Sirius, on the other hand, which had the highest percentage anther extrusion had a higher proportion of florets extruding all three anthers per floret. The parental and F_1 populations thus fell into three distinguishable classes differentiated not only by level of percentage anther extrusion but also by the proportion of open flowering florets which extruded one, two or three anthers.

A similar differential pattern of extrusion of one, two or three anthers was shown by central florets. Since the central florets are invariably smaller than basal florets this was evidence that the pattern of anther extrusion was not dependent on the size of the floret. It may well be that more frequent anther extrusion in basal than in central florets is only a reflection of the fact that basal florets would have less resistance than central florets to opening merely as a result of their position on the ear.

F_2 *populations*

In comparing the range of expression of percentage anther extrusion per ear in the F_2 populations with those of the parental and F_1 populations, the data from each ear of each population at each sowing were pooled, transformed to angles, and the numbers of ears that fell into successive five per cent classes counted to give overall frequency distributions. These distributions were than tested for normality by calculating the theoretical normal distributions and comparing these with the observed distributions by means of chi squared tests for goodness of fit (Table 4) following the methods detailed by Leonard, Mann and Powers (1957). Too few degress of freedom were available to test the normality of the Sona 227 distribution but the distributions of the Sirius and F_1 populations were not significantly different from normality while that of the F_2 population was highly so.

The distribution in the F_2 population would be expected to fit the normal curve if many genes were involved especially if their heritability were low. The normal distributions and large variances of the Sirius and F_1 populations are indicative of the low heritability of anther extrusion so the fact that the F_2 distribution was not a normal distribution suggested that relatively few genes might be involved.

The means of the F_1 and F_2 populations (Table 4) were not significantly different ($t_{1187} = 0.141$, $P = 0{,}8-0.9$) and lay approximately half way between the parental means. This suggested that inheritance of anther extrusion might be controlled by additive gene action. On applying Mather's C scaling test (Mather and Jinks 1971) to the generation means the quantity C ($4 \times F_2$ mean $- 2 \times F_1$ mean $-$ mean Sirius $-$ mean Sona 227) was not significantly different from zero ($C = 1.21 \pm 3.119$). This indicated that the generation means depended only on the additive effects of the genes and that there were no interactions between non-allelic genes and no disturbing factors such as differential viability or fertility.

The simple hypotheses that anther extrusion was controlled by either one or two additive genes were than tested following Powers' Partitioning Method of Genetic Analysis as set out by Leonard et al. (1957). Powers' analysis visualises the F_2 generation as a composite of genotypes each of which fluctuates normally about its own particular mean. The mean and variation of genotypes present in the F_2 but not represented by parental or F_1 genotypes are estimated by making simple assumptions as to the relationship between mean and variance. The corresponding normal distributions are then combined with the observed distributions of parental and F_1 genotypes to develop a genetic hypothesis against which the obtained frequency distribution of the F_2 generation can be tested.

To test the hypothesis of a single additive gene the assumption was made that Sirius, the parental line with pronounced anther extrusion, was homozygous for the gene which caused, or at least did not suppress, anther extrusion, that Sona 227 was homozygous for an allele at the same locus which did not cause, or which suppressed, anther extrusion, and that the F_1 plants were heterozygous. These three genotypes would be expected in the F_2 population in the percentage ratio 25:25:50. The percentage frequencies observed in the two parental types and the F_1 (Table 5) were multiplied by the appropriate expected F_2 genotypic percentage to give the partition frequencies given in Table 6. By summing within each frequency class the expected percentage frequency distribution for an F_2 population based on the segregation of one additive gene was derived.

To test for the similarity or otherwise of this theoretical F_2 distribution to the observed F_2 distribution it was next necessary to apply a chi squared test for homogeneity. To do this the theoretical F_2 distribution arrived at in Table 6 was converted to a numerical basis comparable with the observed distribution by multiplying the percentage in each frequency class by 1118/100. The two distributions were then placed in a contingeny table as shown in Table 7. The proportion of the overall total expected for each cell of the contingency table was then calculated and these are included in Table 7 in parenthesis. Finally a chi squared for 12 degrees of freedom was computed using the observed data and the expected proportion calculated in the contingency table. This chi squared was 198.608 with a probability of less than 0.001. Thus the distributions were not homogeneous and the hypotheses that inheritance of anther extrusion was due to a single additive gene was thus disproved.

Table 4. *Observed and theoretical frequency distributions for anther extrusion and test for goodness of fit to normality*

Popul.	Frequency distribution in numbers. Upper limit of class																	N	d.f.	χ^2	P
	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85				
Sona																					
O	108	15	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	124			
T	117.20	6.77	0.03	—	—	—	—	—	—	—	—	—	—	—	—	—	—	124.00			
Sirius																					
O	—	—	1	1	2	5	11	20	22	20	20	14	1	6	4	—	—	127	4	1.954	0.7—0.8
T	—	—	0.52	1.16	2.98	6.17	11.21	16.69	20.71	20.96	18.57	13.41	8.06	3.99	1.73	0.61	0.18	126.95			
F_1																					
O	4	9	13	18	14	17	8	7	3	2	1	—	—	—	—	—	—	96	2	1.881	0.3 —0.5
T	6.17	7.28	11.62	15.32	16.71	15.06	11.22	6.80	3.58	1.52	0.52	0.15	0.04	—	—	—	—	95.99			
F_2																					
O	107	128	152	158	144	116	81	76	66	40	15	16	6	10	0	2	1	1118	10	79.99	< 0.001
T	135.28	88.88	116.83	142.55	146.57	138.97	121.64	89.78	61.38	38.57	20.35	10.06	4.58	1.68	0.67	0.14	0.06	1117.99			

Population	Mean	Variance	Standard Deviation
Sona 227	0.99	6.25	2.50
Sirius	45.98	136.89	11.70
F_1	22.32	129.28	11.37
F_2	22.60	224.70	14.99

Brackets indicate classes combined to give at least ten individuals per class for computation of χ^2.
O = Observed frequency; T = Theoretical frequency.

Table 5. *Frequency distribution of observed anther extrusion of parental,* F_1 and F_2 *populations expressed as percentages*

Population	Frequency distribution in percentages. Upper limit of class																			1 additive gene	2 additive genes
	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	Total		
Sona 227	87.10	12.10	0.80	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100.00	25.00	6.25
F_1	4.17	9.38	13.54	18.75	14.58	17.71	8.33	7.29	3.13	2.08	1.04	—	—	—	—	—	—	—	100.00	50.00	37.50
Sirius	—	—	0.80	0.80	1.57	3.94	8.66	15.75	17.32	15.75	15.75	11.02	0.80	4.72	3.15	—	—	—	100.03	25.00	6.25
F_2	9.57	11.45	13.60	14.13	12.88	10.38	7.25	6.80	5.90	3.58	1.34	1.43	0.54	0.89	0.00	0.17	0.09	—	100.00		

Table 6. *Partitioning of the frequency distribution of an* F_2 *population on the basis of the frequency distributions of parental and* F_1 *genotypes assuming one additive gene*

Population	Frequency distribution in percentages. Upper limit of class																			
	Genotypes	2	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	Total
Sona 227	aa	21.78	3.03	0.20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25.01
F_1	Aa	2.08	4.69	6.77	9.38	7.29	8.86	4.17	3.65	1.57	1.04	0.52	—	—	—	—	—	—	—	50.02
Sirius	AA	—	—	0.20	0.20	0.39	0.99	2.17	3.94	4.33	3.94	3.94	2.76	0.20	1.18	0.79	—	—	—	25.03
Theoretical F_2	1AA:2Aa:1aa	23.86	7.72	7.17	9.58	7.68	9.85	6.34	7.95	5.90	4.98	4.46	2.76	0.20	1.18	0.79	—	—	—	100.06

Table 7. *Contingency table for chi squared test for homogeneity between the observed and theoretical F_2 distribution assuming one additive gene, calculated on the basis of number of individuals in each class*

Class Centre	F_2 population Observed	(Calculated)	Theoretical	(Calculated)	Subtotals
2.5	107	(186.88)	266.76	(186.88)	373.76
7.5	128	(107.16)	86.31	(107.16)	214.31
12.5	152	(116.08)	80.16	(116.08)	232.16
17.5	158	(132.55)	107.10	(132.55)	265.10
22.5	144	(114.93)	85.86	(114.93)	229.86
27.5	116	(113.06)	110.12	(113.06)	226.12
32.5	81	(75.94)	70.88	(75.94)	151.88
37.5	76	(80.43)	84.86	(80.43)	160.86
42.5	66	(65.98)	65.96	(65.98)	131.96
47.5	40	(47.84)	55.68	(47.84)	95.86
52.5	15	(32.43)	49.86	(32.43)	64.86
57.5	16	(23.43)	30.86	(23.43)	46.86
62.5	6	(4.12)	2.24	(4.12)	8.24
67.5	10	(11.60)	13.19	(11.60)	23.19
72.5	0	(4.42)	8.83	(4.42)	8.83
77.5	2	(1.00)	0.00	(1.00)	2.00
82.5	1	(0.50)	0.00	(0.50)	1.00
87.5	—	—	—	—	—
Sub totals	1118		1118.67		2236.67

Brackets indicate classes combined to give at least ten individuals per class for the computation of χ^2.

The possibility that two genes of equal effect were involved in the inheritance of anther extrusion was then considered. For this purpose it was assumed that Sirius was homozygous for both genes controlling pronounced anther extrusion and thus carried four effective alleles, that Sona 227 was homozygous for alleles at these two loci controlling lack of anther extrusion and thus carried no effective alleles for pronounced anther extrusion, and that the F_1 was heterozygous at both loci and hence carried two effective alleles. The expected percentage ratio of genotypes carrying zero, two and four effective alleles in an F_2 population would be 6.25: 37.50: 6.25 per cent respectively. As before by multiplying the observed percentage frequencies of the two parental types and the F_1 given in Table 5, by the appropriate expected F_2 genotypic percentage the partition frequencies for each genotype were calculated and are given in Table 8. By subtracting within each frequency class these partition frequencies from the observed F_2 percentage frequencies residual frequencies, given at the bottom of Table 8, were obtained. These are the partition frequencies ascribable to genotypes other than those of the parents and F_1 and thus represent the distribution of the genotypes carrying one or three effective alleles.

According to the hypothesis the residual partition distribution is expected to be a composite made up of the normal distributions of two genotype groups, those carrying one or three effective alleles, each having its characteristic mean and variance. Genotypes with one effective allele would be expected to have a mean between that of Sona 227 and the F_1 and genotypes with three effective alleles would be expected to have a mean between that of the F_1 and Sirius. Observations of the means and variances of the parental and F_2 types (Table 4) indicate that there is a positive relationship between them but that this relationship is not linear since the variance of the F_1 is nearly as large as that of Sirius. The variance of genotypes with three effective alleles would thus be expected to be much greater than that of those with one effective allele and this might cause the two distributions to overlap slightly.

It can be seen from Table 4 that the F_1 population mean falls in the 25 per cent frequency class. That part of the residual partition frequency distribution that falls below this class is thus probably due principally to genotypes carrying one effective allele while that part falling above it is probably due principally to those carrying three effective alleles. Each of these two groups of genotypes would be expected to contribute 25 per cent of individuals in an F_2 population. By alloting half the residual frequencies observed in the 20 and 25 per cent frequency classes to each genotype group the residual distribution can be further partitioned and ascribed to particular genotypes as shown in Table 9. The two sub-distributions so formed each consist of about 25 per cent of the F_2 distribution and do overlap slightly. It was possible to calculate means and variances for these two distributions and hence to construct their expected normal distributions.

To calculate the means the upper class limits were expressed as class centres as shown in Table 9. Each partition frequency was multiplied by its class centre with due consideration given to positive and negative values and the sum (SX) was divided by the total of the partition frequencies to give the means. In order to calculate the variances it was assumed that a sufficiently close estimate of the actually non-linear relationship between parental and F_1 means and variances would be given by assuming linearity of variances between Sona 227 and the F_1 and then again between the F_1 and Sirius. On this assumption the total variance of each of the genotype groups in Table 9 could be estimated from the formula $y = mx + b$.

For the genotypes with one effective allele an estimate of m was obtained from:

$$m = \frac{\text{variance } F_1 - \text{variance Sona } 227}{\text{mean } F_1 - \text{mean Sona } 227} = \frac{123.03}{21.33} = 5.77$$

and an estimate of b from:

$$\begin{aligned} b &= \text{variance Sona } 227 - (m \times \text{mean Sona } 227) \\ &= 6.25 - (5.77 \times 0.99) = 0.46 \end{aligned}$$

The total variance was then derived by substituting in $y = mx + b$. For genotypes with three effective alleles the total variance was calculated in a similar manner using the means and variances of the Sirius

Table 8. *Partitioning of the frequency distribution of the observed F_2 population on the basis of the frequency distributions of parental and F_1 genotypes assuming two additive genes*

Population	Frequency distribution in percentages. Upper limit of class																				Theoretical percentage in F_2
	Genotypes	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	Total	
Observed F_2	AABB··· aabb	9.57	11.45	13.60	14.13	12.88	10.38	7.25	6.80	5.90	3.58	1.34	1.43	0.54	0.89	0.00	0.17	0.09	—	100.00	100.00
Sona 227 (0 alleles)	aabb	5.44	0.76	0.05	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.25	6.25
F_1 (2 alleles)	AaBb AAbb aaBB	1.56	3.52	5.08	7.03	5.47	6.64	3.12	2.73	1.17	0.78	0.39	—	—	—	—	—	—	—	37.49	37.50
Sirius (4 alleles)	AABB	—	—	0.05	0.05	0.10	0.25	0.54	0.98	1.08	0.98	0.98	0.69	0.05	0.30	0.20	—	—	—	6.27	6.25
Residual	Aabb aaBb AABb AaBB	2.57	7.17	8.42	7.05	7.31	3.49	3.59	3.09	3.65	1.82	−0.03	0.74	0.49	0.59	−0.20	0.17	0.09	—	50.01	50.00

Table 9. *Frequency distributions of the one effective allele and three effective allele genotypes*

Class centres																					
Genotypes	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	72.5	77.5	82.5	87.5	Total	SX	Mean
Aabb aaBb	2.57	7.17	8.42	3.53	3.66	—	—	—	—	—	—	—	—	—	—	—	—	—	25.35	309.58	12.21
AABb AaBB	—	—	—	3.53	3.66	3.49	3.59	3.09	3.65	1.82	−0.03	0.74	0.49	0.59	−0.20	0.17	0.09	—	24.68	831.69	33.70

Table 11. *Observed or theoretical frequency distributions of F_2 genotypes or genotype groups expressed as percentages*

Population	Upper limit of class																				Theoretical percentage in F_2
	Genotypes	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	Total	
Sona 227	aabb	87.10	12.10	0.80	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100.00	6.25
	Aabb, aaBb,	19.50	20.24	23.19	19.19	11.45	4.69	1.39	0.30	0.04	—	—	—	—	—	—	—	—	—	99.99	25.00
F_1	AaBb, AAbb, aaBB,	4.17	9.38	13.54	18.75	14.58	17.71	8.33	7.29	3.13	2.08	1.04	—	—	—	—	—	—	—	100.00	37.50
	AABb, AaBB,	0.64	1.33	3.29	6.44	10.96	14.79	16.93	16.50	12.77	8.42	4.71	2.09	0.79	0.26	0.06	—	—	—	99.98	25.00
Sirius	AABB	—	—	0.80	0.80	1.57	3.94	8.66	15.75	17.32	15.75	15.75	11.02	0.80	4.72	3.15	—	—	—	100.03	6.25
Theoretical F_2	AABB···aabb	12.04	9.67	11.80	13.49	11.17	11.76	8.25	7.92	5.46	3.87	2.55	1.21	0.25	0.36	0.21	—	—	—	100.01	100.00

Table 10. *Means, variances and standard deviations observed or calculated for particular genotypes or genotype groups*

Population	Genotypes	Mean	Variance	Standard deviation
Sona 227 (0 alleles)	aabb,	0.99	6.25	2.50
1 allele	Aabb, aaBb,	12.21	70.99	8.43
F_1 (2 alleles)	AaBb, AAbb, aaBB,	22.32	129.28	11.37
3 alleles	AABb, AaBB,	33.70	132.96	11.53
Sirius (4 alleles)	AABB,	45.98	136.89	11.70

and F_1 populations. The calculated means, variances and standard deviations of the two genotype groups are given in Table 10 together with the comparable data from the parental and F_1 populations.

The normal distributions corresponding to the means and variances calculated for one and three effective allele genotypes were then built up using the Table of Normal Probability Integral (Fisher and Yates, 1963) and are given in Table 11 together with the observed percentage frequencies of the parental and F_1 populations taken from Table 5. Table 11 thus contains five normal distributions expressed in percentages each one representing the expected distribution of a genotype or group of genotypes. An overall theoretical F_2 distribution was next constructed by multiplying each frequency by the expected percentage F_2 proportion of the corresponding genotype or genotypes and summing within each frequency class. This theoretical F_2 distribution is given at the bottom of Table 11.

As before the similarity of otherwise of this theoretical distribution to the observed F_2 distribution was tested by means of a chi squared test for homogeneity the contingency table for which is given in Table 12. The homogeneity chi squared, this time for 10 degrees of freedom, was 18.070 which was just not significant ($P = 0.05-0.1$). The two distributions could thus be considered homogeneous and it could be concluded that the observed F_2 distribution can be explained by assuming only two additive genes of equal effect. However, while this analysis is suggestive of there being only two genes involved it cannot be regarded as conclusive since it involved assumptions as to the relationship of means and variances and the large variances involved made the distinction of overlapping distributions somewhat arbitrary. We can certainly conclude that the inheritance of anther extrusion involves more than one additive gene but can say no more than that it may possibly be controlled by as few as two.

Table 12. *Contingency table for chi squared test for homogeneity between the observed and theoretical F_2 distribution assuming two additive genes, calculated on the basis of numbers of individuals in each class*

Class Centre	F_2 population				
	Observed	(Calculated)	Theoretical	(Calculated)	Sub totals
2.5	107	(120.82)	134.64	(120.82)	241.64
7.5	128	(118.03)	108.07	(118.03)	236.07
12.5	152	(141.95)	131.90	(141.95)	283.90
17.5	158	(154.40)	150.80	(154.40)	308.80
22.5	144	(134.43)	124.86	(134.43)	268.86
27.5	116	(123.72)	131.45	(123.72)	247.45
32.5	81	(86.59)	92.18	(86.59)	173.18
37.5	76	(82.26)	88.52	(82.26)	164.52
42.5	66	(63.51)	61.03	(63.51)	127.03
47.5	40	(41.63)	43.26	(41.63)	83.26
52.5	15	(21.76)	28.53	(21.76)	43.53
57.5	16	(14.77)	13.54	(14.77)	29.54
62.5	6	(4.38)	2.77	(4.38)	8.77
67.5	10	(7.01)	4.02	(7.01)	14.02
72.5	0	(1.18)	2.37	(1.18)	2.37
77.5	2	(1.00)	0.00	(1.00)	2.00
82.5	1	(0.50)	0.00	(0.50)	1.00
87.5	—	—	—	—	—
Sub totals	1118		1117.94		2235.94

Brackets indicate classes combined to give approximately ten individuals per class for the computation of χ^2.

Discussion

Anther extrusion depends on two events. The floret must open and while it is open the anther filaments must elongate sufficiently to bring the anther outside the floret before the floret closes again. The limiting factors to anther extrusion are thus likely to be the degree of flower opening, the degree of filament elongation, a combination of both or a lack of synchronisation of these events. If each of the limiting factors were equally variable it might be expected that, over a range of environments, the distribution of anther extrusion in individual ears in an F_2 population would be normal. The fact that the results showed this not to be so indicates that one qualitatively inherited limiting factor predominates over the others.

It is a common observation in making hand crosses that dehisced anthers are found forced up by the elongation of their filaments into the top part of closed florets from which they have been unable to escape. This suggests that the extent, duration or timing of flower opening is more critical for anther extrusion than filament elongation. In addition to the fully extruded anthers discussed so far a large number of half extruded anthers were found during the glasshouse observations. These anthers which seemed to be trapped between the closed flower parts were very frequently found in the same florets as fully extruded anthers and may have resulted from the inability of the elongating filaments to force them between the closed or closing flower parts. The results presented in this paper showed that the two parental lines and the reciprocal F_1 generations between them differed not only in the extent of percentage anther extrusion but also in the pattern of extrusion of one, two or all three anthers. It is reasonable to speculate that these differences reflect differences in the degree to which the florets opened.

De Vries (1971) refers to several descriptions in the older literature of the process of flower opening being controlled by the rapid uptake and loss of water by the lodicules. The extent, duration and timing of flower opening are determined by this movement of water into and out of the lodicules. The additive genes which appeared to control percentage anther extrusion in our material may well have operated by controlling the uptake and retention of water by the lodicules possibly by influencing lodicule development if not actually influencing the critical water movements themselves. This interpretation is supported by independent observations that it is very easy to find turgid lodicules in the ears of Sirius at anthesis but very difficult to find any in those of Sona 227.

Obviously much more detailed observations will have to be made before the validity of such speculations can be tested. In the meantime, the results presented here show that the pronounced anther extrusion of Sirius is associated with a high proportion of the florets extruding any anthers that extrude all three. Effective selection for pronounced anther extrusion might thus be carried out in the glasshouse by rapid estimations of the proportions of open flowering florets extruding one, two or three anthers rather than by estimating the actual percentage anther extrusion itself which involves the counting of grain sets after harvest. This and the small number of genes apparently involved in the inheritance of anther extrusion mean that it should be relatively straightforward to select semi-dwarf and other desirable genotypes having the level of anther extrusion of Sirius despite the low heritability of anther extrusion.

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