GENETIC STUDIES ON WILD POPULATIONS
OF *MELANDRIUM* III

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1. INTRODUCTION

IN a previous investigation (Lawrence, 1963) the methods of Jinks (1954) and Hayman (1958) were used to study the genetic variation in flowering time and plant weight found between random samples of plants from six British populations of *Melandrium*. In the following account the same methods are employed in a more detailed study of the variation within and between samples from different *Melandrium* populations.

2. MATERIALS AND METHODS

Two samples of *Melandrium album* seed (W10 and W13), and two of *M. rubrum* (R5 and R8) were obtained. W10 came from a field at Stanway, Gloucestershire; W13 from the botanical gardens, Poznan University, Poland; R5 from a hedgerow in A'ystwyth, Cardiganshire; and R8 from a cliff in the Pleinmount peninsula, Guernsey. Samples W10, R5 and R8 include seed from at least five plants, but the number of plants contributing to sample W13 is unknown.

Three male and three female plants were taken at random from each of these samples, and arbitrarily numbered one to three. Plants of the same number were crossed in all possible combinations, giving a total of forty-eight crosses. Excess pollen was used for all pollinations, and the percentage germination of the resulting seed was high in all cases. The families were arranged in two blocks, each independently randomised. Plots contained twenty individuals at planting and an average of 19.5 plants at maturity.

Four characters were recorded:—

- (i) Flowering time; the number of days from 23 May 1959 to the opening of the first flower.
- (ii) Plant weight; the net weight in ounces, measured in mid-October. At this time the plants were resuming vegetative growth.
- (iii) Stem number.
- (iv) The proportion of female plants.

The data with regard to the first three characters were analysed using Hayman's (1954) method for diallel tables. Since this analysis was developed for crosses between inbred lines, the genetical interpretation of the analysis will be somewhat different in the present case. Comparable estimates of additive (a) and dominance (b) variation in its different forms (b_1 - b_3), can, however, be obtained. With dioecious material consistent (c) and inconsistent (d) variation between reciprocal families can arise not only from maternal or cytoplasmic inheritance, but also from genetic differences between male and female parents and in male progeny from sex chromosome activity.

Analysis of the results summed over the three diallel tables examines the variation between samples, while the interaction of the main effects with the genetic replicates (three diallels) tests the presence of variation within samples. Main effects were

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tested against the (samples $\times$ replicates) item, and this interaction was tested against the residual. One plot had twenty females. The missing male data was estimated from the comparable plot in the second block, adjusting for differences in block totals. One degree of freedom was therefore lost in the analysis of the males and the sex difference. The data were also analysed by means of the covariance (Wr)/variance (Vr) method of Jinks (1954), Dickinson and Jinks (1956) and the covariance (W'r)/covariance (Wr) method of Hayman (1958). The consistency of the estimates of Vr and Wr over blocks and sexes was tested by means of Allard's (1956) analysis. Again, this method was devised for inbred material, and thus the genetical interpretation of the analysis does not apply to the present results. An analysis of the proportion of female plants in the progeny was carried out to determine the influence of each parent on the sex ratio.

3. RESULTS

(i) Flowering time

The average flowering time of males and females in each group of inter- and intra-sample crosses is given in table 1, and the results

TABLE 1

Average flowering time, in days from 23 May 1959
Top figure, female plants; bottom figure, male plants

$\begin{array}{c} \delta \\ \backslash \\ \text{♀} \end{array}$	W ₁₀	W ₁₃	R ₅	R ₈
W ₁₀	25.03 26.46	34.29 34.28	24.86 22.85	23.12 20.48
W ₁₃	40.42 37.23	46.91 44.68	40.36 40.58	34.59 27.75
R ₅	28.68 27.64	34.46 32.25	35.48 28.62	27.83 24.60
R ₈	25.25 25.60	33.76 33.30	29.42 30.45	29.51 31.05

Intra-population cross ♀ average = 34.23

Intra-population cross ♂ average = 32.70

Inter-population cross ♀ average = 31.42

Inter-population cross ♂ average = 29.75

of the analyses of variance in table 2. There is significant variation between samples (item 1) and within them (item 2). The highly significant additive variation (*a*) between samples is over ten times greater than that within samples, but the dominance (*b*) and reciprocal (*c* and *d*) variation is no greater. In the absence of significant *c* or *d* main effects in male plants, it is not surprising to find no evidence of variation between samples in the sex difference. Within samples there is significant additive and dominance variation in both sexes,

TABLE 2
Analysis of variance of flowering time

Item	N	Females		Males		Sex difference	
		MS	VR	MS	VR	MS	VR
1. Samples	15	264.5	3.5**	250.7	3.1**	39.8	1.1
a	3	1122.0	14.8***	891.0	11.1***	37.8	<1
b	6	53.0	<1	85.2	1.1	38.3	<1
b ₁	1	142.1	1.9	156.8	2.0	0.4	<1
b ₂	3	28.4	<1	61.7	<1	66.0	1.8
b ₃	2	45.1	<1	84.7	1.1	15.7	<1
c	3	83.3	1	139.8	1.8	67.4	1.8
d	3	11.5	<1	52.5	<1	17.3	<1
2. Samples × replicates	10	76.0	6.2***	80.0	6.1***	37.0	2.7**
a	6	120.5	9.8***	49.5	3.8**	39.1	2.8*
b	12	84.3	6.9***	134.8	10.3***	56.6	4.1***
b ₁	2	22.7	1.9	256.3	19.6***	127.9	9.3***
b ₂	6	66.8	5.5***	130.0	9.9***	61.0	4.4**
b ₃	4	141.2	11.5***	81.3	6.2***	14.4	1.0
c	6	60.2	4.9***	69.0	5.3***	19.9	1.4
d	6	30.7	2.5*	11.7	<1	13.0	<1
3. Samples × blocks	15	11.8	<1	10.1	<1	11.9	<1
4. Samples × replicates × blocks	30†	12.5	...	14.7	...	14.8	...
5. Blocks	1	33.4	2.7	10.7	<1	6.4	<1
6. Replicates	2	33.8	2.8	50.0	3.8*	25.8	1.9
7. Blocks × replicates	2	5.3	<1	15.7	1.2	14.7	1.1
8. Total	95	...	...	...	...	...	...

* P<0.05 **P<0.01 *** P<0.001

† Only 29 degrees of freedom in males and sex difference.

and also with respect to the sex difference. Significant reciprocal differences are also found within samples.

The analyses of variance gave no evidence of dominance variation between the samples in either sex. Wr/Vr and $W'r/Wr$ analysis,

FIG. 1.— Wr/Vr and $W'r/Wr$ graphs of male and female flowering time.

however, suggests that a small amount of dominance variation is nevertheless to be found. In the absence of dominance no variation is expected in Wr and Vr or in $W'r$ and Wr . It is clear from fig. 1, however, that Wr and Vr , and also $W'r$ and Wr , do in fact differ between samples. This is confirmed by an analysis of variance of Wr and Vr (table 3) calculated from each block and sex separately. The

results show that there is significant variation in the sum of W_r and V_r between samples (Arrays, table 3). Moreover W_r and V_r and also W_r and V_r are linearly related (Joint regression W_r/V_r males $P = 0.05-0.01$, females $P = 0.01-0.001$; W_r/V_r males $P = 0.001$, females $P = 0.01-0.001$) with slopes close to expectation (Dickinson and Jinks, 1956; Hayman, 1958). Regressions from the two blocks are homogeneous (Heterogeneity $P > 0.2$) in all cases except the male W_r/V_r where heterogeneity is just significant at the 5 per cent. level. There can be little doubt therefore that the samples have different numbers of dominant genes affecting flowering time. Table 3 also

TABLE 3
Analysis of variance of V_r and W_r for flowering time

Item	N	MS	VR
Arrays	3	0.0812	14.25*
Sex	1	0.0179	1.23
Dominance	1	0.1658	11.36
Blocks	1	0.0713	12.51*
$S \times D$	1	0.0146	10.43**
others NS	11	0.0086	...
$A \times S \times B$	3	0.0057	14.25*
others NS	7	0.0018	...
$A \times S \times D \times B$	3	0.0004	0.0014
Total	31	...	...

* $P < 0.05$ ** $P < 0.01$ NS = Not significant

shows that array order is consistent in males and females, confirming the absence of sex chromosome variation between samples.

The significant arrays $\times$ sex $\times$ blocks interaction in table 3 is due to a significant ($P < 0.001$) arrays $\times$ blocks interaction in female but not male progeny. Examination of the female data shows that sample W_{13} appears to have the largest number of dominant alleles in one block, and the least in the other. The remaining samples are consistent over blocks. Finally table 3 also shows that the difference in the mean size of W_r and V_r varies in the two sexes (Sex $\times$ dominance). W_r is greater than V_r in both sexes (males $P = 0.01-0.001$, females $P < 0.001$) but as can be seen from fig. 1 the difference is greater in the females.

(ii) Plant weight

The data and results of analyses of variance for plant weight are given in tables 4 and 5 respectively. Like flowering time, there is significant variation both between (item 1) and within (item 2) samples in each sex. The highly significant additive variation between samples (a) is respectively five and nine times greater than the variation within samples in females and males. Unlike flowering time there is

also evidence of dominance variation (*b*) between samples. Inter-sample hybrids are consistently heavier than intra-sample hybrids in each sex (*b*₁). In male, but not female, plants there is also a consistent difference between reciprocal families (*c*). The reason for the significantly subnormal variation in the females is unknown. The presence of consistent reciprocal variation in male progeny suggests sex chromosome variation between samples. This is confirmed by the significant dominance variation (*b*₃) with regard to the sex difference. There is also consistent variation between reciprocal

TABLE 4
Average plant weight, in ounces
Top figure, female plants; bottom figure, male plants

$\begin{array}{c} \delta \\ \diagdown \\ \text{♀} \end{array}$	W ₁₀	W ₁₃	R ₅	R ₈
W ₁₀	$\begin{array}{c} 14.48 \\ 8.14 \end{array}$	$\begin{array}{c} 18.00 \\ 15.27 \end{array}$	$\begin{array}{c} 18.42 \\ 13.63 \end{array}$	$\begin{array}{c} 20.22 \\ 14.12 \end{array}$
W ₁₃	$\begin{array}{c} 17.24 \\ 13.89 \end{array}$	$\begin{array}{c} 16.64 \\ 12.28 \end{array}$	$\begin{array}{c} 22.76 \\ 15.36 \end{array}$	$\begin{array}{c} 21.67 \\ 12.52 \end{array}$
R ₅	$\begin{array}{c} 20.58 \\ 14.86 \end{array}$	$\begin{array}{c} 21.44 \\ 16.77 \end{array}$	$\begin{array}{c} 21.10 \\ 16.62 \end{array}$	$\begin{array}{c} 20.56 \\ 16.12 \end{array}$
R ₈	$\begin{array}{c} 18.36 \\ 13.77 \end{array}$	$\begin{array}{c} 23.34 \\ 19.33 \end{array}$	$\begin{array}{c} 20.64 \\ 20.03 \end{array}$	$\begin{array}{c} 19.48 \\ 15.73 \end{array}$

Intra-population cross ♀ average = 17.93
 Intra-population cross ♂ average = 13.19
 Inter-population cross ♀ average = 20.27
 Inter-population cross ♂ average = 15.47

crosses (*c*) with regard to the sex difference. Within samples there is significant additive and dominance variation in each sex, and significant dominance variation with regard to sex difference (item 2).

The presence of dominance variation and of sex chromosomes activity is also shown in the *Wr/Vr* and *W'r/Wr* graphs (fig. 2). Estimates of *Vr* and *Wr* from the two blocks are consistent in each sex (table 6), but the array order is different in males and females (*Arrays* × *sex*). Results from the two blocks give significant joint regressions (Joint regression *Wr/Vr* males and females both $P = 0.05-0.01$; *W'r/Wr* males and females both $P < 0.001$) and each pair of regressions is homogeneous. The slopes of all regressions are close to expectation (Dickinson and Jinks, 1956; Hayman, 1958). Table 6 also suggests that the mean difference between *Vr* and *Wr* is greater in male progeny (*sex* × *dominance*) but the item is only just significant

TABLE 5
Analysis of variance of plant weight

Item	N	Females		Males		Sex difference	
		MS	VR	MS	VR	MS	VR
1. Samples	15	33.3	1.8	47.1	3.7**	22.7	1.9
a	3	92.3	5.1**	121.9	9.5***	3.4	<1
b	6	30.4	1.7	23.1	1.8	29.1	2.5*
b ₁	1	98.9	5.4*	93.6	7.3*	0.1	<1
b ₂	3	11.4	<1	6.2	<1	9.5	<1
b ₃	2	24.8	1.4	13.3	1	73.5	6.3**
c	3	0.5	<1	50.3	3.9*	46.5	4.0*
d	3	12.7	<1	16.8	1.3	5.6	<1
2. Samples × replicates	30	18.2	3.5***	12.9	3.0***	11.7	1.9*
a	6	33.0	6.3***	25.2	5.8***	3.6	<1
b	12	10.5	2.0*	13.3	3.1**	16.2	2.6*
b ₁	2	5.7	1.1	18.9	4.4*	20.8	3.3*
b ₂	6	16.3	3.1*	17.0	3.9**	19.0	3.0*
b ₃	4	4.3	<1	4.7	1.1	9.8	1.6
c	6	19.4	3.7**	7.1	1.7	8.4	1.3
d	6	17.5	3.3**	5.4	1.2	14.2	2.3
3. Samples × blocks	15	6.3	1.3	3.9	<1	3.8	<1
4. Samples × replicates × blocks	30†	4.7	...	4.5	...	7.5	...
5. Blocks	1	5.0	1.1	2.4	<1	14.3	2.3
6. Replicates	2	20.6	4.4*	26.1	6.0**	2.2	1
7. Blocks × replicates	2	2.1	<1	2.4	<1	7.6	1.2
8. Total	95	...	...	...	...	...	...

* P < 0.05 ** P < 0.01 *** P < 0.001

† Only 29 degrees of freedom in males and sex difference.

at the 5 per cent. level. Further, the dominance item is significant in neither sex if each is analysed separately.

Previous analyses have demonstrated sex chromosome variation between samples. W_r/V_r and W'_r/W_r regressions with respect to the

FIG. 2.— W_r/V_r and W'_r/W_r graphs of male and female weight.

sex difference are not, however, significant. An analysis of variance of V_r and W_r (table 7) shows that the arrays item is not significant. From table 5 it can be seen that the majority of the variation between samples in the sex difference is accounted for by the inconsistent or

TABLE 6

Analysis of variance of Vr and Wr for plant weight

Item	N	MS	VR
Arrays . .	3	0.4193	1.39
Sex . .	1	0.0964	<1
Dominance . .	1	0.0077	<1
Blocks . .	1	0.0022	<1
A × S . .	3	0.3016	16.94***
S × D . .	1	0.0979	5.50*
residual . .	21	0.0178	...
Total	31	...	...

* $P < 0.05$ *** $P < 0.001$

TABLE 7

Analysis of Variance of Vr and Wr for the sex difference in plant weight

Item	N	MS	VR
Arrays . .	3	0.9371	<1.0
Dominance . .	1	16.4560	16.9**
Blocks . .	1	0.0288	<1.0
Residual . .	10	0.9741	...
Total . .	15	...	...

** $P < 0.01$

TABLE 8

*Average stem number**Top figure, female plants; bottom figure, male plants*

$\begin{matrix} \delta \\ \backslash \\ \text{♀} \end{matrix}$	W ₁₀	W ₁₃	R ₅	R ₈
W ₁₀	$\begin{matrix} 11.37 \\ 10.51 \end{matrix}$	$\begin{matrix} 14.40 \\ 14.36 \end{matrix}$	$\begin{matrix} 13.99 \\ 13.91 \end{matrix}$	$\begin{matrix} 12.94 \\ 11.62 \end{matrix}$
W ₁₃	$\begin{matrix} 13.08 \\ 13.29 \end{matrix}$	$\begin{matrix} 13.97 \\ 13.28 \end{matrix}$	$\begin{matrix} 16.77 \\ 16.68 \end{matrix}$	$\begin{matrix} 13.46 \\ 10.97 \end{matrix}$
R ₅	$\begin{matrix} 15.22 \\ 15.08 \end{matrix}$	$\begin{matrix} 21.59 \\ 19.60 \end{matrix}$	$\begin{matrix} 11.69 \\ 11.86 \end{matrix}$	$\begin{matrix} 13.89 \\ 13.90 \end{matrix}$
R ₈	$\begin{matrix} 12.73 \\ 13.21 \end{matrix}$	$\begin{matrix} 15.75 \\ 16.01 \end{matrix}$	$\begin{matrix} 10.35 \\ 11.13 \end{matrix}$	$\begin{matrix} 11.79 \\ 11.26 \end{matrix}$

Intra-population cross ♀ average = 12.21

Intra-population cross ♂ average = 11.73

Inter-population cross ♀ average = 14.51

Inter-population cross ♂ average = 14.15

TABLE 9
Analysis of variance of stem number

Item	N	Females		Males		Sex difference	
		MS	VR	MS	VR	MS	VR
1. Samples	15	41.7	2.2*	35.8	2.9**	4.8	<1.0
a	3	65.9	3.5*	57.7	4.6**	4.0	<1.0
b	6	49.1	2.6*	37.4	3.0*	7.8	1.4
b ₁	1	96.1	5.2*	105.5	8.4**	0.2	<1.0
b ₂	3	28.2	1.5	21.6	1.7	9.1	1.6
b ₃	2	57.0	3.1	27.1	2.2	9.7	1.8
c	3	41.3	2.2	36.6	2.9*	2.4	<1.0
d	3	3.0	<1.0	10.0	<1.0	1.9	
2. Samples × replicates	30	18.6	7.2***	12.6	2.8**	6.5	1.2
a	6	11.3	4.3**	16.9	3.7**	2.8	<1.0
b	12	17.5	6.7***	11.0	2.4*	8.5	1.5
b ₁	2	26.5	10.2***	3.1	<1.0	17.3	3.1
b ₂	6	18.1	6.9***	13.9	3.1	1.9	<1.0
b ₃	4	12.2	4.7**	10.5	2.3	13.9	2.5
c	6	26.9	10.3***	16.9	3.7**	6.8	1.2
d	6	19.9	7.6***	7.1	1.6	5.8	1.1
3. Samples × blocks	15	3.2	1.4	4.9	1.1	5.6	1.0
4. Samples × replicates × blocks	30†	2.3	...	4.3	4.5	5.5	...
5. Blocks	1	0.1	<1.0	39.5	8.8**	35.1	6.4
6. Replicates	2	1.9	<1.0	4.6	1.0	2.8	<1.0
7. Blocks × replicates	2	1.4	<1.0	4.2	<1.0	2.3	<1.0
8. Total	95	...	...	...	...	...	...

* P<0.05 ** P<0.01 ***P<0.001

† Only 29 degrees of freedom in males and sex difference.

residual dominance (b_3). This, together with the absence of a significant W_r/V_r or W'/W_r regression suggests that there is some form of non-allelic interaction among sex chromosome genes, or between sex chromosomes and the autosomes.

(iii) Stem number

The data and results of analyses of variance in stem number are given in tables 8 and 9. Table 9 shows that there is genetic variation

FIG. 3.— W_r/V_r and W'_r/W_r graphs of male and female stem number.

both between and within samples with regard to this character. Significant additive (a) and dominance (b) variation is found between samples. Although the consistent reciprocal variation (c) between

samples just reaches the 5 per cent. level of significance in male but not female plants, the variation in sex difference between samples is not significant. It is unlikely therefore that the sex chromosomes contribute much to the variation in stem number.

A significant W_r/W_r regression is found in each sex (Joint regression, males $P = 0.05-0.01$, females $P < 0.001$) with each pair of regressions homogeneous (Heterogeneity $P > 0.2$), but the W_r/V_r regressions are not significant. An analysis of variance of V_r and W_r also fails to show differences between arrays (table 10). This suggests

TABLE 10
Analysis of variance of V_r and W_r for stem number

Item	N	MS	VR
Arrays . .	3	81.76	1.2
Sex. . .	1	184.12	2.8
Dominance . .	1	323.58	4.9*
Blocks . .	1	240.31	3.6
Residual . .	25	66.60	...
Total . .	31	...	...

* $P < 0.05$

the presence of non-allelic interaction and/or heterozygosity in the gene system controlling stem number. W_r/V_r , but not in general W_r/W_r , regressions are disturbed by these factors.

(iv) *Variation within and between intra-sample families*

The mean variance within and between families in the four groups of intra-sample crosses for each character and sex are given in table 11. The values in table 11 are the average of the variances calculated from separate blocks, and weighted according to the degrees of freedom. In all but one of the twenty-four cases the variation between families is greater than that within, and in thirteen cases the difference is significant. Table 11 also gives the total variance in each group of intra-sample crosses. These total variances are significantly heterogeneous for each character and sex, except for female weight (Flowering time, males and females both $P < 0.001$; Weight, males $P < 0.001$, females $P = 0.5-0.1$; Stem number, males $P = 0.001-0.001$, females $P < 0.001$). The total variance of female progeny is significantly greater than that of the males in six out of twelve cases, but in no case is the reverse found.

(v) *Sex ratio*

The mean percentage females in the progeny is given in table 12, and the results of an analysis of variance of this percentage transformed

TABLE 11

Variance between (first figure) and within (second figure) families in the four groups of intra-population crosses, with respect to the three characters. Third figure is the total variance

		N	Flowering time		Plant weight		Stem number	
			MS	VR	MS	VR	MS	VR
W ₁₀	♀	4	164.8	4.37**	16.0	<1.00	12.8	1.58
		49	37.7		24.2		8.1	
		53	47.3		23.6		8.4	
	♂	4	73.8	3.18*	38.8	3.70*	39.5	6.81***
		35	23.2		10.5		5.8	
		39	28.4		13.4		9.3	
W ₁₃	♀	4	215.0	2.23	105.8	3.34*	241.0	9.18***
		50	96.6		31.7		26.3	
		54	105.4		37.2		42.2	
	♂	4	668.5	6.63**	77.8	5.52***	134.5	10.11***
		57	100.9		14.1		13.3	
		61	138.1		18.3		21.3	
R ₅	♀	4	838.5	3.16*	147.5	3.94***	60.3	3.89**
		77	265.4		37.4		15.5	
		81	293.7		42.8		17.7	
	♂	3	474.3	3.72*	38.7	1.02	60.7	4.10*
		32	127.4		37.8		14.8	
		35	157.1		37.8		18.7	
R ₈	♀	4	1040.2	8.93***	135.3	5.96***	13.8	1.68
		59	116.5		22.7		8.2	
		63	175.2		29.9		8.5	
	♂	4	453.5	5.96***	134.3	4.33**	10.8	1.08
		48	76.1		31.0		10.0	
		52	105.1		39.0		10.1	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

TABLE 12

Percentage females in progeny

♀ \ ♂	♂	W ₁₀	W ₁₃	R ₅	R ₈
	♀				
W ₁₀	.	69.2	60.8	58.0	47.9
W ₁₃	.	52.7	55.5	47.5	53.8
R ₅	.	54.2	60.8	57.3	50.0
R ₈	.	63.3	54.2	35.6	47.4

to angles (Fisher and Yates, 1957) in table 13. The samples have significantly different sex ratios (item 1), the majority of the variation

TABLE 13
Analysis of variance of percentage females transformed to angles

Item	N	MS	VR
1. Samples . . .	15	159.0	2.0*
♂ parent . . .	15	265.9	3.4*
♀ parent . . .	3	177.7	2.2
residual . . .	9	117.2	1.5
2. Samples × replicates	30	91.3	1.3
♂ parent . . .	6	95.6	1.3
♀ parent . . .	6	179.3	2.5*
residual . . .	18	60.6	< 1.0
3. Samples × blocks .	15	66.4	< 1.0
4. Samples × replicates × blocks .	30	74.1	...
5. Blocks . . .	1	0.4	< 1.0
6. Replicates . . .	2	10.2	< 1.0
7. Blocks × replicates .	2	43.1	< 1.0
8. Total . . .	95	...	...

* $P < 0.05$

being attributable to the male parent. The influence of the female parent is just above the 5 per cent. level of significance. Within samples there is a significant effect of the female, but not male, parent.

4. DISCUSSION

Genetic variation was found both within and between the population samples with regard to each character studied. In all cases, however, there was considerably more variation between the samples. Hayman's (1954) analysis separates this variation into an additive (a) and three dominance (b_1 - b_3) items. In the present case, the genetical interpretation of these items will be somewhat different from that given by Hayman (1954), who considered crosses between inbred lines only. However formulæ appropriate to the general case can be derived from Dickinson and Jinks (1956). Thus (a) is the variance of array means and equals:—

$$\frac{1}{2n}(D_I + \frac{1}{2}H_I - \frac{1}{2}H_{II} - \frac{1}{2}F_I) + E.$$

This has the same form as the formula given by Hayman and depends substantially on additive variation. Similarly (b) is the mean variance of arrays minus the variance of array means, and equals:—

$$\frac{1}{4}H_{II} + E^1.$$

This shows that significance of the (b) item depends only on dominance and a function of gene frequency and inbreeding.

Hayman analyses of the data therefore show that there was greater additive variation between the samples than within them for flowering time, weight and stem number. They also show that there was greater dominance variation between samples for weight and stem number, though not flowering time. Alternative tests for the presence of dominance variation between samples are provided by W_r/V_r and $W'r/W_r$ analyses (Jinks, 1954; Dickinson and Jinks, 1956; Hayman, 1958). Using these methods, dominance variation was found for all characters. Since such analyses are probably the more sensitive, this is likely to be the correct result. The W_r/V_r and $W'r/W_r$ graphs also suggest that dominance for flowering time was ambidirectional and incomplete. In heterozygous material $\bar{W}_r - \bar{V}_r$ is not an unambiguous test for inequality in D and H . In the absence of non-allelic interaction and using P_1 for the parental diagonal, it can be seen from Dickinson and Jinks (1956) that

$$\bar{W}_r - \bar{V}_r = \frac{1}{8}(D - H) + \frac{1}{8}(H_{III} - \frac{1}{2}H_{IV} - \frac{1}{2}F_I).$$

Since, however, the frequency of heterozygotes was probably quite low in the present material (see later) the size of the biasing factor

$$\frac{1}{8}(H_{III} - \frac{1}{2}H_{IV} - \frac{1}{2}F_I)$$

is unlikely to adequately explain the inequality of $\bar{W}_r$ and $\bar{V}_r$. The slopes of the W_r/V_r graphs for flowering time do not suggest the presence of non-allelic interaction. Dominance for plant weight is complete and, as shown by the significant b_1 item in the Hayman analysis, predominantly in the direction of increased weight. The suggestion from the analysis of V_r and W_r that $\bar{W}_r - \bar{V}_r$ is greater in males than females probably arises from heterozygosity and/or non-allelic interaction. These factors tend to scatter the points about the W_r/V_r but not the $W'r/W_r$ regression, and it can be seen that as a consequence the slope of the male W_r/V_r graph is only 0.75. The significant $W'r/W_r$, but insignificant W_r/V_r , regression for stem number indicates that the low heritability of this character probably arises from heterozygosity and/or non-allelic interaction.

Additive and dominance variation within samples was also found for all characters. The significance of c and d items within samples probably arose largely from genetic differences between male and female parents, although sex chromosomal variation could also have contributed. In a previous experiment the mean variance between families in groups of intra-sample crosses differed from the same mean variance in groups of inter-sample crosses (Lawrence, 1963), but this is not found in the present results. In the groups of intra-sample crosses the variance between families is on the average over four times greater than the variance within them, indicating a certain amount of sib or parent-offspring mating in the populations from which the samples were drawn (see table 19 in Mather, 1949 and table 4 in

Hayman and Mather, 1955). These variances are not purely genetic but in the present material it is impossible to obtain estimates of the environmental component. As the environmental component to the variation within families is likely to be the larger, however, the conclusion concerning inbreeding is probably correct. An analysis of variance of the cube root of the variance ratio (between/within families) failed to detect variation in the extent of inbreeding in any sample, sex or character. The total variance of progeny nevertheless varies considerably between samples. Female progeny tend to exhibit greater variation than males, presumably due to an indirect effect of the sex chromosomes.

Sex chromosome variation was found in both flowering time and plant weight, but not in stem number. With flowering time, such variation was found only within samples, the sex chromosomes from different samples having similar average effects. Sex chromosome

TABLE 14

The average difference between reciprocal crosses for male weight and the sex difference in weight. (Male arrays subtracted from female arrays)

	W10	W13	R5	R8
Males	+0.50	-9.60	-1.27	+10.36
Females-males	-0.02	+8.49	+2.01	-10.48

variation in plant weight, however, was found both within and between samples. Between samples the variation appears to arise from X rather than Y chromosome activity. The variance ratio female parents/male parents (variance of rows versus variance of columns in the diallel tables) is 1.57 in male progeny, 0.98 in female progeny, and 1.92 for the sex difference. Although none is significant, bigger ratios in the males and for the sex difference than in the females suggests X chromosome variation. Table 14 shows that the X chromosomes of samples W13 and R8 have the greatest activity. The similarity in size of the average reciprocal difference in male weight and the sex difference in weight arise from the absence of reciprocal variation in female offspring. With regard to the sex difference, the sign of average reciprocal difference indicates the mean dominance of the X chromosome. A larger sex difference in progeny of female as opposed to male descent indicates a relatively recessive X chromosome and *vice versa* a dominant X chromosome. The sign of the average reciprocal difference in male progeny shows the direction in which the X chromosomes act. Table 14 therefore suggests that the X chromosomes display undirectional dominance towards greater weight. Undirectional dominance of this kind was also found in the Hayman

analysis of male and female data. The X chromosomes of sample W₁₃ appear to have a preponderance of recessive alleles, of R₈ a preponderance of dominant alleles, and of W₁₀ and R₅ more or less equal numbers of dominants and recessives. This conclusion can also be independently inferred from the W_r/V_r and W'_r/W_r graphs of male and female weights. Sample 13 appears more recessive (*i.e.* lies further from the origin) in female than male offspring, R₈ appears more dominant (nearer the origin) and the others show little change of position.

The analysis of X chromosome activity can be taken further, and an attempt made to relate this activity to the size of the sex difference. Differences between males and females can arise from the X chromosomes in several ways, including:—

- (i) From a direct effect, where the differences are due to the dominance or non-allelic interaction of X borne genes.
- (ii) From an indirect effect, or sex limitation (Morgan, 1914), where there is an interaction between autosomal and/or sex chromosome genes and sex.
- (iii) From a gene dosage effect, or different additive effects of X chromosomes when in the haploid or diploid state.

The third alternative, except in certain very simple situations which do not occur in the present data, will give results indistinguishable from the second. For the third alternative to give rise to a variable sex difference, certain genes must have a greater dosage effect than others. Table 4 and fig. 2 show that these cannot exclusively be dominant or recessive genes, or genes acting either exclusively toward greater or lesser weight. A direct effect of the X chromosomes, the first alternative, does not appear likely. As the dominance variation is much greater between than within samples, a larger sex difference should be found in the inter-sample than in the intra-sample, hybrids. This is not found (inter-sample hybrids 4.80 oz., intra-sample hybrids 4.74 oz.). Further the relative sizes of the sex differences should be predictable from the dominance properties of the X chromosomes, but this is not possible. No predictions can be made for sex limited effects. The suggestion of non-allelic interaction and/or heterozygosity for the sex difference is compatible with sex limitation.

A different effect of the sex chromosomes is shown by the variation in sex ratio between the samples. As found before (Lawrence, 1963), the majority of the variation is due to the male parent. Deviations from 50 per cent. females in the progeny are due to different growth rates of X and Y bearing pollen (Correns, 1928). Variation in sex ratio therefore depends on variations in this pollen growth rate differential. Such variation may be sex chromosomal or sex limited. A distinction between these modes of control cannot be made in the present data as second generation hybrids are necessary for this purpose. The effect of the female parent within, and possibly between, samples

may either depend on a small amount of zygote selection, or on a stylar effect on pollen growth rates.

The results and conclusions discussed above bear a striking resemblance to those from a previous experiment (Lawrence, 1963), using different material. The two experiments agree with respect to the distribution of variation within and between samples, the mode of inheritance of flowering time and plant weight, the type of action of the sex chromosomes, the presence of inbreeding in the populations and the control of the sex ratio. They differ in two main ways. First, in the earlier experiment the X chromosomes had a considerable influence on the variation in flowering time between samples but less on weight, a situation which is reversed in the present results. Second, there was no suggestion in the present results of differences in the level of heterozygosity between samples. It is possible that these dissimilarities depend on gene-environment interactions.

The overall consistency of the results from the two experiments demonstrates the value of the methods of analysis employed. As pointed out by Dickinson and Jinks (1956), the accuracy of W_r/V_r analysis applied to dioecious material depends on the ratio of the genetic variance within and between samples. It can be seen from the results that there is considerably greater variation between samples for all characters studied. The sensitivity of the W_r/V_r and W'_r/W_r methods is particularly well illustrated by the analysis of sex chromosome activity. For the present purpose, the success of the system of analysis also depends on how far the results may be generalised from the sample to the population. This in turn depends not only on the ratio of variation within and between populations but also on the method and extent of sampling. Sampling occurred at three stages. First, in both experiments the populations were sampled by taking seed from a number of plants which were then grown to reconstruct the populations. The relation of the derived population to the original will depend on the number of plants sampled and possibly on a change in the action of selection. In the first experiment a minimum of ten plants were sampled and in the second a minimum of five, with the possible exception of W_{13} for which information is lacking. Since the populations sampled were small and since the variation studied clearly depends on many genes, the correspondence between derived and original populations is likely to be good. Second, the sampling of the diallel parents from the derived populations was random, and therefore entailed no bias. Third, little effect of sampling the progeny of the diallel cross could be detected. The agreement between results from the two blocks was good, a significant difference being found only for the flowering time of W_{13} females. This difference could also arise from genotype-environment interaction. It is concluded, therefore, that the variation between the samples reflects variation between the populations from which they were drawn. Such differences have, no doubt, been brought about by natural selection.

5. SUMMARY

The genetic variation within and between random samples of plants from two populations of *Melandrium album* and two of *M. rubrum* has been studied. Greater variation in flowering time, plant weight, stem number and sex ratio was found between samples than within them. With regard to the first three of these characters the variation contained both additive and dominance components. X chromosome variation within and between samples was found with respect to weight, but only within samples for flowering time. Weight differences between the sexes were probably the result of sex limitation.

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