GENOTYPE-ENVIRONMENT INTERACTION AND DEVELOPMENTAL REGULATION IN *ARABIDOPSIS THALIANA*

IV. WILD MATERIAL; ANALYSIS

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Received 6.vi.70

1. Introduction

Previous papers in this series (Westerman and Lawrence, 1970; Westerman, 1970*a*, 1970*b*) have concerned the investigation of genotype-environment interaction in inbred lines of the species. Though this material poses fewer analytical problems than that from natural populations, it suffers from the disadvantage that the variation observed cannot be confidently ascribed to an adaptive response by the lines to a variable environment. For this purpose, we must consider material sampled from a wild population.

The present paper, therefore, presents a genetic analysis of the average and developmental phenotypes of the descendants of plants sampled from a disused railway-track population at Wixford, Warwickshire. Seed was collected from this location in the summer of 1967, and prior to this experiment the descendants of 16 of the original plants sampled had been inbred by self-fertilisation for two generations. This paper concerns a diallel set of crosses between seven of these lineages, chosen to represent the full range of early- and late-flowering times.

2. Material and methods

The diallel progenies were sown directly on to agar medium, and then vernalised for 4 weeks at $1 \pm 1°$ C. After the vernalisation period, they were raised in four environments, set at 10°, 15°, 20° and 25° C. respectively, and with a constant photoperiod of 16 hours. In each environment, ten seeds per family were sown in each of two independently randomised blocks. All other details are similar to those described in Westerman and Lawrence (1970).

The quantitative characters scored were flowering time, height, number of leaves in the basal rosette, and number of siliquae produced by each plant.

3. Results

The first plants flowered on day 18, and scoring was terminated after approximately 90 days of flowering in each environment. Percentage germination was 96 per cent., and less than 2 per cent. of the plants failed to flower; these non-flowering plants, most of which occurred at 25° C. (table 1), have been excluded from the data presented here. From the family means for each character in each environment (tables 1-4), it is clear that, as expected, the population sample comprises a mixture of early-

TABLE 1

Mean flowering time of diallel families at each temperature. Numbers of non-flowering plants are in brackets

10° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	69·30	76·79	74·90	70·11	74·95	67·25	75·39	71·52
2	70·28	54·86	53·41	83·93	54·14	70·50	55·66	63·91
3	75·93	53·15	52·10	78·25	50·65	73·18	59·14	63·46
4	71·35	83·97	89·50	94·22	81·80	74·15	87·50	81·65
5	73·75	55·91	49·90	81·55	52·55	70·01 (1)	50·95	63·00
6	61·73	71·79	71·16	71·35	72·60	65·40	78·05	70·46
7	70·28	55·45	55·10	81·20	60·70	73·89	56·81	65·50

15° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	68·22	73·07 (1)	74·45	75·51	76·67	59·10	77·00	71·07
2	75·27	41·15	42·55	44·65	45·65	63·94	44·77	54·47
3	73·58	41·87	38·47	77·89 (1)	39·70	67·52	46·08	55·70
4	82·98	89·26 (1)	89·30	95·20 (3)	84·94	80·16 (1)	86·14	81·00
5	69·25	41·84	39·80	78·83	39·11	71·61	42·20	56·15
6	60·85	71·18	67·05	73·17	69·00	57·94	67·89	67·14
7	60·81 (1)	46·24	44·35	80·72	48·40	72·62	45·91	57·79

20° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	41·39	45·94	46·15	51·34	47·44	36·50	47·22	44·94
2	48·39	23·39	23·64	73·95	26·30	39·06	24·75	37·80
3	40·67	24·72	21·75	66·40	22·65	47·85 (1)	24·55	35·44
4	53·84	67·45 (1)	59·96	78·58 (3)	62·44	54·69	59·70 (4)	63·06
5	43·56	22·55	23·35	59·75 (2)	23·21	45·67	22·78	35·62
6	41·00	57·60	49·30	51·77 (1)	48·43	40·50	43·31	46·16
7	44·35	25·05	23·48	64·47 (1)	24·36	50·05	24·97	36·00

25° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	46·65	55·05	53·95	65·45	50·81	49·36	56·41 (1)	51·21
2	51·90 (1)	23·59	23·15	77·92 (5)	22·10	41·28	22·50	38·92
3	48·55	24·05	22·50	65·25 (3)	21·55	57·28 (1)	24·84	37·58
4	65·10	79·98 (8)	70·67 (8)	85·83 (10)	73·42 (3)	65·68	67·55 (6)	70·70
5	47·20	23·70	22·65	70·77 (4)	22·70	54·24 (1)	21·75	37·35
6	41·11	51·97	46·56 (2)	60·00	43·55	39·61	44·25	48·75
7	38·80	24·10	22·65	56·45 (3)	25·65	47·95	23·65	35·73

$\bar{r}$ = Array mean.

TABLE 2

Mean height at flowering time of diallel families at each temperature

10° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	38·00	51·16	59·00	60·39	52·50	36·40	59·59	50·20
2	49·49	47·92	42·13	75·67	37·74	59·25	47·35	51·82
3	59·47	36·65	34·75	81·95	40·71	55·89	45·19	49·52
4	59·85	77·59	73·71	68·22	71·40	69·25	82·72	70·40
5	56·10	38·02	33·34	71·25	35·02	53·71	34·90	47·13
6	30·22	67·25	53·37	60·20	52·75	34·95	63·80	53·00
7	52·66	47·35	42·40	65·15	47·40	70·03	52·13	54·49

15° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	29·61	42·34	48·90	45·64	36·06	22·26	44·94	39·11
2	41·77	29·20	29·95	36·95	35·90	42·40	39·88	37·50
3	47·50	31·43	30·25	52·69	29·65	49·16	34·69	39·77
4	46·68	47·51	51·05	47·20	49·06	51·39	51·09	47·73
5	44·35	30·72	33·25	52·49	30·80	48·06	32·75	37·98
6	28·40	47·66	48·72	43·30	40·82	26·54	41·60	40·20
7	39·45	40·11	39·34	46·06	36·95	46·00	40·70	41·02

20° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	82·61	69·90	67·60	86·84	75·92	72·95	84·17	77·12
2	73·11	66·65	66·67	67·83	69·90	80·06	74·02	71·26
3	71·49	65·37	65·15	71·00	60·45	76·64	73·60	70·72
4	71·08	83·23	87·06	76·50	78·79	91·06	82·24	78·81
5	78·01	66·64	69·60	85·83	61·00	85·95	71·46	72·22
6	79·15	75·95	82·05	83·34	74·43	66·65	72·52	78·20
7	84·24	71·70	68·23	62·09	72·07	87·37	76·81	75·52

25° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	58·65	57·90	57·78	87·95	68·06	64·27	78·25	68·57
2	64·32	64·92	66·10	90·92	63·70	73·24	74·25	68·89
3	71·90	65·65	64·70	80·55	65·30	71·83	74·19	69·42
4	89·30	71·15	84·54	74·54	78·60	85·48	90·15	81·38
5	63·30	69·75	67·20	64·19	69·15	66·97	71·60	67·77
6	65·06	64·78	66·77	81·56	66·35	58·78	82·70	71·09
7	74·60	72·80	70·28	85·45	65·40	88·72	80·45	77·81

$\bar{r}$ = Array mean.

TABLE 3

Mean leaf number of diallel families at each temperature

10° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	19·16	22·37	23·95	19·84	23·25	18·33	23·24	20·88
2	20·59	13·86	12·91	22·97	13·94	22·05	13·62	17·07
3	21·45	12·10	11·40	22·15	11·55	20·43	13·90	16·54
4	20·60	24·24	24·21	23·23	23·95	21·00	23·61	22·74
5	20·99	12·67	11·55	23·85	11·95	22·37	10·80	17·00
6	17·78	19·84	21·23	22·00	23·35	17·95	22·25	20·63
7	21·66	14·00	13·25	23·45	15·85	22·25	12·34	17·33

15° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	21·50	24·08	25·95	23·28	26·05	18·93	25·37	23·14
2	24·77	12·00	11·50	12·80	13·30	19·99	12·64	16·22
3	24·17	11·60	10·41	25·63	10·76	20·74	12·54	16·62
4	25·41	25·68	25·80	23·70	25·67	25·22	26·19	23·85
5	24·10	11·61	10·80	25·26	10·27	23·89	11·75	17·29
6	19·05	22·90	20·31	23·62	23·59	19·34	21·57	21·60
7	19·74	12·15	12·01	23·39	14·70	23·87	13·05	17·29

20° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	11·00	12·90	13·95	12·59	14·05	10·17	13·78	12·87
2	14·56	6·76	6·81	24·11	7·00	11·45	7·37	11·23
3	12·27	7·35	5·70	19·87	6·50	16·15	6·80	10·50
4	16·09	21·54	17·34	20·92	18·13	16·43	16·73	18·54
5	13·17	7·15	6·25	17·88	6·11	12·84	6·34	10·27
6	11·70	16·30	15·10	16·79	15·30	12·00	13·05	13·83
7	12·89	7·15	7·25	20·17	7·00	14·39	6·46	10·42

25° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	11·75	17·20	17·61	20·26	15·25	13·94	17·37	15·17
2	17·11	7·01	6·25	23·92	6·51	13·01	6·90	11·67
3	14·55	6·75	6·05	18·70	5·74	16·61	6·90	10·66
4	20·40	23·00	18·93	26·04	22·19	21·92	19·36	21·30
5	14·05	6·10	5·75	23·41	6·25	16·52	5·50	11·06
6	10·83	16·12	12·96	16·22	13·55	11·00	12·30	14·28
7	10·25	6·45	6·31	17·81	7·80	13·94	6·30	10·25

$\bar{r}$ = Array mean.

TABLE 4

Mean siliqua number of diallel families at each temperature

10° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	36·69	32·43	34·10	27·23	31·85	37·45	30·35	32·85
2	30·55	34·05	34·12	30·30	31·04	28·45	32·87	32·02
3	33·00	33·40	33·90	30·30	32·15	31·51	37·07	33·20
4	29·60	30·71	30·56	28·43	32·15	29·16	30·65	29·59
5	32·26	36·31	34·10	29·80	34·90	29·17	37·25	32·76
6	35·56	28·25	31·56	28·90	29·05	33·43	31·75	31·30
7	32·11	31·75	35·10	28·00	33·75	30·60	34·52	32·88

15° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	31·28	25·28	25·11	27·26	24·45	29·40	24·87	26·92
2	25·50	26·40	27·00	25·25	26·70	23·46	28·17	26·05
3	23·77	27·01	25·52	23·55	25·31	25·36	27·12	25·71
4	26·98	24·79	24·95	25·15	22·45	25·77	23·78	24·98
5	24·45	25·84	26·65	24·77	25·29	25·20	26·40	25·16
6	31·90	25·46	25·05	24·99	25·05	32·47	23·18	26·63
7	25·40	27·48	28·05	24·89	24·40	23·10	26·60	25·72

20° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	19·29	7·89	8·89	5·48	9·57	12·92	9·29	9·14
2	11·46	10·76	9·72	6·45	10·70	8·06	10·90	9·07
3	6·78	9·39	11·60	4·91	10·28	7·50	10·78	9·07
4	7·05	5·65	4·49	2·75	9·98	8·80	5·40	6·13
5	11·58	9·92	10·80	8·09	11·83	9·25	10·30	10·27
6	9·18	5·12	7·18	9·68	8·36	11·11	8·68	8·82
7	9·21	10·21	12·95	4·42	11·24	6·54	8·64	9·09

25° C.

	1	2	3	4	5	6	7	$\bar{r}$
1	9·40	7·65	8·89	5·71	6·31	8·19	5·50	7·68
2	6·62	11·40	11·20	5·57	11·31	5·96	10·95	8·97
3	8·10	11·45	11·70	5·56	11·80	6·45	9·42	9·46
4	6·89	4·50	4·26	4·92	4·09	6·62	4·36	5·32
5	6·90	11·75	12·70	4·90	12·25	7·07	12·20	9·36
6	10·56	5·75	9·11	6·45	7·30	9·61	5·80	7·44
7	7·45	10·05	10·11	5·72	10·25	5·67	11·25	8·57

$\bar{r}$ = Array mean.

and late-flowering types. The obvious differences between environments are least between 20° and 25° C., a fact which can be attributed in part to irregularities in the 20° C. environment. At both 20° and 25° C., the high temperatures caused some degree of irregular flowering and incomplete siliqua development. The mean siliqua numbers at these temperatures are therefore unexpectedly low (table 4), and indeed the plants appeared less healthy than those grown at 10° and 15° C.

TABLE 5

Hayman analyses of variance of the average phenotype. Entries are mean squares

Source	d.f.	FT	HT	LN	SN
a	6	10658·7510***	2347·4718***	1065·0078***	115·5225***
b	21	1066·9244***	460·0133***	151·7518***	37·4514***
b_1	1	3091·2988***	2603·8431***	627·9360***	139·8930***
b_2	6	43·5170**	276·0748***	8·4442***	9·5152***
b_3	14	1360·9294***	388·7134***	179·1562***	42·1068***
c	6	179·8924***	86·7781*	11·6090***	4·2750
d	15	53·1078***	63·5882*	8·7861***	1·6467
t	48	1838·2060***	525·4084***	203·7142***	31·8743***
Environments	3	15950·2427***	25699·0829***	1259·6660***	14401·0711***
$E \times a$	18	219·0159***	251·2261***	31·3817***	16·2552***
$E \times b$	63	33·3332***	100·6398***	5·5232***	4·7870***
$E \times b_1$	3	38·2677*	92·9461*	3·2596	5·4601
$E \times b_2$	18	15·0000	47·9350	2·8398	3·4933
$E \times b_3$	42	40·8378***	123·7771***	6·8350***	5·2933***
$E \times c$	18	62·6889***	34·0702	7·9413***	2·8959
$E \times d$	45	39·9210***	53·2047**	4·2540***	2·3245
$E \times t$	144	62·2717***	96·3184***	8·6612***	5·2146***
Blocks	1	2·0574	828·2551***	0·4758	413·3819***
$B \times t$	48	12·8033	48·8610*	2·6646	2·7432
$E \times B$	3	81·2341***	230·9006**	12·3121***	62·5761***
$E \times B \times t$	144	14·3624	41·9813*	2·3361	2·7738
Replicates	3134*	14·5029	34·7302	2·0017	2·4822

FT = flowering time, HT = height, LN = leaf number, SN = siliqua number.
(* = 3037 for SN.)

(a) *Average phenotype*

The Hayman (1954) analyses of variance (table 5) indicate the presence of both additive and non-additive variation for all four characters; there are also significant differences between reciprocal crosses with respect to flowering time and leaf number. The model appropriate for the genetic effects is Eisenhart's (1947) Model I, since these families comprise a quota sample of those originally collected. The significance of the b_1 item in all cases implies that the non-additive variance is directional, dominance being in the direction of late flowering, tallness and a large number of basal leaves (tables 1-3). For the fitness character (table 4), parent 4 possesses the greatest number of dominant alleles and produces thd least siliquae, thus suggesting that dominance is in the direction of a small number of siliquae. At the higher temperatures only, this dominance of parent 4 could be due

to an underestimate of its score for siliqua number because of the failure of plants to flower (table 1). However, we are confident that this rather surprising outcome may be ascribed to the obvious truncation of growth suffered by some of the plants in this experiment, in consequence of their having exhausted the supply of nutrients and water in the agar medium. Clearly, under conditions of agar culture, the longer the interval between germination and flowering, the less moisture and nutrients will be retained by the medium at flowering time. Thus when family 4, which is by far the latest parent (table 1), began to flower, the agar lost its moisture very rapidly, leading to early death, and, hence, truncation of siliqua production at a premature stage. On the other hand, families which flowered earlier were subject to less stress during growth, and often finished flowering before the agar had dried up completely. In conjunction with this effect, members of array 4 were in general the largest plants, bearing most leaves and most shoots. Consequently, they required more nutrients and moisture from the medium at all stages during their growth than did earlier flowering, smaller types. Indeed, the latter effect may be the more important since, even after a vernalisation treatment of 12 weeks, parent 4 still produced the lowest number of siliquae, although its time to flowering was markedly reduced (Jones, personal communication).

Turning now to the inheritance of the developmental phenotype, it is clear that, as was the case for the average phenotype, the additive mean square ($E \times a$) is the largest item with respect to all characters. Analysis of the data within environments shows that the magnitude of the additive effects increases with temperature for flowering time and leaf number. There appears however to be no linear relationship in this respect for the remaining characters. In contrast to the average phenotype, the mean dominance deviation ($E \times b_1$) is small, indicating that the direction of dominance does not change with temperature. The significant non-additive variation ($E \times b_3$) is remarkably constant in magnitude over environments for flowering time and leaf number, but decreases with increasing temperature for height and siliqua number. Reciprocal differences, both consistent (c) and specific (d), interact with environments effectively only with respect to flowering time and leaf number, and are largest at 15° C.

(b) *Developmental phenotype*

In the earlier papers which were concerned with diallel crosses between inbred lines, the linear and non-linear components of the developmental phenotype were estimated by regressing family means on to environmental means, the latter being calculated as the average performance of the parents in that environment (Perkins, 1970). The specification of the environment in this way is less informative in the present case where we cannot assume that the parents are homozygotes. Family means have been regressed, therefore, on to environmental values defined as the average performance of all 49 families raised in that environment. Then the phenotype of family i in environment j is

$$Y_{ij} = \mu' + d'_i + (1 + \beta'_i)\varepsilon'_j + \delta_{ij} \quad \text{(Perkins and Jinks, 1968)}$$

where d'_i is now defined as the genetic effect of the ith family, rather than the additive genetic effect of that family, as in analyses of inbred lines.

The genetic analysis of the linear and non-linear components of genotype-environment interaction were performed in exactly the same manner as described in Westerman (*loc. cit.*). The total sum of squares with respect to the linear components of interaction now becomes however

$$(t^2-1)\sigma_e^2 + \sum_{i=1}^{t^2} \beta_i'^2 \sum_{j=1}^{s} \varepsilon_j'^2 \quad \text{with } (t^2-1) \text{ degrees of freedom;}$$

and with respect to the non-linear component of interaction is

$$(t^2-1)(s-2)\sigma_e^2 + \sum_{j=1}^{s} \sum_{i=1}^{t^2} \delta_{ij}^2 \quad \text{with } (t^2-1)(s-2) \text{ degrees of freedom,}$$

where σ_e^2 = replicates mean square

s = number of environments

t = number of diallel parents.

TABLE 6

Hayman analyses of variance of the linear and non-linear components of the developmental phenotype

	FT				HT			
	Linear		Non-linear		Linear		Non-linear	
Source	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
a	6	352·6742***	36	60·0079***	6	126·0296***	36	148·5525***
b	21	40·0149***	126	20·9338***	21	126·8051***	126	61·0978***
b_1	1	15·1160	6	21·6724	1	125·6285	6	47·4496
b_2	6	23·8028	36	11·1622	6	21·2590	36	55·3408*
b_3	14	48·7484***	84	25·0688***	14	172·1232***	84	64·5400***
c	6	40·8329**	36	32·1968***	6	22·5693	36	30·6447
d	15	38·9744***	90	21·1702**	15	51·5029	90	42·0447
t	48	78·8744***	288	27·2998***	48	90·1467***	288	62·2689***
Replicates	3134	14·5029	3134	14·5029	3134	34·7302	3134	34·7302

	LN				SN			
	Linear		Non-linear		Linear		Non-linear	
Source	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
a	6	58·8339***	36	7·0599***	6	13·6032***	36	9·1779***
b	21	10·0418***	126	2·8482***	21	4·7593**	126	3·2911*
b_1	1	10·0006*	6	1·9916	1	1·8773	6	3·0203
b_2	6	3·9774	36	2·2413	6	3·5908	36	3·4257
b_3	14	12·6437***	84	3·1694***	14	5·4723**	84	3·2517*
c	6	5·5559*	36	4·5119***	6	4·2016	36	2·1767
d	15	6·5871***	90	2·5070	15	1·3707	90	2·5692
t	48	14·5006***	288	3·4760***	48	4·7361***	288	3·6620***
Replicates	3134	2·0017	3134	2·0017	3037	2·4822	3037	2·4822

The results of these analyses are presented in table 6. The linear component of the developmental phenotype is in all cases larger than the non-linear component, the former accounting for 84, 67, 90 and 66 per cent. of the total variation attributable to genotype-environment interaction for flowering time, height, leaf and siliqua number, respectively. We noted

earlier that additive effects appear to be important in respect of the interaction of these families with the environment. The present analyses show that the additive mean square is in general the largest item with respect to both the linear and the non-linear response; that is, its importance is

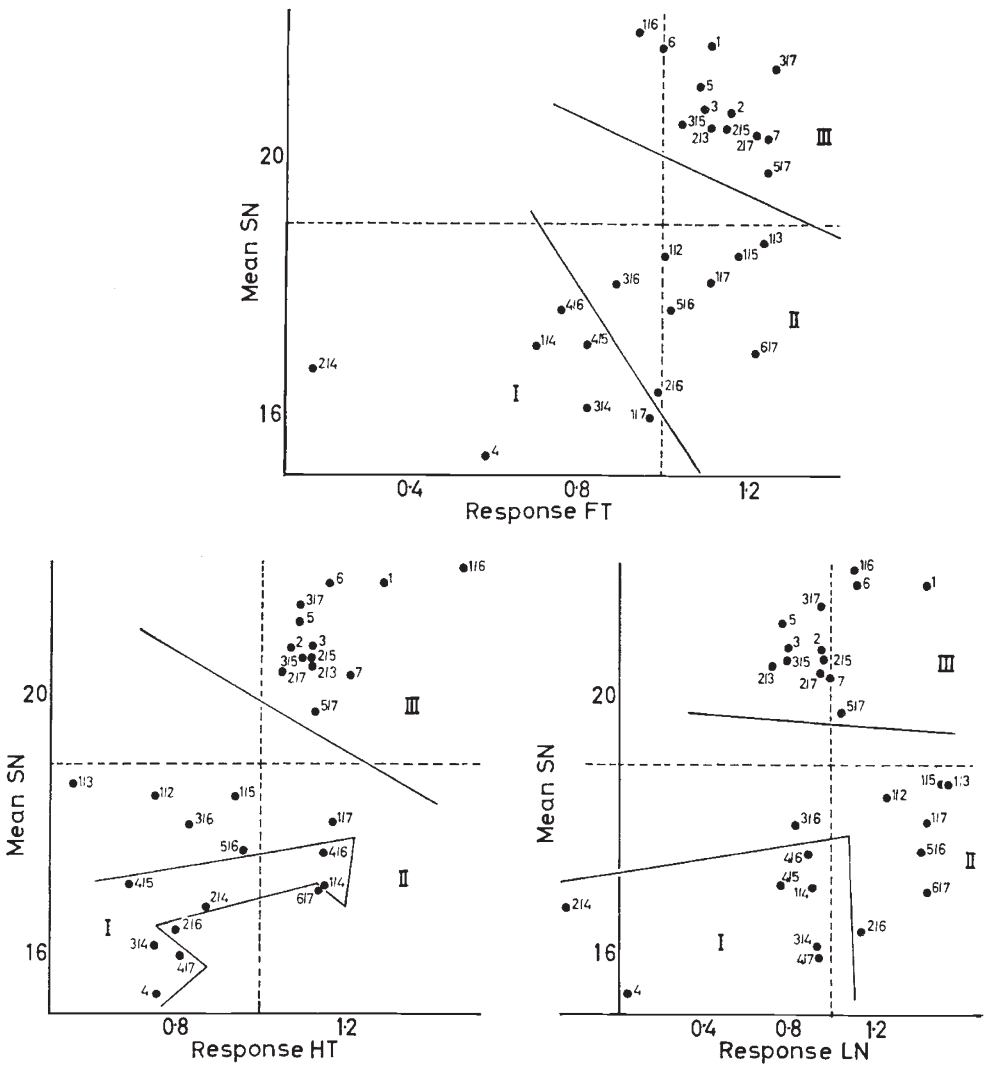

FIG. 1.—The relationship of mean siliqua number and the response of the three primary characters. The unbroken lines indicate the position of the three groups (see text).

not confined to one component of this response. The same is apparently true with regard to the non-additive and reciprocal effects displayed by genes determining the developmental phenotype.

(c) *Relationship of primary characters with siliqua number*

In fig. 1 mean siliqua number is plotted against the response metric,

$(1+\beta_i')$, for each of the three primary characters. The diagrams are divided into four parts by the average of the $(1+\beta_i')$'s, which is of course unity, and by the average siliqua number of the 49 families.

At first sight, the interpretation of the diagram for flowering time appears unambiguous. All the points lie on a significant regression line running from the top-right to the bottom-left quarter; in other words, the predominant mode of developmental regulation appears to be such that flexibility is advantageous. Closer examination of this diagram, however, reveals a more complex situation; the 28 points fall into three groups, as indicated by the unbroken lines on fig. 1. The first group, which consists of the seven families having parent 4 as one parent, lies in the bottom left-hand quarter; that is, these families produce a low number of siliquae, and their flowering time changes relatively little over environments. The second group of points falls on the whole in the bottom right-hand quarter, and concerns hybrids between an early (2, 3, 5, 7) and a late (1, 6) flowering parent. Since the reproductive output of these F_1's is much lower than that of their parents, they display considerable non-allelic interaction with respect to siliqua number; their response for flowering time is, however, similar to the response of their parents. Finally, crosses between two late or two early parents constitute the third set of points, in the top right-hand quarter. These 13 points, formed by crosses within early- and late-flowering types, fall on a significant regression line running from the top-left to the bottom-right corner of this quarter; that is, these families manifest various degrees of developmental stability, with the late parents (1 and 6) and their hybrid being the most stable.

Turning to the diagram for height (fig. 1), we find that exactly the same three groups of points can again be distinguished, although the first and second groups now overlap. Thus, the hybrids between an early- and a late-flowering parent (Group II) not only produce fewer siliquae, but also tend to respond less with respect to height, than do their parents. Within the third group, in the top right-hand quarter, there is some tendency for the 13 points, and in particular those which concern hybrids, to exhibit varying proportions of developmental flexibility, the late families 1 and 1×6 being now the most flexible.

An examination of the diagram for leaf number (fig. 1) indicates that the general picture is similar to that for the other primary characters. In the first group, we notice that the hybrid 2×4 lies outside the diagram, since it has a $(1+\beta\ell)$ value of less than zero; in other words, its response to temperature, though slight, is opposite in direction to that of the other 27 families. The relative reponse of parent 4 over environments is even less for leaf number than for flowering time and height, thus emphasising the contrast between the developmental phenotype of this parent and that of the remaining six parents. The explanation of this consistent and marked difference in the level of variability exhibited by parent 4 is, however, not clear. Furthermore, we recall that the low reproductive output of this parent may be ascribed to truncation by growth on agar medium. For both these reasons, families having parent 4 as one parent will be excluded from further discussion. The hybrids in the second group appear in general to change more over environments with respect to leaf number than do their parents; that is, they are less stable. However, the development of members of the third group, consisting of crosses between two early or two

late parents, is apparently not regulated in any specific manner. The mode of developmental regulation of leaf number has been previously found (Westerman and Lawrence, 1970; Westerman, 1970b) to be more diverse than that of the other primary characters. Thus, although the average phenotypes of flowering time and leaf number are always highly, but not completely, correlated, the developmental phenotypes of these two characters are in general relatively unassociated.

4. Discussion

The families in this natural population of *Arabidopsis* fall into two distinct groups, an early-flowering type with a low number of basal leaves (families 2, 3, 5, 7) and a late-flowering type with a large number of leaves (families 1, 6). These types also differ in their response to vernalisation, in that the early type requires no vernalisation, while the late type has a marked vernalisation requirement (Jones, personal communication). This population was chosen for study in the belief that the bimodal distribution of variation with respect to flowering time and leaf number indicated a polymorphic situation.

In a polymorphic population, crosses between the two morphs should of course on average be at least as fit as crosses within the morphs, assuming that the environmental niches of the morphs are equally represented in the sample used. We recall, however, that hybrids between an early- and a late-flowering parent produce fewer siliquae than do either of their parents. Furthermore, the low reproductive output of these hybrids does not appear to be a result of truncation of their growth since, when array 4 is omitted, there is no association between flowering time and siliqua number. Regarding high siliqua number as synonymous with high fitness, we are therefore forced to conclude that it is unlikely that the early- and late-flowering types share a common gene pool; that is, they are independent populations.

The interpretation of these results, assuming that there are two independent populations, is not quite straightforward. With respect to flowering time, for example, interpopulation hybrids might be expected to be less stable than intrapopulation hybrids. We noted earlier (fig. 1), however, that the large difference in reproductive output between non-co-adapted and co-adapted crosses is not apparently accompanied by any difference in the variability of this primary character. Thus the conclusion that the early- and late-flowering types comprise sympatric populations is obviously speculative. Further information would be desirable, for instance, on the amount of outcrossing that occurs under natural conditions.

Despite the discontinuity in average phenotype between the early and late populations, their developmental phenotypes are nevertheless remarkably similar; the genetic systems controlling these two aspects of the total phenotype are therefore apparently unrelated. The optimum for flowering time in this material appears to be brought about by stabilisation of the expression of the genes concerned, with the late-flowering families being the most stable. The response of inbred lines to temperature (Westerman and Lawrence, 1970; Westerman, 1970a) and to photoperiod (Westerman 1970b) has also been consistently found to be such that stability of expression is advantageous. We may argue then that the genotype-environmental

interactions displayed by this character are not adaptive; a thesis which is further supported by the synchrony of the flowering response observed in the wild.

With respect to height, on the other hand, a high level of variability appears to be the adaptive optimum; this has been observed both for inbred lines (Westerman and Lawrence, 1970; Westerman, 1970b) and for this wild material. We conclude that height is therefore an opportunistic character, possessing the capacity to express different optimal phenotypes in different environments.

The last point is concerned with some assessment of the method used to examine the evolutionary role of genotype-environment interaction. This method relates the average phenotype of a fitness character to the developmental phenotype of a primary character; the relationship may be direct or via a correlation between these and the average phenotype of the primary character. We have seen above that the same direct association has been consistently observed in all four experiments with respect to each of the two characters, flowering time and height. On the other hand, the correlations of both mean siliqua number and the response of the primary character with the mean expression of the primary character are not uniform over experiments for either character. We may be confident, therefore, that this method provides an informative and convenient means of ascertaining whether the variation exhibited in respect of genotype-environment interaction is or is not adaptive.

5. Summary

1. The diallel progenies of seven partly inbred descendants of a natural population of *Arabidopsis* were analysed genetically with respect to four metrical characters, flowering time, height, leaf and siliqua number.

2. The inheritance of all characters is determined by genes with both additive and non-additive effects; there are also significant differences between reciprocal crosses for flowering time and leaf number.

3. All characters exhibit genotype-environment interaction, and for flowering time and leaf number the interaction is largely accounted for by a linear regression to the environmental values.

4. Both linear and non-linear response to environment is controlled by additive and non-additive (b_3) variation, and, with respect to flowering time and leaf number, reciprocal differences.

5. The optimum for flowering time is brought about by stabilisation of the expression of the genes concerned, the late-flowering families being the most stable. With respect to height, on the other hand, a high level of variability appears to be the adaptive optimum.

6. The results suggest that the early- and late-flowering families comprise two independent populations, rather than one polymorphic population.

Acknowledgments.—I am indebted to Dr M. J. Lawrence for his advice and guidance. I also wish to thank Mr Malcolm Perry for technical assistance. This work was carried out during the tenure of a C.S.I.R.O. Postgraduate Studentship, and supported by a grant from the S.R.C.

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