

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

II. INBRED LINES; ANALYSIS

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1. INTRODUCTION

It was shown in a previous paper (Westerman and Lawrence, 1970) that the capacity of inbred lines of *Arabidopsis thaliana* to respond to the environmental variable, temperature, varied considerably from one line to another. Despite the diversity of this response, measured in terms of three flowering time or primary characters and one fitness character, two main conclusions were possible. Firstly, the relationship between the performance of a line and the environmental value was essentially linear with respect to all four characters measured; and secondly, while flowering time appears to be a character whose optimum is brought about by the stabilisation of the expression of the genes concerned, with respect to height most families manifest a variable degree of developmental flexibility. The development of the third primary character examined, leaf number, is apparently not regulated in any particular manner.

The present paper is concerned with a genetical analysis of the developmental phenotypes of seven of these inbred lines.

2. MATERIAL AND METHODS

The seven lines chosen (table 1) are approximately a quota sample of the developmental phenotypes of the 33 lines studied in the previous paper, particular emphasis being placed on the character flowering time in this

TABLE 1

The parent lines

(See fig. 1 of Westerman and Lawrence, *loc. cit.*)

Line no.	Name	Country of origin	Accession number
1	Eifel	Germany	2
2	Maine	France	8
3	Langridge	Unknown	11
4	Limburg	Germany	13
5	Landsberg-1	Germany	16
6	Le Mans-2	France	20
7	Wilna-2	U.S.S.R.	26

selection. The lines were crossed in all possible combinations to produce a 7×7 diallel set of progenies. These were raised in four controlled environments at 10°, 15°, 20° and 25° C., 10 sibs being grown in each of two independently and completely randomised blocks in each environment.

Germination was in general good, in that 96 per cent. of the seed sown germinated. Flowering time characters, as in the previous experiment, were scored daily for a total period of 90 days in each environment, except at 10° C., where the growth of the plants was sufficiently slow to warrant scoring on alternate days only. Three per cent. of the plants in the experiment failed to flower within the scoring period. All other technical details were similar to those described in the previous paper (Westerman and Lawrence, *loc. cit.*).

3. RESULTS

(a) *The average phenotype*

The family means for each character at each temperature are shown in tables 2-5. As in the earlier paper, the data were transformed before analysis on to a square root scale in an attempt, only partly successful, to remove the dependence of family variance on family mean. The data were then analysed by partitioning the total variation into the three main items attributable to

TABLE 2
Mean flowering time of diallel families at each temperature

	1	2	3	4	5	6	7
10° C.							
1	45.64	42.72	54.87	51.19	50.95	45.83	70.46
2	42.42	44.85	51.60	48.77	52.67	42.30	69.55
3	57.70	58.17	82.23	65.60	77.00	51.23	69.95
4	58.33	58.35	66.45	70.78	69.47	52.60	76.90
5	59.57	56.41	93.44	77.56	71.82	54.40	84.50
6	43.60	43.03	47.68	48.86	67.56	37.65	64.20
7	76.32	65.00	77.82	76.56	77.72	72.40	78.15
15° C.							
1	27.15	25.01	30.95	32.36	31.75	31.02	34.46
2	24.70	29.36	32.80	29.43	31.49	27.01	29.75
3	34.31	37.31	40.87	39.36	44.18	29.12	39.39
4	36.06	34.89	40.65	44.23	39.12	32.18	23.25
5	36.46	36.62	44.18	47.20	41.93	34.88	42.73
6	27.17	26.46	31.67	29.61	24.34	25.64	31.26
7	33.62	32.86	37.29	39.40	43.67	39.45	36.00
20° C.							
1	12.62	11.95	14.51	14.46	14.07	14.80	15.95
2	12.63	12.70	13.65	15.40	14.16	14.04	15.28
3	16.95	17.56	16.60	18.40	18.46	17.23	17.70
4	17.00	17.66	16.86	17.78	17.15	18.20	16.90
5	18.20	17.50	18.86	26.67	19.95	18.15	18.60
6	15.00	14.04	16.33	15.75	15.61	14.70	14.95
7	16.65	15.10	18.24	18.65	20.16	19.95	15.85
25° C.							
1	4.88	5.01	4.90	5.00	5.49	5.78	4.10
2	5.55	6.22	5.85	5.65	5.30	5.10	4.16
3	6.08	8.12	6.15	5.40	5.79	5.74	5.06
4	7.00	7.02	5.83	6.15	5.20	6.10	4.65
5	7.10	6.45	7.25	23.17	9.43	6.30	4.64
6	4.99	5.03	5.35	5.25	4.23	5.73	3.90
7	3.85	4.10	3.86	5.54	4.89	5.68	3.15

TABLE 3

Mean height at flowering time of diallel families at each temperature

	1	2	3	4	5	6	7
	10° C.						
1	12·09	10·50	36·65	27·94	23·02	23·76	44·12
2	11·92	12·58	36·70	31·77	32·11	20·00	35·93
3	43·25	50·83	75·73	72·15	82·67	52·97	58·18
4	36·00	40·54	76·67	77·95	80·19	50·15	62·00
5	36·31	41·16	65·50	57·28	74·32	50·75	64·20
6	23·50	24·10	38·26	44·84	41·45	26·70	50·50
7	48·66	39·25	75·60	62·67	61·28	60·11	50·76
	15° C.						
1	29·04	23·74	50·86	51·50	47·19	51·09	43·92
2	24·28	40·19	70·37	48·57	54·35	43·72	27·41
3	68·25	82·11	95·31	99·99	89·76	63·00	70·35
4	70·75	61·52	104·32	99·86	73·15	65·95	72·09
5	75·06	75·81	89·76	48·57	83·14	74·74	59·23
6	37·52	43·29	65·38	54·89	44·17	56·60	43·67
7	40·04	48·29	71·11	53·18	57·04	61·78	49·12
	20° C.						
1	23·27	22·70	43·57	43·58	40·18	43·30	35·70
2	24·86	25·00	38·40	46·50	40·75	42·34	35·40
3	60·70	56·34	59·55	68·70	68·53	72·46	50·80
4	51·80	51·30	67·26	66·34	68·65	66·65	45·50
5	55·65	54·34	73·27	39·67	52·90	63·57	49·80
6	45·95	52·39	69·39	67·00	64·06	60·00	51·75
7	34·35	31·95	51·41	55·95	50·22	52·21	35·95
	25° C.						
1	60·71	60·43	72·05	70·05	72·36	70·07	52·20
2	57·80	60·06	80·20	74·24	73·25	70·90	57·88
3	78·11	83·36	93·60	85·50	82·57	86·24	70·78
4	75·25	80·54	90·79	84·65	84·05	86·10	69·45
5	81·55	77·05	87·00	77·25	78·19	79·70	63·71
6	69·23	73·90	83·80	83·39	78·65	74·51	67·05
7	52·45	52·85	63·89	67·55	59·66	67·59	58·60

TABLE 4

Mean leaf number of diallel families at each temperature

	1	2	3	4	5	6	7
	10° C.						
1	14·28	13·73	15·27	15·90	15·59	15·35	21·05
2	13·21	14·47	14·15	14·36	15·05	13·40	20·50
3	16·25	16·78	16·00	17·40	18·84	13·58	22·21
4	17·39	16·83	18·00	17·55	17·71	14·30	22·10
5	16·67	16·22	26·73	24·23	19·04	14·65	23·60
6	12·60	12·50	12·86	12·83	19·22	11·88	19·41
7	24·36	22·10	21·51	23·17	22·31	22·65	23·20
	15° C.						
1	12·12	11·27	12·56	12·93	12·17	13·18	13·74
2	11·71	11·65	12·40	12·21	11·87	12·90	13·46
3	12·99	13·00	12·56	12·43	14·05	12·62	14·54
4	13·61	13·09	12·73	13·56	12·39	12·98	13·84
5	13·60	12·18	14·05	18·32	13·57	13·02	16·03
6	12·34	11·80	12·56	11·71	10·00	12·49	13·68
7	14·18	13·36	13·60	14·55	15·35	14·44	14·56

TABLE 4—*continued*

	1	2	3	4	5	6	7
	20° C.						
1	11·10	10·75	10·86	10·55	10·66	11·95	12·85
2	10·96	11·10	10·55	11·25	10·91	10·96	12·18
3	11·65	11·39	10·10	11·05	10·37	11·93	13·15
4	11·70	12·41	10·27	10·99	10·80	11·85	12·80
5	11·80	12·09	10·91	16·00	11·59	11·96	13·50
6	11·35	10·85	11·97	11·06	11·52	11·05	11·92
7	13·30	12·30	12·71	11·95	13·45	13·84	13·20
	25° C.						
1	8·02	7·70	7·65	8·10	7·48	8·65	8·45
2	8·25	8·39	8·25	8·08	7·35	8·45	7·90
3	8·30	8·90	7·25	7·40	7·65	8·33	8·01
4	8·10	7·89	6·55	7·30	7·55	8·10	8·00
5	9·00	7·95	8·00	14·42	8·60	8·55	8·28
6	8·26	8·10	7·90	7·93	7·86	7·82	7·85
7	8·00	8·20	7·88	8·89	8·28	8·73	7·75

TABLE 5

Mean siliqua number of diallel families at each temperature

	1	2	3	4	5	6	7
	10° C.						
1	24·08	25·06	20·96	22·98	23·38	24·70	26·52
2	23·01	25·64	20·45	21·61	21·11	23·90	25·77
3	21·45	18·05	16·06	15·10	17·06	19·12	20·01
4	21·30	19·78	18·00	18·34	17·25	20·50	21·10
5	22·67	20·75	23·04	23·22	15·48	21·55	21·85
6	24·55	24·81	21·69	21·25	24·36	25·65	25·51
7	24·89	25·20	20·08	21·39	22·58	26·57	25·96
	15° C.						
1	16·00	15·54	13·90	14·65	15·84	15·43	17·72
2	15·91	13·26	11·84	14·65	13·43	13·88	17·60
3	12·81	10·53	10·93	10·40	12·02	14·06	13·31
4	13·00	14·65	9·77	10·16	11·36	16·21	12·59
5	12·29	11·53	12·02	22·04	13·70	14·10	13·90
6	17·43	17·41	15·08	16·31	15·33	16·22	18·48
7	16·68	15·57	13·36	17·71	15·65	17·73	18·12
	20° C.						
1	16·64	15·75	14·53	13·49	13·82	13·50	16·10
2	16·36	14·30	14·05	12·60	12·71	14·43	16·03
3	11·50	10·78	11·30	8·70	9·38	12·20	14·15
4	11·85	12·77	10·83	9·24	9·15	13·60	14·35
5	12·65	11·84	8·26	17·34	11·76	13·15	14·00
6	14·20	15·84	12·52	12·33	14·00	16·80	16·66
7	15·45	17·60	14·56	12·95	13·63	15·20	17·20
	25° C.						
1	15·10	13·35	13·75	15·00	13·91	14·77	16·60
2	14·40	14·55	14·00	13·09	15·00	14·15	16·85
3	14·02	12·59	14·80	13·25	14·58	16·23	17·46
4	14·10	13·84	13·40	15·30	14·90	16·00	17·10
5	14·75	14·05	12·50	13·84	14·01	16·50	18·30
6	15·11	16·04	15·55	15·44	15·67	14·86	16·05
7	17·30	17·75	16·56	17·87	18·35	17·66	19·65

genetic effects, environments and blocks, their interactions, and replicates. The latter, which serves as an error item, is calculated as the average variation between individuals within families, environments and blocks. The genetic effects are further partitioned according to Hayman's (1954) analysis of variance of diallel tables.

The results of the analyses of variance with respect to the four characters are presented in table 6. The block and second-order interaction mean squares were homogeneous and not significant, and were therefore pooled with the replicates mean square.

TABLE 6

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

Source	d.f.	FT	HT	LN	SN
<i>a</i>	6	8.6704***	56.5889***	1.5048***	3.5252***
<i>b</i>	21	0.2997***	0.8768***	0.1070***	0.0911***
<i>b</i> ₁	1	0.0124	0.3211	0.2600***	0.0359
<i>b</i> ₂	6	0.1986***	0.5060**	0.0589***	0.0816*
<i>b</i> ₃	14	0.3635***	1.0753***	0.1166***	0.0991***
<i>c</i>	6	1.0519***	3.1806***	0.3110***	0.1932***
<i>d</i>	15	0.3181***	0.6865***	0.1288***	0.1684***
<i>t</i>	48	1.4458***	8.0693***	0.3140***	0.5573***
Environments	3	528.2736***	72.0863***	28.6172***	21.1194***
<i>E</i> × <i>a</i>	18	2.0692***	6.0023***	0.4810***	0.2262***
<i>E</i> × <i>b</i>	63	0.1195***	0.4387***	0.0353***	0.0565***
<i>E</i> × <i>b</i> ₁	3	0.0766*	0.9582***	0.0209	0.0605
<i>E</i> × <i>b</i> ₂	18	0.0900***	0.4040***	0.0181**	0.0784***
<i>E</i> × <i>b</i> ₃	42	0.1353***	0.4165***	0.0437***	0.0469*
<i>E</i> × <i>c</i>	18	0.0878***	0.4138***	0.0196***	0.0718**
<i>E</i> × <i>d</i>	45	0.1027***	0.2212**	0.0261***	0.0606***
<i>E</i> × <i>t</i>	144	0.3529***	1.0631***	0.0862***	0.0809***
Blocks	1	0.7493***	1.4885***	0.0000	2.0361***
<i>B</i> × <i>t</i>	48	0.0307	0.1045	0.0086	0.0250
<i>E</i> × <i>B</i>	3	1.2347***	0.4457*	0.0527***	0.1484**
<i>E</i> × <i>B</i> × <i>t</i>	144	0.0244	0.1607	0.0074	0.0380
Replicates	3080	0.0249	0.1380	0.0082	0.0312

FT = flowering time, HT = height, LN = leaf number, SN = siliqua number.

The interpretation of the genetic effects is straightforward. There is clear evidence of additive and non-additive genetic variation, the latter, in general, being ambidirectional; there are also significant differences between reciprocal crosses.

Since these main genetic effects are large in comparison with their interactions with the environment, the non-additive variation may be investigated by means of *Wr/Vr* graphs (Jinks, 1954). The values of *Wr* and *Vr* for each array were adjusted for environmental effects in the usual manner. It turns out that the regressions of *Wr* on *Vr* are significant for all characters (fig. 1). In addition, the slopes of the regression lines do not differ from unity, except in the case of leaf number; thus the assumptions of no epistasis and no correlated gene distributions hold for all characters except leaf number. An inspection of the grand family means with respect

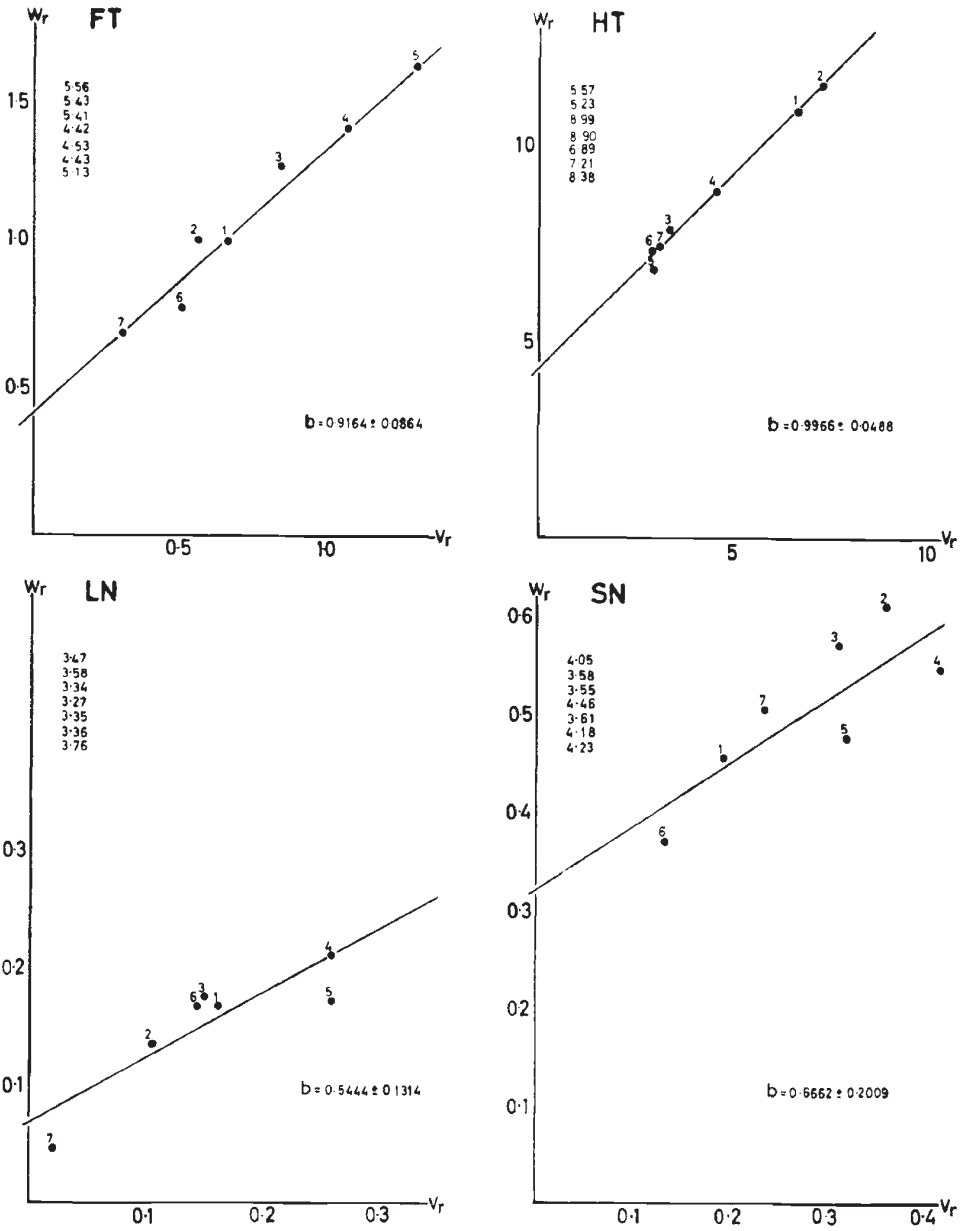


FIG. 1.— W_r/V_r graphs for the four characters with respect to the average phenotype. In the top-left corner, the parental means are ranked according to their position on the graph (symbols as in table 6).

to this character reveals that cross 5 × 4 is the probable cause of the failure. A comparison of the order of points on the graph and the parental means shows that dominance is ambidirectional for all characters except height, where dominance is in the direction of tallness. Furthermore, parent 7 carries the greatest number of dominant genes with respect to the partially correlated

characters flowering time and leaf number, and is one of the most dominant lines also for height at flowering time.

We may now turn to the items which measure genotype-environment interaction. It is clear that for all characters the expression of both additive and non-additive variation and, somewhat surprisingly, of consistent and specific reciprocal effects depends to a considerable extent on the environment.

(b) *Developmental phenotype*

We now wish to examine the nature of the genotype-environment interaction manifested by each character. Thus we may partition the interaction sums of squares of the previous analysis of variance into linear and non-linear components. Accordingly, for each family, a linear regression coefficient is obtained from the regression of family means on to environmental means, where the latter are defined as the average performance of all *parents* in that environment (Perkins, 1970). Thus the phenotype of parent *i* in environment *j* is

$$P_{ij} = \mu' + d'_i + (1 + \beta'_{di}) \epsilon'_j + \delta_{dij}$$

and the phenotype of the (*il*)th F_1 in environment *j* is

$$F_{(il)j} = \mu' + f'_{(il)} + (1 + \beta'_{f(il)}) \epsilon'_j + \delta_{f(il)j}$$

The linear portion of the interaction is specified therefore by the regression coefficients β'_{di} and $\beta'_{f(il)}$, and the non-linear portion by δ_{dij} and $\delta_{f(il)j}$ for parents and F_1 's, respectively.

This approach may, however, be extended in order to examine the inheritance of these two components of genotype-environment interaction. Considering the analysis of the linear portion first, a Hayman (*loc. cit*) analysis of variance may be performed directly on the t^2 regression coefficients available, *t* being the number of diallel parents. The total sum of squares for differences between regression coefficients is then

$$((t^2 - 1) / \sum_j \epsilon_j'^2) \sigma_e^2 + \sum_i \beta_{di}'^2 + \sum_{i,l} \beta_{f(il)}'^2 - \sum_{i,l} \beta_{f(il)}' \epsilon_j'^2 / t^2$$

with $(t^2 - 1)$ degrees of freedom, where $\sigma_e^2 =$ replicates mean square. There is no correction term in respect of the β_{di} 's since, by definition, they sum to zero. In order to compare this total sum of squares with the replicates item, it is clear that it, and therefore all its component sums of squares, must be multiplied by the constant factor $\sum_j \epsilon_j'^2$.

Accordingly, the total sum of squares with respect to the linear component of genotype-environment interaction is

$$(t^2 - 1) \sigma_e^2 + \sum_i \beta_{di}'^2 \sum_j \epsilon_j'^2 + \sum_{i,l} \beta_{f(il)}'^2 \sum_j \epsilon_j'^2 - \sum_{i,l} \beta_{f(il)}' \sum_j \epsilon_j'^2 / t^2 \tag{1}$$

We may now turn to the analysis of the non-linear portion of the interaction. In each of the *s* environments, a Hayman (*loc. cit*) analysis of variance of the $t \delta_{dij}$'s and $t(t - 1) \delta_{f(il)j}$'s was performed. The grand analysis of variance was then obtained by summing each interaction term over environments. The total sum of squares has the form

$$(t^2 - 1)(s - 2) \sigma_e^2 + \sum_j \sum_i \delta_{dij}^2 + \sum_j \sum_{i,l} \delta_{f(il)j}^2 - \sum_j \sum_{i,l} \delta_{f(il)j} / t^2 \tag{2}$$

with $(t^2 - 1)(s - 2)$ degrees of freedom, and can thus be compared directly with the replicates mean square.

Since blocks are for present purposes regarded as environments in their own right, the total sum of squares for genotype-environment interaction $(1 + 2)$ equals.

$$(\text{Environments} \times t + \text{Blocks} \times t + \text{Environments} \times \text{Blocks} \times t)$$

in the previous analysis of variance (table 6). The sums of squares with respect to the non-linear component of intreaction may therefore alternatively be obtained by difference.

The results obtained from the present data using the analysis described above are presented in table 7. Two general points emerge:

TABLE 7

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

Source	FT				HT			
	Linear		Non-linear		Linear		Non-linear	
	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
<i>a</i>	6	5.7269***	36	0.0939***	6	8.3678***	36	1.7760***
<i>b</i>	21	0.2314***	126	0.0375***	21	0.3486***	126	0.2366***
<i>b</i> ₁	1	0.0033	6	0.0723**	1	1.2143**	6	0.3100*
<i>b</i> ₂	6	0.2282***	36	0.0267	6	0.3940**	36	0.1848
<i>b</i> ₃	14	0.2477***	84	0.0396***	14	0.2672*	84	0.2536***
<i>c</i>	6	0.1662***	36	0.0242	6	0.2684	36	0.2168*
<i>d</i>	15	0.1499***	90	0.0455***	15	0.1794	90	0.2025**
<i>t</i>	48	0.8844***	288	0.0454***	48	1.2880***	288	0.4147***
Replicates	3080	0.0249	3080	0.0249	3080	0.1380	3080	0.1380

Source	LN				SN			
	Linear		Non-linear		Linear		Non-linear	
	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
<i>a</i>	6	1.1724***	36	0.0496***	6	0.0570	36	0.1467***
<i>b</i>	21	0.0562***	126	0.0137***	21	0.0696***	126	0.0374
<i>b</i> ₁	1	0.0186	6	0.0155	1	0.0204	6	0.0338
<i>b</i> ₂	6	0.0515***	36	0.0070	6	0.1667***	36	0.0348
<i>b</i> ₃	14	0.0668***	84	0.0164***	14	0.0422	84	0.0384*
<i>c</i>	6	0.0329***	36	0.0106	6	0.0265	36	0.0510**
<i>d</i>	15	0.0353***	90	0.0117**	15	0.0663**	90	0.0396*
<i>t</i>	48	0.1863***	288	0.0172***	48	0.0616***	288	0.0534***
Replicates	3080	0.0082	3080	0.0082	3080	0.0312	3080	0.0312

FT = flowering time, HT = height, LN = leaf number, SN = siliqua number.

(1) With two exceptions only, the mean squares for linear interaction are larger than the corresponding mean squares for non-linear interaction with respect to all three primary characters. Indeed, we find that the percentage of linear response to environment, as estimated from the components of mean squares, is 98, 81 and 95 per cent. for flowering time, height and leaf number, respectively.

(2) For these three characters, the mode of inheritance of both the linear and non-linear components of genotype-environment interaction is predominantly additive; that is, it is the expression of the additive effects of genes which is least consistent in both their linear and non-linear response to environment. With respect to siliqua number, however, the inheritance of the non-linear component of interaction only is predominantly determined by additive variation.

Considering now the analyses of the linear regression coefficients in more detail, for flowering time and leaf number both additive and non-additive genetic effects, and reciprocal items show significant linear interactions with environments. There are no reciprocal differences between regression coefficients with respect to height, while for siliqua number only b_2 and d appear to be involved in the inheritance of that portion of the genotype-environment interaction which is a linear function of the environment. Indeed, only 58 per cent. of the interaction with respect to this fitness character can be attributed to linear response, a proportion which is appreciably lower than that obtained with the flowering time characters.

The non-additive variation in respect of the linear portion of interaction can be examined in greater detail by means of Wr/Vr graphs (Jinks, *loc. cit.*). For all primary characters, the regressions of Wr on Vr are significantly different from zero, yet not different from unity (fig. 2). The linear response of non-additive effects to environment appears therefore to be due solely to dominance. Furthermore, parent 7 is in all cases near the origin, while the remaining parents are grouped some distance along the regression line. In this respect especially, these graphs resemble the Wr/Vr graphs discussed earlier (fig. 1). Thus, with regard to the primary characters, line 7 carries the greatest number of dominant genes both for the linear component of the developmental phenotype and for the average phenotype.

We may now examine the inheritance of the non-linear component of interaction in greater detail. As mentioned earlier, for all characters the inheritance of the deviations from regression is largely controlled by additive effects of genes. However, with respect to the primary characters, the genes determining response also display non-additive variation, mainly b_3 , and specific reciprocal effects. For siliqua number, on the other hand, consistent reciprocal effects interact in a non-linear fashion with environments. Analyses of the deviations from regression within environments reveal that at 10° C. there is in all cases very little non-linear response, and this is determined only by additive variation. Indeed, non-additive and reciprocal components with respect to siliqua number are found only at 25° C. Thus for all characters, and in particular for this fitness character, deviations from linear regression increase and become more complex as temperature rises.

Where there is evidence of both additive and non-additive variation it is of course possible to plot Wr/Vr graphs of the non-linear response within environments, and we find that for the three primary characters, parent 7 is always nearest the origin. Thus for all three primary characters, this parent contributes the greatest number of dominant alleles to its progeny in respect of both the average and the developmental phenotype. Indeed, in the present material there appears to be a fairly general association between the genes determining these two aspects of the phenotype. This is, however, an accident of sampling, since, with the possible exception of height, there is no consistent relationship between the genetic systems which determine the

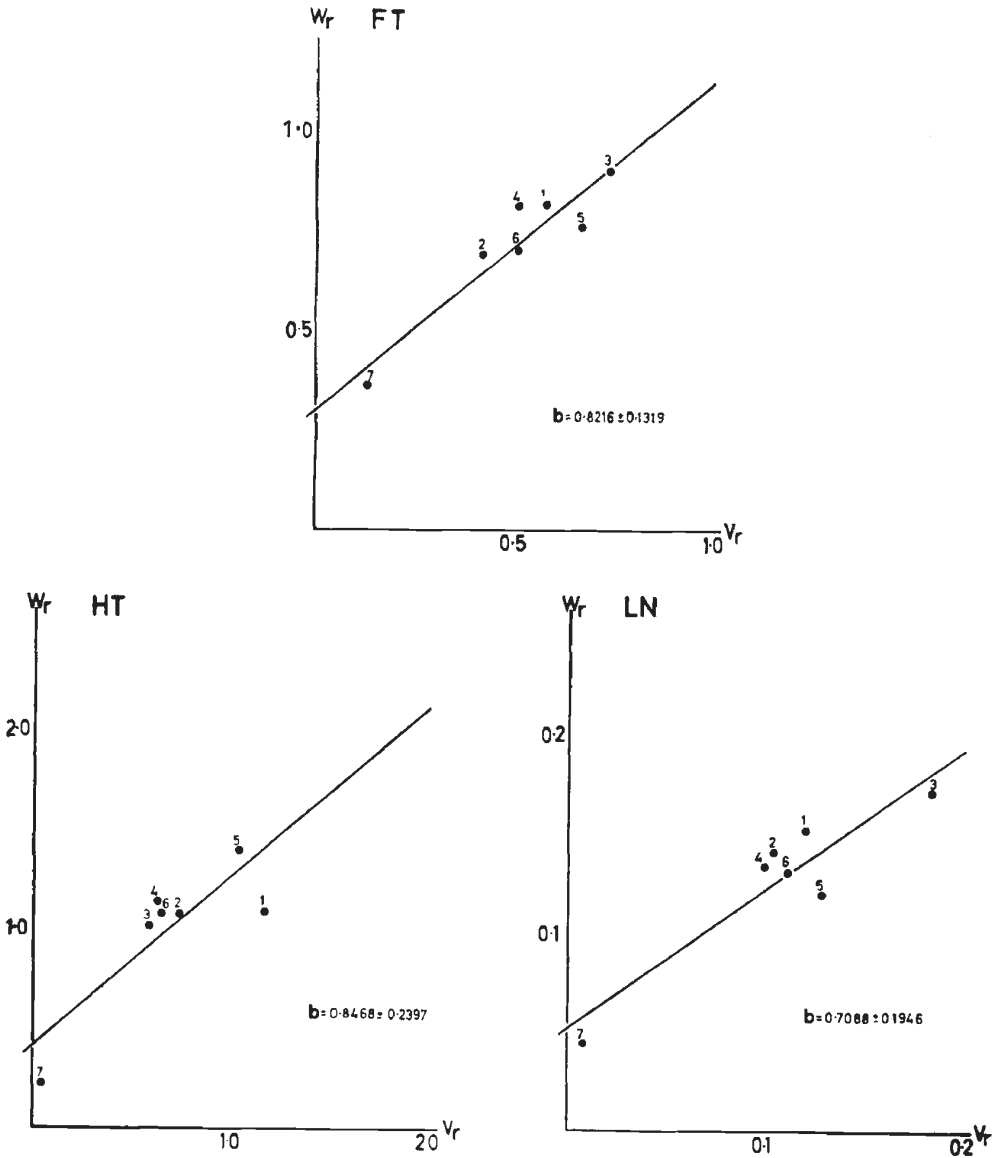


FIG. 2.— W_r/V_r graphs for the three primary characters with respect to the linear component of the developmental phenotype.

average and the developmental phenotype (Westerman and Lawrence, *loc. cit.*).

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

As in the previous paper, the predominant linear nature of the genotype-environment interaction displayed by the primary characters suggests the use of the linear regression coefficients β'_{di} or $\beta'_{f(i)}$ as a measure of the response of a parent or F_1 respectively to environmental change. In fig. 3 mean

siliqua number is plotted against $(1 + \beta'_{di})$ or $(1 + \beta'_{f(i)})$, the response metrics used, for flowering time, height and leaf number, respectively, reciprocal families having been averaged in these diagrams. The average siliqua number of the seven parents and the average of the $(1 + \beta'_{di})$'s

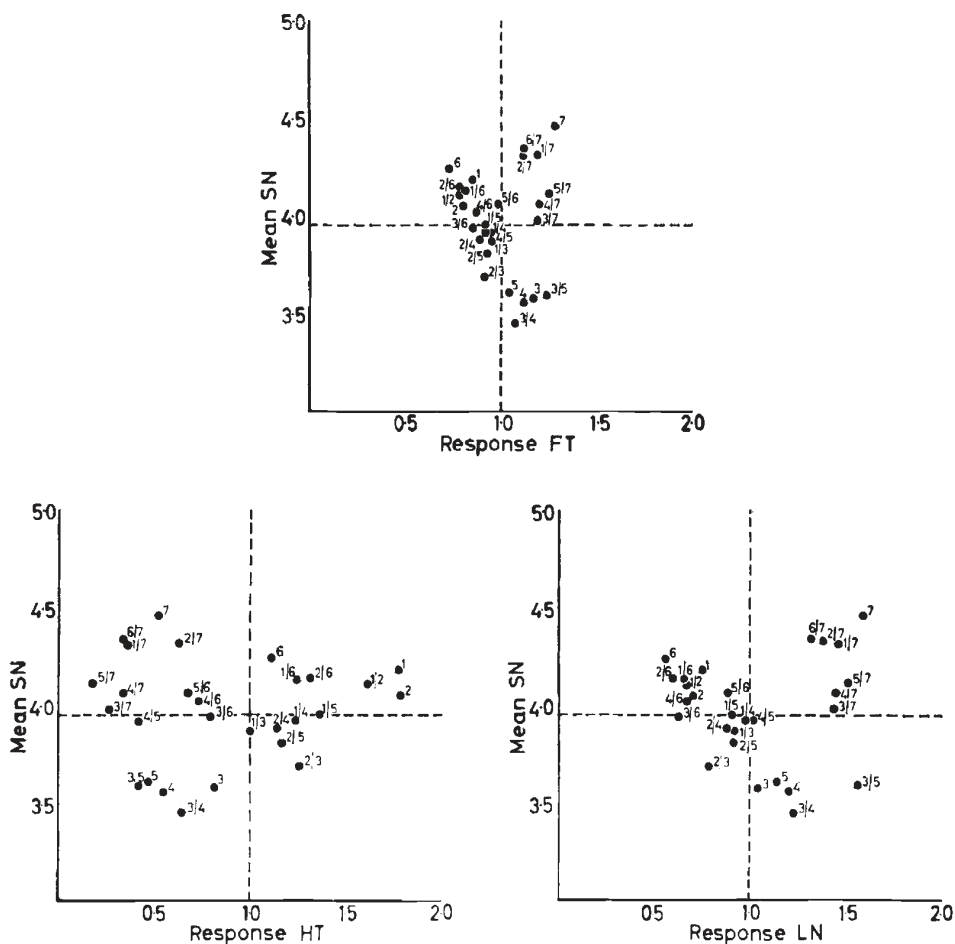


FIG. 3.—The relationship of mean siliqua number and the response of the three primary characters.

divide the diagrams into four parts. The relationship of each primary character with the fitness character can then conveniently be ascertained (see table 1 of the previous paper).

The interpretation of the diagrams for flowering time and leaf number is straightforward. All the points lie on a significant regression line running from the top-left to the bottom-right quarter, except for parent 7 and its progeny. This distinct group of seven families falls in the top-right quarter, so that above average siliqua production is correlated with a large change in both time of flowering and in leaf number over environments; that is, these families are developmentally flexible with respect to these two characters.

From the diagrams, there is little doubt that parent 7 carries the most dominant alleles for the response metric, thus underlining the conclusions drawn earlier from the W_r/V_r graphs (fig. 2). The remaining parents show various degrees of developmental stability. Lines 1, 2, and 6 are relatively stable, a high reproductive output being associated with little change in flowering time or leaf number over environments, while parents 3, 4, and 5 are unstable.

Turning now to the F_1 's, we have the relationship

$$\beta'_{f(i)} = 1/2 (\beta'_{di} + \beta'_{di}) + \beta'_{h(i)}$$

(Perkins, *loc. cit*) where $\beta'_{h(i)}$ is the linear regression coefficient for the dominance-environmental interaction component of the (i)th F_1 hybrid. In other words, the response metric of each F_1 is made up of the average of its parents' response, plus a regression coefficient for the interaction of the dominance component with the environment. Accordingly while, for example, $\beta'_{f(47)}$ is larger than $\beta'_{f(67)}$, the relative magnitudes of β'_{d4} and β'_{d6} imply that $\beta'_{h(47)}$ is much smaller than $\beta'_{h(67)}$. On average, however, the $\beta'_{h(i)}$'s are small in comparison with the β'_{di} 's, and the mean of the $\beta'_{h(i)}$ values does not differ significantly from zero for either flowering time or leaf number. The conclusion here is then clear. Three of the four possible types of developmental regulation are illustrated in these two diagrams (fig. 3) and furthermore, although stability is the chief mode of regulation, it is in this material recessive to flexibility.

An examination of the diagram (fig. 3) for height reveals that the dominant parent, 7, and all its progeny are again quite distinct. They are now grouped in the top-left quarter of the diagram, and therefore manifest developmental stability with respect to this character. The remaining families fall on a line running from the top-right to the bottom-left quarter, the regression being significant at the 1 per cent. level of probability. Thus lines 1, 2 and 6 are developmentally flexible, and lines 3, 4 and 5 are inflexible, in that they produce fewer siliquae than average, and their height changes relatively little over environments. The dominance of stability to flexibility with respect to height is confirmed by finding that 18 out of a total of 21 $\beta'_{h(i)}$'s are negative, and their mean value of -0.1839 is significantly less than zero. The linear interaction of the dominance component of the F_1 's with environments is on average therefore in the direction of less change over environments.

A correlation between mean performance and variability over environments has frequently been observed (Jinks and Jones, 1958; Eberhart and Russell, 1966; Perkins and Jinks, 1968). In the present data, there is a strong positive association between the average phenotype and the linear component of the developmental phenotype in respect of flowering time and leaf number. In general, plants which flower later and produce more leaves change more over environments than do early-flowering forms with few basal leaves. On the other hand, while late-flowering plants are on average taller, these taller genotypes respond relatively less to environment than do shorter genotypes; that is, mean performance and linear interaction are negatively correlated with respect to height. These associations lead us to the same conclusion as that reached in the previous section; namely, that the genetic systems controlling these two aspects of the phenotype are not

entirely independent. However, this conclusion only applies to the primary characters. Mean expression, linear and non-linear components of genotype-environment interaction all appear to be entirely unrelated with respect to siliqua number.

The most striking point to emerge from an examination of these diagrams (fig. 3) is their confirmation of the trends that were apparent in the corresponding diagrams in the previous paper. In other words, using the behaviour of the seven selected lines on the earlier diagrams as a basis for prediction,

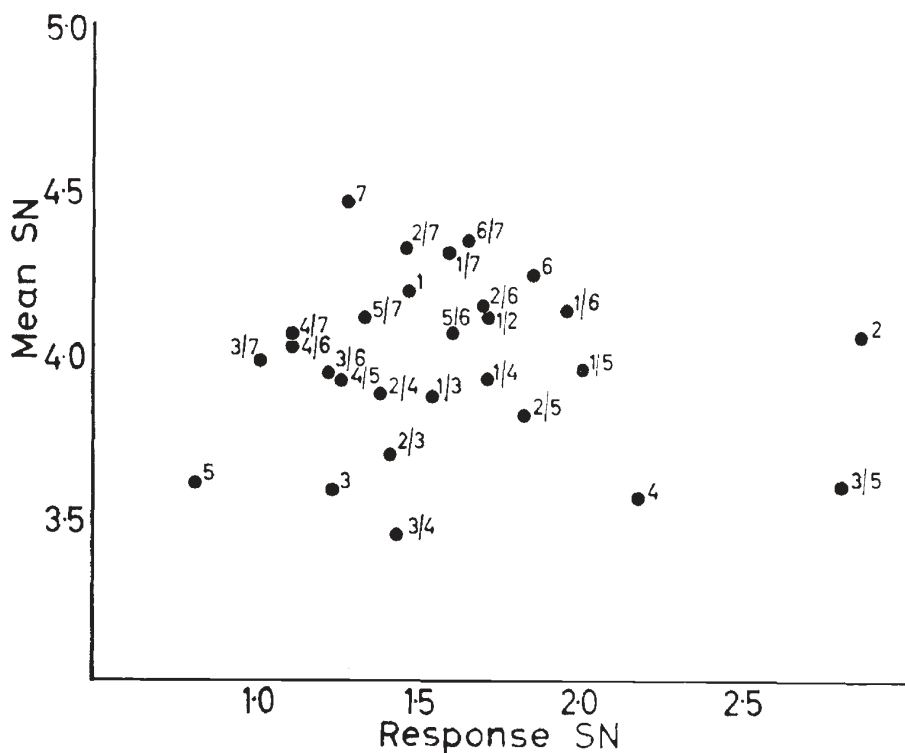


FIG. 4.—The relationship of mean siliqua number and the response with respect to siliqua number.

the agreement of observed with expected is very good indeed for all three primary characters. With the exception of line 5, all parents have reacted in a similar manner in these experiments. In the earlier diagrams, line 5 tended to fall with parents 1, 2 and 6, whereas it now groups very distinctly with lines 3 and 4. This change in its response pattern can be attributed in part only to the inclusion of the 10° C. environments in this experiment.

One final point requires mention. We wish to determine if there is any consistent relationship between mean reproductive output, and the variability of this character over environments. Since only 58 per cent. of the genotype-environment interaction with respect to siliqua number is linear in nature, there is little doubt that the use of $(1 + \beta_{di})$ and $(1 + \beta_{f(i)})$ as response metrics for this character is less satisfactory than for the primary characters. Hence, in order to carry out this comparison the mean of each family was plotted against its total sum of squares over environments (fig. 4).

With the exception of parent 2, the distribution is somewhat triangular; that is, above average siliqua production is, in general, associated with intermediate variability of this character over environments. This result lends some support to the use of mean siliqua number as a measure of reproductive performance.

4. SUMMARY

1. Genetical analysis of the average and developmental phenotypes, of seven inbred lines with respect to three primary characters, namely flowering time, height and leaf number, and one fitness character, siliqua number, has been carried out by means of a diallel cross.

2. The inheritance of the average phenotype for all characters examined is predominantly controlled by additive variation, though non-additive and reciprocal effects are also present.

3. All characters display considerable genotype-environment interaction, and for the three primary characters the interaction is largely a linear function of the environmental values.

4. In general, it is the expression of the additive effects of genes which is least consistent in both their linear and non-linear response to environment. Furthermore, such non-additive effects as are present appear to be due solely to dominance.

5. Although stability is the chief mode of developmental regulation for flowering time and leaf number, it is apparently recessive to flexibility in this material.

6. With respect to height, on the other hand, most families manifest a variable degree of developmental flexibility; dominance, however, is in the direction of less change over environments.

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