THE POPULATION GENETICS OF *ARABIDOPSIS THALIANA*

III. THE EFFECT OF VERNALISATION

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Received 14.vii.70

1. INTRODUCTION

PREVIOUS experiments concerning material sampled from natural populations of *Arabidopsis* have shown that there are considerable differences between populations as well as between families within populations, with respect to several metrical characters including flowering time (Jones, 1971*a, b*). Observations on populations of the species in its natural habitats, however, suggest that only a small part of the variation detected in laboratory experiments, at least with respect to flowering time, is expressed. Indeed, in many populations flowering time appears to be strikingly synchronised in the natural environment. Furthermore, despite the apparently favourable nature of the glasshouse environment, not all the plants came into flower during the course of the experiments and showed no sign of doing so had their duration been extended.

There are two major environmental factors which control floral initiation in a specific manner, namely, photoperiod and low temperature (Lang, 1952). All the available information on the response of *Arabidopsis* to photoperiod suggests that it is a quantitative long-day plant (Laibach, 1943; Ratcliffe, 1961). Thus, if the individuals under investigation had a similar photoperiodic requirement the daylength of 18 hours used in the experiments would not have been a limiting factor for flowering and flower initiation.

From investigations on inbred lines there is a considerable amount of evidence that low temperature is an important factor affecting floral initiation in this species (Napp-Zinn, 1957; 1960*a, b*). Furthermore, low temperature is effective in inducing flowering in non-flowering material from natural populations (Cetyl, 1965; Cetyl, Dobrovolná and Effmertová, 1968). Under natural conditions there is also ample opportunity for any low-temperature requirement to be satisfied for, at least in some of the habitats which it occupies, the species behaves as a winter annual (Ratcliffe, 1961, 1965). After germination in the autumn a prostrate rosette of leaves is formed, at which stage the plant overwinters and flowering then takes place in the following spring. Flowering often takes place therefore after the plant has experienced a period of low temperature, *i.e.* it has been vernalised. Under such conditions it might be expected that all the individuals in a population would have a uniform requirement for vernalisation. However, it is clear from investigations concerning material from natural populations in Czechoslovakia that there are considerable differences between populations in the proportion of plants with such a requirement (Cetyl, Dobrovolná and Effmertová, 1968), which suggests that this is a character of complex adaptive significance. Little is known of either the quantitative effect of a period of low temperature and its consequence on flowering time, nor, in

British populations at least, of the frequency of natural populations with such a requirement and the type of habitat in which they are found.

The present experiment was designed to investigate the quantitative effect of vernalisation on the time of flowering of a number of families from three natural populations of *Arabidopsis thaliana*. The populations were chosen to represent three types of habitat in which the species is commonly found, namely, gardens, disused railway tracks, and limestone slopes in the Derbyshire Dales.

2. MATERIAL AND METHODS

The experimental material was obtained from 12 plants sampled at random in each of the three populations (table 1). Before treatment, the

TABLE 1
Origin and habitats of the populations

Population	Origin	Habitat
1	Cannon Hill Park, Birmingham	Flower beds
2	Wixford, Warwickshire	Disused railway track
3	Winnats Pass, Derbyshire	Limestone slope

seed was sterilised in equal volumes of hydrogen peroxide (20 vols.) and absolute alcohol for 10 minutes, washed in sterile distilled water, and placed on filter paper in petri dishes, where it was allowed to imbibe water for 24 hours at room temperature. It was then vernalised in the dark at a temperature of $1 \pm 1^\circ \text{C}$., a procedure which is technically more convenient than the treatment of the young plant and which has, moreover, been shown to be as effective at least in laboratory inbred lines (Napp-Zinn, 1960a, 1965).

Seed samples from each of the 36 families were treated in this way, at 14-day intervals, over a period of 11 weeks, giving the following six treatments in all:

Treatment	Weeks at $1 \pm 1^\circ \text{C}$.
1	11
2	9
3	7
4	5
5	3
6	1

Successive treatments were initiated 14 days after the previous one so that all the treatments were completed at the same time, 11 weeks after the start of the experiment. The seed was then sown on agar medium in test-tubes (Langridge, 1957; Brown and Smith, 1964). Eight seeds were sown from each of the 216 family-treatment combinations (3 populations $\times$ 12 families $\times$ 6 treatments) in each of two independently and completely randomised blocks. The blocks, which were sown on consecutive days, were housed in separate controlled environment cabinets. These were maintained at a temperature of 25°C ., a light intensity of approximately $22,000 \text{ lm/m}^2$ at the plant level and a daylength of 16 hours. Flowering time (in days) was measured from the day on which the first plant came into flower (15 days

after sowing), following which plants continued to come into flower for the following 59 days. By this time some plants had still not come into flower. As these showed no sign of flowering, however, the experiment was terminated. These are referred to as non-flowering individuals.

3. RESULTS

(i) *Variation between populations*

The distribution of flowering time in the three populations in each of the six treatments is shown in fig. 1. Three main points emerge from a

FIG. 1.—Histograms showing the distribution of flowering time in each of the three populations after 1, 3, 5, 7, 9 and 11 weeks of vernalisation. The non-flowering individuals (N) are shown separately.

comparison of the populations which concern, respectively, the proportion of plants which have a requirement for vernalisation (*i.e.* a necessity for a period of cold treatment before normal flowering will occur), the mean expression of flowering time shown by those individuals which flowered and, lastly, the variation of scores about these means.

Turning first to the proportion of non-flowering plants, it is clear that all individuals from the Winnats Pass Population have an absolute requirement for vernalisation as no plants flowered after 1 week of treatment. Some individuals from Wixford also have a requirement for vernalisation, but these comprise a much smaller proportion of the population (approximately 25 per cent. after 1 week of vernalisation). Cannon Hill, on the other hand, contains no individuals with such a requirement.

As expected, the proportion of non-flowering individuals decreases with increasing treatment. For instance, in Wixford most individuals flower

after 3 weeks and only a few require 5 weeks of vernalisation before they will flower. Most individuals from Winnats Pass, on the other hand, require a much longer period of vernalisation before flowering occurs, a requirement which in some cases exceeds 11 weeks. There are thus marked differences between these populations in their proportions of non-flowering plants.

The three populations also show considerable differences in their mean flowering times. Cannon Hill is clearly the earliest flowering population, as all individuals flowered within the first 20 days after only 1 week of treatment. Winnats Pass, on the other hand, is a late-flowering population whilst Wixford is intermediate in its flowering time. In all three populations an increasing period of vernalisation reduces the mean flowering time, even of the population from Cannon Hill.

TABLE 2
Cannon Hill: mean flowering times

		Treatment (weeks)												Family mean
		11		9		7		5		3		1		
Block	Family	1	2	1	2	1	2	1	2	1	2	1	2	
	1	4.63	6.80	3.00	4.00	6.00	3.75	4.67	5.00	6.25	6.33	9.71	9.00	5.762
	2	9.83	9.80	7.67	12.50	10.50	10.29	13.14	9.25	14.63	10.71	14.83	13.60	11.375
	3	4.14	3.71	4.14	5.60	4.50	5.86	4.17	4.20	7.71	5.38	9.63	9.25	5.691
	4	7.50	5.00	6.43	8.00	6.80	7.33	4.50	5.20	9.00	7.00	11.80	10.17	7.394
	5	4.25	4.83	4.75	5.60	8.14	6.00	5.80	4.00	9.88	7.60	10.88	10.29	6.835
	6	8.17	7.00	3.50	5.40	7.33	5.13	7.14	4.00	8.60	7.71	10.63	9.00	6.968
	7	4.60	7.00	5.00	5.75	5.75	4.83	4.33	5.17	8.00	6.83	9.71	10.33	6.442
	8	6.00	4.00	3.00	7.00	5.25	7.43	5.13	6.83	9.25	7.75	11.17	10.60	6.951
	9	4.33	7.75	5.00	3.88	5.14	5.80	7.25	6.80	7.00	6.14	10.30	9.00	6.539
	10	6.00	9.25	7.00	4.67	8.00	8.00	9.67	8.25	9.50	8.50	11.00	10.20	8.337
	11	4.00	10.00	3.14	6.00	7.67	4.50	9.00	8.00	7.00	6.80	10.71	10.25	7.256
	12	5.29	6.00	3.60	4.60	6.50	6.71	7.43	4.88	8.86	6.60	9.50	9.67	6.637

Turning to the last point concerning the effect of vernalisation on the population variance, it has clearly had little effect on the variance of the population from Cannon Hill. In Wixford, however, the variance is markedly reduced with an increasing period of treatment. Thus, after 1 week of vernalisation, individuals flower over the entire scoring period, whilst after 11 weeks of vernalisation 99 per cent. of individuals flower within the first 20 days. A direct comparison of these two relatively early flowering populations and Winnats Pass is not possible in the present experiment because several individuals in the latter failed to flower even after 11 weeks of vernalisation. However, this population appears to possess at least as much genetic variance as Wixford, for the variation shown by this material after 11 weeks of vernalisation is similar to that shown by Wixford after 1 week of vernalisation, though it is possible that, with an increasing duration of treatment, the variance of this population would decline in a similar way to that of Wixford.

(ii) *Variation within populations*

(a) *Cannon Hill*

The mean flowering time of each family-treatment combination is shown in table 2 and the analysis of variance of these means in table 3. An

TABLE 3

Cannon Hill: Analysis of variance

	Item	d.f.	M.S.
	Families (F)	11	26.929***
Families	{ Family 2 v. rest	1	230.147***
	{ Remainder	10	6.607***
	Treatments (T)	5	80.060***
	Blocks (B)	1	1.381
	F $\times$ T	55	1.410
	F $\times$ B	11	1.078
	T $\times$ B	5	7.981***
	F $\times$ T $\times$ B	55	1.530***
	Within	656	0.770

*** $P < 0.001$; ** $P = 0.01-0.001$; * $P = 0.05-0.01$.

FIG. 2.—Cannon Hill: the mean response of individual families to vernalisation.

TABLE 4

Wixford: mean flowering times

		Treatment (weeks)												*Family mean
		11		9		7		5		3		1		
Block		1	2	1	2	1	2	1	2	1	2	1	2	
Family	1	3.33	4.33	2.60	6.29	2.75	4.00	6.60	5.43	7.13	5.40	13.50	13.43	5.025
	2	3.00	5.33	4.25	5.00	3.60	6.00	7.50	4.40	8.00	5.88	16.33	11.86	5.579
	3	2.33	3.71	4.67	7.00	3.50	3.80	8.50	3.40	5.83	4.83	13.38	10.38	5.191
	4	—	—	16.00	10.00	13.00	9.33	13.50	10.50	16.33	14.00	44.67 (3)	30.00 (6)	12.833
	5	3.00	4.71	4.50	2.63	3.86	4.00	9.13	4.50	4.50	5.20	11.88	12.57	4.790
	6	—	7.50	26.00	24.00	17.83	6.67	12.00	13.71	46.00 (5)	22.75 (3)	— (7)	— (5)	21.120 (8)
	7	2.40	3.80	4.71	4.86	6.00	3.00	2.20	5.88	5.33	4.63	12.38	11.17	4.576
	8	9.20	—	11.00	11.20	15.40	13.86	15.75	12.29	17.75	15.63	— (7)	43.33 (1)	14.110
	9	3.75	—	3.13	4.67	3.33	5.50	11.00	4.00	6.86	7.17	15.67	12.50	5.708
	10	8.00	19.00	15.14	10.33	14.00	12.00	13.67	12.50	21.38	15.14	43.50 (4)	39.50 (5)	14.270
	11	2.75	4.00	3.33	5.50	4.60	3.00	4.50	3.57	7.88	4.88	11.29	11.75	4.658
	12	6.75	25.50	15.20	12.50	10.50	10.60	13.00	11.40	20.40	14.60	36.00 (1)	—	13.525

The number of non-flowering individuals are shown in brackets.

* The family mean is based on the observation from 9, 7, 5 and 3 weeks of treatment only.

The dashes refer to the family-treatment combinations in which either all the individuals were lost or no individuals came into flower.

TABLE 5

Wixford: analysis of variance on results from 9, 7, 5, and 3 weeks of treatment only

	Item	d.f.	M.S.
Families	Families (F)	11	250.176***
	Between groups	1	2378.500***
	Within groups	10	37.344***
	Treatments (T)	3	87.054***
	Blocks (B)	1	96.420***
F × T	F × T	33	18.983*
	Between groups × T	3	61.779***
	Within groups × T	30	14.703*
	F × B	11	12.279***
	T × B	3	12.558
	F × T × B	33	7.905***
	Within	418	3.413

examination of the means shows that one family (2) is consistently later than all the other families over all treatments (table 2; fig. 2), and indeed this family

FIG. 3.—Wixford: histograms showing the distribution of flowering time in each family after 1 week of vernalisation. The non-flowering individuals (N) are shown separately.

accounts for most of the variation with respect to differences between families (table 3). Despite this discontinuity, however, all the families appear to respond in the same way to treatment (table 3; fig. 2).

(b) *Wixford*

The data from this population are incomplete both because of the relatively high incidence of non-flowering plants after 1 week of treatment, and because of losses after 11 weeks of treatment (table 4). For this reason the analysis of variance is restricted to the results from 9, 7, 5 and 3 weeks of treatment only (table 5).

TABLE 6

Wixford: analyses of variance on the early and late groups separately

Item	Early group		Late group	
	d.f.	M.S.	d.f.	M.S.
Families (F)	6	1.566	4	91.102***
Treatments (T)	3	12.108*	3	136.425***
Blocks (B)	1	4.219	1	163.378***
F × T	18	1.684	12	34.232*
F × B	6	0.812	4	14.755
T × B	3	9.770	3	19.008
F × T × B	18	3.264***	12	12.863*
Within	246	1.026	172	6.827

It is clear that there is much more variation between families in this population than in Cannon Hill. The families, however, fall into two distinct groups:

1. Families 1, 2, 3, 5, 7, 9 and 11, which comprise an early-flowering group with no apparent requirement for vernalisation (table 4; fig. 3).

2. Families 4, 6, 8, 10 and 12, which comprise a late-flowering group in which all families have at least a partial requirement for vernalisation (table 4; fig. 3).

TABLE 7

Wixford: analysis of variance on both late and early families with the omission of family 6

Item		d.f.	M.S.
Families	Families (F)	10	152.891***
	Between groups	1	1509.317***
	Within groups	9	2.177
	Treatments (T)	3	35.525***
	Blocks (B)	1	42.994***
F × T	F × T	30	3.518
	Between groups × T	3	13.769*
	Within groups × T	27	2.380
	F × B	10	3.798***
	T × B	3	6.623
	F × T × B	30	3.106***
Within		388	1.339

Much of the variation between families in this population thus falls to a comparison between these groups, although there clearly remains some variation between families within groups (table 5). It turns out, however, that all this within-group variation can be ascribed to differences between families in the late group (table 6) and that, furthermore, this variation is due to one family (6) which on average flowers later than the remaining four families in this group (tables 4 and 7).

FIG. 4.—Wixford: Mean response to vernalisation of the early group of families (Δ), family 6 ($\square$) and the late group of families with the omission of family 6 ($\circ$). The mean flowering times of the late group of families after 1 week of treatment, and of family 6 after 3 weeks of treatment, are underestimates because of the presence of non-flowering individuals in these treatments.

TABLE 8

Wixford: within family variances based on observations from 9, 7, 5, and 3 weeks of treatment

Family	Variance
1	1.452 (36)
2	1.030 (31)
3	0.630 (28)
4	3.343 (26)
5	1.621 (39)
6	30.240 (30)
7	0.356 (42)
8	1.096 (42)
9	1.721 (32)
10	1.648 (43)
11	0.458 (38)
12	2.037 (31)

The degrees of freedom are shown in brackets.

In contrast with the previous population, families in this population respond differentially to treatment (table 5). This is due both to a differential response of the two groups of families (table 5; fig. 4), and also to a differential response of families within groups (table 5). As was the case with the average expression of the character, it turns out that only families in the late group show this differential response to treatment (table 6) and that family 6 is again responsible for this heterogeneity (table 7; fig. 4).

TABLE 9
Winnats Pass: mean flowering times

		Treatment (weeks)									
		11		9		7		5		3	
Block		1	2	1	2	1	2	1	2	1	2
Family											
1	31.00	29.67	37.50	44.00	51.50	46.00	—	50.00	—	—	—
			(2)	(4)	(4)	(5)		(7)	(4)	(8)	(7)
2	30.14	29.00	36.50	—	—	—	—	36.00	—	—	—
			(4)	(4)	(7)	(7)		(7)	(6)	(4)	(8)
3	18.00	41.00	—	41.00	—	38.00	—	—	—	23.00	40.50
	(2)			(2)	(6)	(7)		(8)	(8)	(5)	(6)
4	30.67	—	—	—	—	—	—	—	—	—	—
	(2)	(1)		(2)	(4)	(4)		(5)	(7)	(5)	(7)
5	32.00	45.25	50.50	35.60	49.00	58.00	—	—	—	—	—
			(3)		(3)	(5)		(4)	(8)	(6)	(7)
6	30.20	27.57	38.17	41.50	45.00	—	—	—	—	—	—
		(1)	(2)	(3)	(7)	(8)		(3)	(8)	(7)	(8)
7	—	20.50	24.00	24.00	32.67	34.00	—	49.00	50.00	—	—
					(2)	(4)		(8)	(5)	(7)	(8)
8	—	26.71	47.40	37.00	—	—	—	—	—	—	—
			(2)	(3)	(4)	(8)		(3)	(7)	(7)	(7)
9	40.17	—	40.40	—	60.00	—	—	—	—	—	—
	(2)		(1)	(3)	(6)	(5)		(8)	(7)	(8)	(8)
10	23.67	21.00	40.50	20.25	52.50	45.40	53.00	—	—	—	—
					(2)	(1)		(6)	(7)	(5)	(8)
11	54.00	32.00	44.00	47.00	48.00	44.0	—	24.00	—	—	—
	(4)	(1)	(2)	(5)	(4)	(4)		(8)	(6)	(8)	(8)
12	—	43.00	—	—	—	—	—	—	—	—	—
	(7)	(2)	(5)		(8)	(5)		(2)	(4)	(3)	(2)

The number of non-flowering individuals are shown in brackets.

Family 6 also differs from the other families in two further respects. Firstly, it is the only family in which no individuals flowered after 1 week of treatment, and furthermore, contains some non-flowering individuals after 3 weeks of treatment. It differs, secondly, in that its within-family variance is at least six times greater than that of any of the other families in this population (table 8). It appears, therefore, that this family is showing marked segregation for genetic differences with respect to flowering time.

(c) *Winnats Pass*

Because of the large number of non-flowering individuals in this population (table 9), the data is too incomplete to allow any useful quantitative analysis. However, by treating the response to vernalisation as a threshold character, a qualitative assessment of the effect of vernalisation on this material can be made. The proportion of plants that came into flower in each family in each treatment is shown in fig. 5.

It is clear that, although all the families respond to vernalisation, they differ considerably in this respect. For example, all the individuals in families 7 and 10 came into flower after 9 weeks of treatment, whilst only 28 per cent. and 10 per cent. of those in families 11 and 12 respectively did so after 11 weeks of treatment. Since, in both families 10 and 11, a similar

FIG. 5.—Winnats Pass: the proportion of plants coming into flower in individual families in response to vernalisation.

proportion of plants were induced to flower after only 5 weeks of treatment, it is also evident that families differ in their response to continuing periods of vernalisation.

4. DISCUSSION

The mean flowering times and vernalisation requirements of the three populations clearly reflect their diverse origins. As expected from previous

results on this and other weed populations (Jones, 1971*a, b*), individuals from the Cannon Hill population are early flowering with no vernalisation requirement. The early-flowering nature of this population and its possible relationship with the type of selection to which it has been subject has already been discussed in a previous paper (Jones, 1971*b*).

In contrast to the somewhat sheltered habitat of the Cannon Hill population, individuals in the Winnats Pass population are found growing in exposed conditions on freely draining, south-facing, limestone slopes over 305 m above sea-level. According to Ratcliffe (1961), these are subject to summer drought, and germination is thus prevented until the autumn, following which the plants overwinter as rosettes. It is presumably during this stage that any vernalisation requirement is satisfied. Under such conditions, although individuals with no vernalisation requirement could well come into flower in the same season, it is unlikely that they could set seed before the onset of winter. Thus genotypes manifesting this response would be at a disadvantage relative to those with a distinct requirement for a period of vernalisation, which would flower only in the following season. Furthermore, individuals similar to those in the Wixford population, which require only a short period of vernalisation, might well flower early in the spring when conditions are again likely to be disadvantageous. Thus individuals in this population require a relatively long period of vernalisation. A similar difference in the vernalisation requirements of populations from extreme and sheltered habitats has been reported in Subterranean clover (Morley and Davern, 1956). The contrast in this latter case was between individuals from sheltered coastal habitats in North Africa with no vernalisation requirement, compared with plants from adjacent mountain areas with a definite requirement for vernalisation.

As expected from previous investigations on populations from disused railway tracks (Jones, 1971*a, b*), the population from Wixford displays a wide range of variation with respect to flowering time. Furthermore, the distribution of variation in this population is similar to that shown by a somewhat smaller sample of families taken from a site at Luddington which is six miles along the track from Wixford (see Jones, 1971*b*: Population 3). The two distinct groups of families found in both this and the Wixford population suggest that these populations have a polymorphic structure, and indeed the type of disruptive selection which would result in this situation can be readily envisaged. After germination in the late summer or autumn, the early-flowering genotypes could flower and set seed before winter. The late-flowering genotypes on the other hand, because of a vernalisation requirement, would overwinter as rosettes and flower in the following spring, together with the progeny of the early-flowering individuals which flowered in the previous autumn. At this stage, therefore, crossing between the two morphs may occur. Any intermediates which might well flower in the late autumn would be unable to set seed before the onset of winter and would thus be at a severe selective disadvantage relative to the two extreme types.

On this hypothesis then, assuming conditions are suitable, the early-flowering genotypes would produce two generations a year, while the late-flowering genotypes would produce only one. For these two morphs to constitute a balanced polymorphism, the advantage of the late-flowering genotypes must clearly on average be twice that of the early-flowering genotypes. It is possible, however, that the two groups of genotypes represent

two co-existing populations, which originated from two populations which have evolved independently, in which case no prediction of their fitness relationship can be made. Clearly, at this stage, there is no means of discriminating in favour of either of these hypotheses. However, a more detailed analysis of the Wixford population will be presented in a later paper in the series.

5. SUMMARY

1. The effect of vernalisation on the time of flowering has been examined in three natural populations of *Arabidopsis thaliana* from diverse habitats, namely, gardens, disused railway tracks and limestone slopes in the Derbyshire Dales.

2. The populations show considerable differences in their vernalisation requirements. On the one extreme the garden population has no requirement for vernalisation whilst on the other all the families from the Derbyshire population show a marked requirement for vernalisation. The population from the disused railway track appears to have a polymorphic structure in this respect, as five families have a vernalisation requirement whilst the remaining seven do not.

3. In all three populations an increasing duration of treatment results both in a reduction in the mean flowering time and in the number of non-flowering individuals. The interaction of families within populations in their response to treatment has been examined.

4. The results are discussed in relation to the type of selection which may have brought about these differences between populations.

Acknowledgments.—I am grateful to Dr M. J. Lawrence for his advice and encouragement throughout the course of this work. I would also like to thank Miss Jennifer Bird for her excellent technical assistance. The work was undertaken whilst the author was in receipt of a Science Research Council Studentship.

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