MATING SYSTEMS AND POPULATION STRUCTURE IN TWO CLOSELY RELATED SPECIES OF THE WHEAT GROUP

I. VARIATION BETWEEN AND WITHIN POPULATIONS

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SUMMARY

Samples of seven wild populations of the predominantly selfing species *Triticum longissimum* were compared with samples of five populations of the closely related, but predominantly outcrossing species, *T. speltoides*. For most of the 36 quantitative characters which were examined, the differences between populations, the total variances of the populations and the mean within-family variances, were greater in the selfer than in the outbreeder. Theoretical models were analysed in an attempt to explain these results, using concepts of classical population genetics.

1. INTRODUCTION

THE existence of substantial genetic variability in predominantly self-pollinating species of plants has been known since the earliest days of cultivation. Only in recent years has the naturally occurring variability in such species been evaluated and quantified (*e.g.* Weil and Allard, 1964; Allard, 1965; Imam and Allard, 1965; Moore and Lewis, 1965; Allard, Jain and Workman, 1967; Jain and Marshal, 1967; Antonovics, 1968; Pederson, 1968; Jain, Marshal and Wu, 1970; Jones, 1971*a, b*).

The genetic variability within species can be partitioned into several components: variance between populations within a species, variance between families within the population and variance arising from the differences between individuals within families. One of the objects of the analysis of these effects in samples originally collected in the wild is to make inferences on the possible selective regimes experienced by the wild population.

The analysis of possible mechanisms for preserving variability is concomitant to the analysis of variability itself. Conservation of variability in inbreeding systems by means of selection has been discussed by Hayman (1953), Hayman and Mather (1953), Allard *et al.* (1967) and Karlin (1968). The significance of linkage and its possible interaction with selection in conserving variability was pointed out by Lewis and John (1963), Parsons (1957), Jain and Allard (1966), Allard *et al.* (1967) and Karlin (1968). The mating system itself is one of the crucial determinants of the degree of variability but, as the above-named authors have pointed out, its effects can be overwhelmed by, for example, selection.

Since it is reasonable to assume that the amount of gene flow between populations of selfing species is smaller than in outbreeders, we can predict greater differences between populations of the selfing species than between populations of the outbreeder. That such is the case has been demonstrated by Knowles (1943) in *Bromus mollis*, Weil and Allard (1964) in *Collinsia*

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heterophilla, Imam and Allard (1965) and Jain and Marshal (1967) in *Avena fatua* and *A. barbata*, Antonovics (1968) in *Agrostis tenuis* and *Anthoxanthum odoratum*, and Jones (1971a) in *Arabidopsis thaliana*. The same isolation effect might, on the other hand, be expected to produce significant differences between families within populations of a predominantly selfing species (Knowles, 1943; Lawrence, 1969; Jain *et al.*, 1970; Jones, 1971b). Allard *et al.* (1967) have remarked, "Individuals within a population are often heterozygous for many genes governing quantitative characters. The variability that is commonly observed within individual families is therefore not exclusively environmental but much of it can be ascribed to segregation. It is clear that the genetic organisation of a population cannot be determined solely from the rate of outcrossing that occurs in the population." The experiments to be reported here further emphasise the truth of this statement.

The above-mentioned studies of the genetic variances in selfing species demonstrated the presence of variation between and within populations where selfing is the predominant mating system. These studies do not and cannot examine the direct effect of the mating system on the amount of genetic variation. We believe that such an evaluation can be done by comparing two closely related species which differ in their mating system. Such pairs are not common.

The genus *Triticum*-*Aegilops* (Bowden, 1959; Chennaveeraiah, 1960; Morris and Sears, 1967; MacKey, 1968; Sears, 1969) consists of species at various levels of ploidy. These species are indigenous to an extended area in western and central Asia (Zohary, 1966). Among the diploid species ($2n = 14$) there are two closely related species, namely *Triticum longissimum* (= *Aegilops longissima*) and *T. speltoides* (= *Ae. speltoides*) which seem to be morphologically very similar. The former, however, is predominantly a selfer while the latter is predominantly an outcrosser. The physiology of the flowering of *T. longissimum* appears to preclude all but rare outcrossing events (Zohary and Imber, 1963; Simchen, Zarchi and Hillel, 1971). The mature anthers open and discharge most of the pollen grains within the floret before emerging from it. This process ensures that self-pollination occurs although the actual proportion of selfing as against outcrossing has not been measured. In *T. speltoides*, on the other hand, the anthers emerge from the florets still unsplit. From progeny tests, Zohary and Imber (1963) have estimated the extent of outcrossing in populations of *T. speltoides* to be 75 to 95 per cent. It should be noted that, although this examination has been carried out for several populations of *T. speltoides*, not all of the populations considered in this paper were represented. One should also bear in mind that Zohary and Imber tested their populations more than six years before our experiments. In the series of experiments reported here our object was to compare populations of these two species with respect to quantitative characters and relate the differences between them to the mating system and other possible evolutionary factors.

2. MATERIALS AND METHODS

(i) Population survey

Seven populations of *T. longissimum* and five of *T. speltoides* were sampled from various sites in Israel. Table 1 and fig. 1 summarise the locations and prevailing environmental conditions for the 12 populations.

(ii) *Experimental design*

Ten spikes, each from a different plant, were sampled at random from each of the 12 natural populations. Each spike was used to establish a family, consisting of four offspring from the same mother plant, in the following manner. The seeds from each family (*i.e.* spike) were sown in a common petri dish in the laboratory on 8th October 1969. Germination was completed 5 days after sowing, at which stage four seedlings were sampled at

FIG. 1.—Approximate locations of the populations: Populations of *T. longissimum* (1-7) are represented by squares and the populations of *T. speltoides* (8-12) are represented by triangles. (Reprinted from Zarchi *et al.*, 1972.)

random from each petri dish (*i.e.* family). The seedlings were randomly allocated to peat flower-pots in a wire-mesh-covered house.

Seventy days later the pots were moved to experimental plots at the Talpiot experimental farm in Jerusalem. The field was divided into two blocks. Two seedlings were allocated randomly to each block. In this way the members of each family were allocated randomly to each block so that randomisation was complete. The two marginal rows in both sides of each

TABLE 1
Description of the populations and their habitats
 Reprinted from Zarchi *et al.*, *Chromosoma*, 1972)

Population: code and location	Average annual rainfall (mm.)*	Elevation (metres)	Distance from the coast (km.)	Type of soil	Size†	Habitat and principal accompanying plants	Interference by man
<i>T. longissimum</i>							
01 Pardess-Hanna	590	60	10	Red sandy, mixed with coarse sand	Large	Sparse forest of <i>Quercus ithaburensis</i> with <i>Eragrostis bipinnata</i> and <i>Andropogon</i>	Nature conservation in the previous five years
02 Beit-Lid	538	50	5	Red sandy	Large	<i>Eragrostis bipinnata</i>	Not in recent years
03 Taibe	200	600	55	Terra rossa, on hard limestone	Small	Mediterranean scrub with <i>Triticum dicoccoides</i>	Grazed field
04 Eyal	545	100	13	Red sandy	Large	<i>Eragrostis bipinnata</i> and some species of <i>Centaurea</i>	Not in recent years
05 Mikve-Israel	540	20	4	Red sandy	Medium	Ruderal	Pine trees plantation
06 Kanot	475	60	13	Red sandy	Large	Ruderal, with many <i>Centaurea procurrens</i>	Roadsides
07 Gilat	310	100	20	Loess, mixed with some sand	Medium	Steppe scrub plants (<i>e.g. Avena caudii</i>)	Roadsides, Eucalyptus plantation
<i>T. spelioides</i>							
08 Acre	600	20	2	Heavy alluvial	Small	Ruderal	Grazed roadsides
09 Haifa	685	250	6	Terra rossa, on hard limestone	Large	Mediterranean scrub	Eucalyptus plantation
10 Hod Hacarmel	560	30	4	Alluvial	Medium	Ruderal	None
11 Maanit	560	70	14	Heavy alluvial	Medium	Ruderal	Roadsides, Eucalyptus plantations
12 Ashkelon	420	100	6	Heavy alluvial	Medium	Ruderal	Eucalyptus and Pine trees
							Not in recent years

* Based on the years 1900-1960.

† Size of population estimated as follows: large > 2000 plants, medium 500-2000 plants, small < 500 plants.

block were guards, as were the two end plants in each row. The distance between plants in the field were 1.5×0.5 metres. This generation of plants we called S_0 .

The same procedure was carried out for another set of seeds obtained by selfing the progeny of seed taken from the wild in 1968. This generation we called S_1 . Both S_0 and S_1 were randomised and grown together in the same blocks. In all that follows, unless the S_1 generation is referred to specifically, we are considering the S_0 generation.

(iii) *Description of characters*

Forty measurements were made on each plant during the experiment. Thirty-six of them are detailed in tables 2-6. Germination and chiasma characteristics will be considered separately (Hillel, unpubl.; Zarchi, Simchen, Hillel and Schapp, 1972). The number of leaves and tillers of the plants at 2 weeks of growth are not reported since they showed no interesting properties. Characters 21, 22, 23 and 24 are measured on a scale of five points. Thus for character 21, which measures the erectness of the plant, 1 represents the most horizontal while 5 represents fully erect plants. For character 22, green-coloured plants are denoted by 1 and fully violet plants by 5. For character 23, juicy plants are indicated by 1 and dry plants by 5. For character 24, normal emergence of the spikes through their sheath is denoted by 1 and those encountering the most difficulty in emergence were indicated by 5.

Heading and flowering time (characters 1-3 and 5-7) were measured for the first three spikes as the number of days from the arbitrary date, 1st March. The range from the first to the third headings and flowering times (characters 4 and 8) were computed directly from characters 1-3 and 5-7, respectively. The ranges between heading and flowering for each of the first three spikes were also calculated directly from 1-3 and 5-7. Total tiller height without awns and height without spikes were measured for the first three flowered spikes at the flowering time (character 12-17) and again at harvesting time (characters 25-30). Spike length (characters 18-20) was computed by subtracting the total without spike from the total height.

3. RESULTS

(i) *General*

Table 2 summarises the complete analysis of variance for the nested design and consists of the F ratios, for the differences between species, between populations within species and between families within populations. Since the differences between the two blocks and the block $\times$ family interaction in each of the 12 populations were insignificant for the various measurements, we tested the significance of the between-families mean squares against the within-families mean squares. In 24 out of the 36 traits the individual differences between the species were not significant. The 12 characters which showed significant differences between the species were those connected with the seed production and dispersal unit, namely, spike length, number of spikelets in a spike, spike weight of the first three spikes, and the difficulty of spike emergence. Colour and erectness were significant

TABLE 2
Analyses of variance: F ratios of the total analysis for measurements

Characters			Between species†	Between populations† within species	Between families† within populations
No.	Description	Serial flowering (or heading) order	F (1, 10)	F (10-100)	F (100, 308)
1	Heading time	1st	1.7 n.s.	137.4 ***	1.5 ***
2		2nd	1.7 n.s.	126.4 ***	1.3 *
3		3rd	1.4 n.s.	125.2 ***	< 1 n.s.
4	Range between 1st and 3rd heading time		2.9 n.s.	5.3 ***	1.0 n.s.
5	Flowering time	1st	1.5 n.s.	144.1 ***	1.2 n.s.
6		2nd	1.3 n.s.	105.9 ***	1.2 n.s.
7		3rd	1.1 n.s.	99.7 ***	< 1 n.s.
8	Range between 1st and 3rd flowering time		3.1 n.s.	9.1 ***	< 1 n.s.
9	Range between heading and flowering time	1st	< 1 n.s.	8.7 ***	1.2 n.s.
10		2nd	< 1 n.s.	11.1 ***	1.4 *
11		3rd	< 1 n.s.	10.5 ***	1.3 n.s.
12	Total tiller height at flowering time	1st	1.1 n.s.	12.9 ***	1.1 n.s.
13		2nd	1.4 n.s.	25.1 ***	< 1 n.s.
14		3rd	< 1 n.s.	17.8 ***	1.1 n.s.
15	Tiller without spike height at flowering time	1st	< 1 n.s.	31.2 ***	1.2 n.s.
16		2nd	< 1 n.s.	33.5 ***	1.3 n.s.
17		3rd	< 1 n.s.	32.3 ***	1.1 n.s.
18	Spike length at flowering time	1st	23.5 ***	6.1 ***	1.8 ***
19		2nd	21.2 ***	7.3 ***	1.2 n.s.
20		3rd	20.8 ***	7.4 ***	1.3 *
21	Erectness		5.9 *	4.5 ***	1.1 n.s.
22	Dryness		2.5 n.s.	34.5 ***	< 1 n.s.
23	Difficulty in spike emergence		12.3 **	2.5 **	1.1 n.s.
24	Colour		42.0 ***	5.5 ***	1.2 n.s.
25	Total tiller height at harvesting time	1st	4.4 n.s.	26.8 ***	< 1 n.s.
26		2nd	4.7 n.s.	27.2 ***	< 1 n.s.
27		3rd	4.6 n.s.	23.9 ***	< 1 n.s.
28	Tiller without spike height at harvesting time	1st	1.1 n.s.	25.6 ***	1.0 n.s.
29		2nd	1.3 n.s.	26.2 ***	< 1 n.s.
30		3rd	1.2 n.s.	25.0 ***	< 1 n.s.
31	Number of spiklets	1st	12.2 **	13.3 ***	1.1 n.s.
32		2nd	13.3 **	11.7 ***	1.4 *
33		3rd	12.5 **	14.4 ***	1.2 n.s.
34	Spike's dry weight	1st	11.0 **	11.7 ***	< 1 n.s.
35		2nd	13.1 **	10.8 ***	< 1 n.s.
36		3rd	13.1 **	11.7 ***	< 1 n.s.

† Population 3 has not measured for flowering time, thus the degrees of freedom for characters 5-11 will be as follows:

- (a) Between species = 1.
 - (b) Between populations within species = 9.
 - (c) Between families within populations = 97.
 - (d) Within families = 267.
- n.s. = Non-significant difference.
 * = Difference significant $0.01 < P \leq 0.05$.
 ** = Difference significant $0.001 < P \leq 0.01$.
 *** = Difference significant $P < 0.001$.

also. That 24 characters showed no significant differences between species further attests to the similarity of the two species.

In every character there were differences between populations within species. The largest differences were found among the populations of *T. longissimum*.

Thirty of the 36 characters showed no significant differences between families within the 12 populations.

FIG. 2.—Means of the populations of *T. longissimum* and *T. speltoides* for six characters.

(ii) *Differences between populations within each species*

From tables 3 and 4 and fig. 2 it can be seen that the differences between *T. longissimum* populations are higher than those between the populations of *T. speltoides*. In nine characters there were no significant differences between

TABLE 3
Means of populations and species for the 36 measurements

Characters		Populations of <i>T. longissimum</i>										Populations of <i>T. speltoides</i>				
No.	Description	Serial flowering (or heading) order										Species mean				
1	Heading time	1st	1	2	3	4	5	6	7	7	7	8	9	10	11	12
2		2nd	58	56	28	53	50	55	55	55	55	63	50	54	50	64
3		3rd	61	59	31	56	52	58	13	47	47	65	53	56	52	66
4	Range between 1st and 3rd heading time		62	61	33	59	55	60	19	50	50	65	53	58	54	67
5	Flowering time	1st	4.2	4.5	4.7	5.9	4.5	4.4	11.1	5.7	5.7	2.5	3.0	4.1	4.6	2.7
6		2nd	76	77	*	74	72	76	36	69	69	81	73	76	74	83
7		3rd	77	78	*	75	74	78	42	71	71	83	74	77	76	84
8	Range between 1st and 3rd flowering time		78	80	*	77	75	79	47	73	73	84	75	78	76	84
9	Range between heading and flowering time	1st	2.8	2.8	*	2.9	3.4	3.8	11.5	4.4	4.4	2.1	1.8	1.6	2.0	1.8
10		2nd	19	20	*	21	22	20	29	22	22	19	23	22	24	19
11		3rd	18	19	*	20	21	20	30	21	21	19	21	21	23	18
12	Total tiller height at flowering time (cm.)	1st	17	19	*	19	20	19	29	20	20	18	21	20	22	18
13		2nd	73	82	40	74	74	78	51	67	67	61	56	59	57	53
14		3rd	73	75	38	74	74	78	45	65	65	57	52	57	56	52
15	Tiller without spike height at flowering time (cm.)	1st	68	75	35	75	70	74	44	63	63	57	51	58	58	50
16		2nd	56	62	26	57	54	54	34	49	49	49	45	46	45	43
17		3rd	56	57	25	57	53	52	28	47	47	46	42	45	44	42
			56	57	23	57	51	52	28	46	46	45	41	47	45	41

TABLE 3—(continued)

Characters			Populations of <i>T. longissimum</i>							Populations of <i>T. speltioides</i>							
No.	Description	Serial flowering (or heading) order	1	2	3	4	5	6	7	Species mean		8	9	10	11	12	Species mean
			17	20	14	18	20	24	17	19	12	11	12	12	10	11	
18	Spike length at flowering time (cm.)	1st	17	18	13	17	21	23	17	18	12	10	12	12	10	11	
19		2nd	16	18	13	17	20	21	16	17	12	10	12	13	9	11	
20		3rd	3.7	3.6	3.0	3.2	3.2	3.4	3.5	3.4	3.1	2.9	2.7	2.9	2.9	2.9	2.9
21	Erectness		1.6	1.8	3.8	2.0	2.1	1.7	3.6	2.4	1.5	1.9	1.7	1.8	1.6	1.7	
22	Dryness		1.2	1.0	1.0	1.3	1.3	1.0	1.0	1.1	1.5	1.2	1.5	1.4	1.6	1.4	
23	Difficulty in spike emergence		1.2	1.3	1.0	1.7	1.8	1.7	1.0	1.4	2.5	3.1	3.3	2.4	2.6	2.8	
24	Colour		60	69	42	67	62	83	55	63	53	46	54	50	49	50	
25	Total tiller height at harvesting time (cm.)	1st	60	68	41	67	62	80	55	62	52	45	54	51	47	50	
26		2nd	60	67	40	66	62	80	54	61	51	45	53	50	47	49	
27		3rd	46	54	29	52	45	60	37	46	44	38	43	41	41	41	
28	Tiller without spike height at harvesting time (cm.)	1st	47	54	29	51	46	56	36	46	44	37	43	41	39	41	
29		2nd	47	53	28	49	45	57	35	45	43	37	43	40	39	40	
30		3rd	15	15	12	14	15	17	14	15	12	10	12	11	11	11	
31	No. of spikelets	1st	14	14	12	14	15	18	14	14	12	10	12	11	12	11	
32		2nd	15	14	12	14	15	18	14	15	13	10	11	11	11	11	
33		3rd	47	53	32	53	50	72	53	51	31	33	38	33	25	32	
34	Spike's dry weight (10 mg.)	1st	47	52	30	55	48	67	53	50	29	31	36	31	23	30	
35		2nd	43	50	31	52	48	69	52	49	28	33	33	30	24	30	
36		3rd															

* Population 3 has not been measured for flowering time for technical reasons.

TABLE 4
Analyses of variances for individual species: *F* ratios and variance components of the differences between populations
(tested against *MS* between families within populations)

No.	Characters		F ratio		Variance components	
	Description	Serial flowering (or heading) order	<i>T. longissimum</i> F (6, 56)	<i>T. speltoides</i> F (4, 43)	<i>T. longissimum</i>	<i>T. speltoides</i>
1	Heading time	1st	217.4 ***	26.3 ***	361	45
2		2nd	182.4 ***	28.8 ***	326	43
3		3rd	165.1 ***	25.6 ***	290	38
4	Range between 1st and 3rd heading time		6.0 ***	2.2 n.s.	4	4
5	Flowering time	1st	206.7 ***	26.3 ***	239	18
6		2nd	142.8 ***	27.3 ***	184	19
7		3rd	151.8 ***	23.8 ***	148	18
8	Range between 1st and 3rd flowering time		10.7 ***	<1 n.s.	9	0
9	Range between heading and flowering time	1st	10.0 ***	6.0 ***	11	4
10		2nd	12.6 ***	6.7 ***	17	3
11		3rd	12.3 ***	5.5 ***	15	2
12	Total tiller height at flowering time	1st	16.6 ***	3.2 **	147	9
13		2nd	39.9 ***	2.2 **	210	5
14		3rd	23.3 ***	4.4 **	195	14
15	Tiller without spike height at flowering time	1st	29.8 ***	1.8 n.s.	167	2
16		2nd	57.1 ***	<1 n.s.	184	0
17		3rd	53.4 ***	2.1 n.s.	189	3

TABLE 4—(continued)

Characters			F ratio		Variance components	
No.	Description	Serial flowering (or heading) order	<i>T. longissimum</i> F (6, 56)	<i>T. spelioides</i> F (4, 43)	<i>T. longissimum</i>	<i>T. spelioides</i>
18		1st	7.0 ***	2.5 n.s.	8	1
19	Spike length at flowering time	2nd	8.1 ***	4.5 **	8	1
20		3rd	8.1 ***	5.5 **	7	2
21	Erectness†		6.0 ***	1.5 n.s.	9	1
22	Dryness†		66.5 ***	1.1 n.s.	81	0
23	Difficulty in spike emergence†		3.7 ***	2.1 n.s.	1	2
24	Colour†		8.7 ***	4.1 **	11	11
25		1st	36.2 ***	3.8 *	174	8
26	Total tiller height at harvesting time	2nd	34.6 ***	5.8 ***	159	11
27		3rd	30.4 ***	3.7 *	156	7
28		1st	34.8 ***	3.4 *	111	5
29	Tiller without spike height at harvesting time	2nd	33.7 ***	5.4 **	100	7
30		3rd	33.7 ***	3.7 *	105	5
31		1st	23.3 ***	3.4 *	3	0
32	No. of spikelets	2nd	16.5 ***	4.0 **	3	0
33		3rd	20.0 ***	5.7 **	3	1
34		1st	15.0 ***	3.6 *	144	15
35	Spike's dry weight	2nd	12.6 ***	5.0 **	127	19
36		3rd	14.0 ***	3.9 **	129	12

† Population 3 was not measured for flowering time, thus the degrees of freedom for Characters 5-11 will be as follows:

(a) between populations of *T. longissimum* = 5.(b) between families within population of *T. longissimum* = 53

‡ The variance components are multiplied by 100.

the five populations of *T. speltoides* while for all 36 characters the between-populations variance of *T. longissimum* was significant. Thus more characters in the selfer *T. longissimum* produced significant variances, and the variance components due to differences between populations within each species were higher in *T. longissimum* than in *T. speltoides*. It should be noted that in some characters the main contribution to the differences among the populations of *T. longissimum* arises from the difference between populations 7 and 3 and the other populations (e.g. character 1, 13, 16; see table 3 and fig. 2 and the discussion).

FIG. 3.—Variances within populations of *T. longissimum* and *T. speltoides* for five of the characters.

TABLE 5
Total variances within the populations of *T. longissimum* and *T. speltoides* and the mean variances calculated for each of the two species

Characters		Populations of <i>T. longissimum</i>										Populations of <i>T. speltoides</i>					
		Serial flowering (or heading) order										Species					
No.	Description	1	2	3	4	5	6	7	mean	8	9	10	11	12	mean		
1	Heading time	102	59	85	129	144	75	129	103	141	118	79	110	112	112		
2		81	69	77	172	161	91	221	125	88	116	89	118	75	97		
3		74	80	96	160	132	103	324	138	73	124	80	116	73	93		
4	Range between 1st and 3rd heading time	25	19	13	39	26	23	294	63	22	11	18	25	18	19		
5	Flowering time	40	38	*	49	115	24	160	71	52	43	45	46	42	46		
6		38	39	*	47	77	60	239	83	52	51	42	55	34	47		
7		40	45	*	61	67	57	273	91	47	63	41	63	30	49		
8	Range between 1st and 3rd flowering time	22	19	*	30	63	36	400	95	13	16	5	13	12	12		
9	Range between heading and flowering time	25	47	*	46	28	28	256	72	55	38	66	64	49	54		
10		22	32	*	41	38	42	303	80	29	39	60	53	27	42		
11		24	26	*	34	28	40	294	74	24	43	43	44	24	36		
12	Total tiller height at flowering time	596	1601	203	600	294	1131	396	689	355	291	196	322	259	285		
13		276	598	116	744	354	763	515	480	231	253	291	200	193	233		
14		457	1033	143	894	415	1195	571	673	275	288	246	360	195	273		
15	Tiller without spike height at flowering time	327	377	111	249	158	184	196	229	239	188	131	277	190	205		
16		263	339	84	271	187	335	239	245	173	158	171	185	154	168		
17		289	428	103	426	238	293	260	291	213	188	145	300	139	197		

TABLE 5—(continued)
Populations of *T. longissimum*

No.	Description	Serial flowering (or heading) order	Species												Species mean	
			1	2	3	4	5	6	7	Species mean	8	9	10	11		12
18	Spike length at flowering time	1st	178	60	28	30	55	105	87	78	71	39	14	15	20	32
19		2nd	178	94	11	55	57	60	120	82	33	22	20	32	17	25
20		3rd	178	35	8	31	52	79	66	64	30	43	24	32	30	32
21	Erectness†		32	24	0	42	38	30	33	33	50	30	32	32	33	35
22	Dryness†		49	58	29	91	71	39	48	55	82	44	46	66	76	63
23	Difficulty in spike emergence†		14	3	0	40	32	3	0	13	56	20	52	47	66	48
24	Colour†		22	56	0	102	92	133	4	58	113	93	62	100	83	90
25	Total tiller height at harvesting time	1st	154	236	97	231	148	182	221	181	95	137	62	81	84	92
26		2nd	169	162	87	195	220	276	208	188	91	109	56	93	73	84
27		3rd	112	192	74	298	233	254	228	199	76	108	62	82	65	79
28	Tiller without spike height at harvesting time	1st	100	163	71	137	77	111	128	112	73	86	43	57	74	67
29		2nd	112	101	57	127	135	194	99	118	60	75	40	60	68	61
30		3rd	82	148	57	210	144	153	109	129	52	76	47	59	60	59
31	No. of spikelets	1st	5	4	2	6	5	8	7	5	12	3	4	3	7	6
32		2nd	6	6	2	6	4	10	10	6	10	2	2	2	5	4
33		3rd	4	4	2	5	8	6	11	6	7	4	3	3	4	4
34	Spike's dry weight	1st	254	470	86	555	382	582	537	409	190	246	211	168	101	183
35		2nd	302	482	75	421	410	486	663	406	220	178	172	209	66	169
36		3rd	240	331	71	410	375	540	618	368	166	222	161	117	94	152

* Population 3 was not measured for flowering time.
† The variances are multiplied by 100.

FIG. 4.—Summary of ranking of population variances for all 36 characters.

(iii) *Within-population variances*

Table 5 summarises the total variance within each of the 12 populations for each of the 36 characters. It can be seen that for most of the characters *T. longissimum* shows more variability except in population 3, which demonstrates the lowest variability in most of the traits. This point is discussed later. Fig. 3 exhibits the five extreme characters in which the populations of *T. longissimum* have the most variability. There seems to be homogeneity of variances between the *T. speltoides* populations but not in *T. longissimum*.

In order to exhibit more clearly the overall picture we have included fig. 4, which indicates the number of characters (on the ordinate) whose variance has the rank specified (on the abscissa) with 1 indicating highest and 12 the lowest ranking. Thus *T. longissimum* is seen to produce the highest ranks for most characters and *T. speltoides* the lower ranks. If there were no differences between the species we would expect to find 21 of the characters of *T. longissimum* at each rank ($36 \times 7/12$) and 15 of *T. speltoides*. The deviations as shown in fig. 4 were highly significant ($\chi^2_{11} = 32$, $P < 0.001$). The reversal at ranks 11 and 12 is due to the anomolous behaviour of population 3. This is discussed later.

(iv) *Within-family variances*

The results of the within-family variances are summarised in table 6. Six characters with the most extreme results are exhibited in fig. 5. From these results we can conclude:

TABLE 6
Within-family variances in the populations of T. longissimum and T. speltoides and the mean variances in each of the two species

Characters			Populations of <i>T. longissimum</i>										Populations of <i>T. speltoides</i>					
No.	Description	Serial flowering (or heading) order	1	2	3	4	5	6	7	Species mean	8	9	10	11	12	Species mean		
1	Heading time	1st	33	31	18	43	73	46	45	41	77	41	36	32	42	46		
2		2nd	37	35	15	69	69	65	119	58	54	42	37	35	32	40		
3		3rd	36	43	18	88	66	66	196	73	44	43	33	37	31	38		
4	Range between 1st and 3rd heading time		9.2	8.8	6.7	22.2	17.1	14.2	154.7	33.2	12.0	7.2	6.2	13.5	6.3	9.0		
5	Flowering time	1st	8.0	13.3	*	21.5	61.6	18.3	76.5	33.2	32.5	15.5	22.3	22.0	14.6	21.4		
6		2nd	13.5	14.1	*	20.7	31.3	32.0	136.9	41.4	36.6	15.4	19.0	24.8	12.9	21.7		
7		3rd	22.6	20.8	*	32.4	30.6	29.7	217.1	58.9	36.6	16.0	19.3	22.9	11.7	21.3		
8	Range between 1st and 3rd flowering time		12.8	16.2	*	18.4	35.3	20.4	266.4	61.5	8.3	8.6	3.7	5.7	3.8	6.0		
9	Range between heading and flowering time	1st	11.1	27.9	*	14.5	27.4	9.4	120.1	35.1	27.2	24.4	14.1	29.4	26.4	24.3		
10		2nd	10.9	19.0	*	20.2	19.2	33.1	93.4	32.6	15.0	27.4	11.5	34.0	15.7	18.0		
11		3rd	13.0	18.7	*	17.5	14.5	22.6	109.2	32.5	11.6	21.8	16.2	26.8	15.2	18.3		
12	Total tiller height at flowering time	1st	280	921	107	366	178	360	167	340	148	116	105	155	160	137		
13		2nd	218	289	67	510	187	398	293	280	83	88	83	117	75	89		
14		3rd	227	475	74	565	227	496	279	335	86	157	111	167	76	119		
15	Tiller without spike height at flowering time	1st	138	117	65	138	77	98	104	105	115	97	82	129	120	109		
16		2nd	140	152	39	116	93	202	122	123	77	57	67	49	70	64		
17		3rd	190	228	49	189	141	184	125	158	76	105	82	89	61	83		

TABLE 6—(continued)

Characters		Populations of <i>T. longissimum</i>										Populations of <i>T. spelioides</i>						
		Serial flowering (or heading) order										Species						
No.	Description	1st	2nd	3rd	1	2	3	4	5	6	7	8	9	10	11	12	mean	
18	Spike length at flowering time	1st	2nd	3rd	58	15	12	21	20	27	37	31	15	7	8	10	14	
19					57	25	7	35	35	28	84	13	8	10	20	7	12	
20					62	10	6	19	27	37	38	13	23	14	9	11	14	
21	Erectness†				27	22	54	88	32	32	231	57	32	29	24	22	33	
22	Dryness†				56	58	29	104	78	39	57	60	48	45	60	83	64	
23	Difficulty in spike emergence†				11	3	0	39	31	3	12	14	23	54	43	66	47	
24	Colour†				24	60	0	109	95	149	4	63	120	79	59	69	77	
25	Total tiller height at harvesting time	1st			147	263	96	236	154	176	240	109	103	57	80	97	89	
26			2nd		167	169	88	213	234	274	257	111	85	61	84	82	85	
27			3rd		93	187	67	336	250	257	267	86	93	60	74	66	76	
28	Tiller without spike height at harvesting time	1st			86	177	69	138	82	104	137	76	71	42	53	86	66	
29			2nd		111	115	61	138	140	178	125	73	65	46	47	78	62	
30			3rd		68	161	52	251	161	142	124	57	73	50	49	54	57	
31	No. of spikelets	1st			6.5	4.6	2.5	6.7	5.2	6.2	9.0	8.5	3.2	3.8	2.7	8.3	5.3	
32			2nd		7.0	6.6	2.3	5.4	2.6	8.4	11.4	7.0	1.3	1.9	2.3	5.3	3.6	
33			3rd		4.2	4.8	1.8	4.8	7.1	5.9	13.9	6.0	3.0	2.4	3.2	4.0	3.7	
34	Spike's dry weight	1st			301	529	91	635	344	633	491	173	205	220	161	110	174	
35			2nd		361	514	70	485	467	409	643	184	143	202	218	72	164	
36			3rd		188	352	55	479	388	577	615	164	207	164	122	99	151	

* Population 3 was not measured for flowering time.

† The variances are multiplied by 100.

FIG. 5.—Within-family variances in individual nomenclatures: six selected characters—see text for discussion

(a) In most of the characters the mean variances within families are higher in *T. longissimum* populations than in those of *T. speltoides*. As in the previous paragraph, the deviation from expectation is highly significant ($\chi^2 = 41.38$, $P < 0.001$). Fig. 6, for ranking of the within-family variances, is analogous to fig. 4 for the total variances.

FIG. 6.—Summary of ranking of within-family variances for all 36 characters.

(b) Population 3 has the lowest values for the variances in most of the characters.

(c) Population 7 has exceptionally high values for the variances of flowering time (characters 5-11 in table 6 and character 8 in fig. 5).

(d) The only character exhibiting clearly more variance in *T. speltoides* than in *T. longissimum* is difficulty of emergence (character 23 in table 6 and fig. 5). It should be noted that those spikes having most difficulty in emergence are nearly always devoid of viable seeds.

(v) Correlations

In table 7, two sets of correlations are presented. The first is correlation between population means and within family variances; these are seen in most cases to be insignificant. The second set of correlations is between population means of plants from the S_0 and the S_1 generations. These are seen to be extremely high, especially in *T. longissimum*.

TABLE 7
Correlations: Set 1. Between S_0 means and within-family variance
Set 2. Between S_0 means and S_1 means

Character No.	Set 1		Set 2	
	<i>T. longissimum</i>	<i>T. speltoides</i>	<i>T. longissimum</i>	<i>T. speltoides</i>
1	n.s.	n.s.	***	**
2	n.s.	n.s.	***	**
3	n.s.	n.s.	***	**
4	***	n.s.	**	n.s.
5	—	n.s.	—	*
6	—	n.s.	—	**
7	—	n.s.	—	*
8	—	*	—	n.s.
9	—	n.s.	—	*
10	—	n.s.	—	*
11	—	n.s.	—	**
12	n.s.	n.s.	***	*
13	n.s.	n.s.	***	*
14	n.s.	*	***	*
15	n.s.	n.s.	***	*
16	n.s.	n.s.	***	n.s.
17	**	n.s.	***	n.s.
18	n.s.	n.s.	**	n.s.
19	n.s.	n.s.	**	n.s.
20	n.s.	n.s.	*	n.s.
21	n.s.	n.s.	*	n.s.
22	n.s.	n.s.	***	*
23	**	*	n.s.	n.s.
24	**	*	**	**
25	n.s.	n.s.	***	*
26	n.s.	n.s.	***	n.s.
27	n.s.	n.s.	***	*
28	n.s.	n.s.	***	*
29	*	n.s.	***	n.s.
30	n.s.	n.s.	n.s.	*
31	n.s.	n.s.	***	**
32	n.s.	n.s.	***	n.s.
33	n.s.	n.s.	**	n.s.
34	*	*	***	**
35	n.s.	n.s.	***	**
36	*	n.s.	***	*

n.s. = Non-significant correlation.

* = Correlation significant $0.01 < P \leq 0.05$.

** = Correlation significant $0.001 < P \leq 0.01$.

*** = Correlation significant $P < 0.001$.

Population 3 of *T. longissimum* was not measured for flowering time; therefore the correlation coefficient for characters 5-11 are not presented here.

4. THEORETICAL CONSIDERATIONS

(i) *Population variances*

In the experiments described above, the total variance within the populations may be partitioned into between- and within-family variances. The total variance calculated from the experiment represents an estimate of the total variance of the population in the wild one generation following the original sampling. Assuming the wild population to be in equilibrium we can therefore use the total variance in the experiment for inference on the

variance of the original wild population. The experimental variance between families corresponds, in the wild population, to that part of the total variance produced by differences between the groups of descendants from different mother plants. In the wild population, corresponding to the within family, experimental variance would be that part of the total variance arising from the mean differences between individuals coming from the same mother plant.

Thus in a situation of 100 per cent. selfing it would be correct to extrapolate from high experimental variances between families to a considerable genetic diversity among mother plants in the wild. But in a mixed mating system, which is probably the most common situation, there is no control over the genotype of the pollen donor, and the inferences to the genetic diversity in the wild become more complex.

It is possible to derive a one-locus theory for hypothetical circumstances under which we might expect greater *total variance* from a selfing population than in an outcrossing population. The difficulties involved in extending this type of analysis to multi-locus quantitative characters are well known and discussed, for example, by Mather and Jinks (1971). Consider a character for which the genotypes *AA*, *Aa* and *aa* contribute *d*, *h* and $-d$ respectively ($d > 0$). Hillel, Simchen and Jinks (1972) have shown that if *u* is the frequency of *A*, $v = 1 - u$ that of *a* and *f* the inbreeding coefficient, the total variance is

$$2uv(1+f)d^2 + 2uv(1-f)[1-2uv(1-f)]h^2 - 4uv(1-f)(u-v)dh. \quad (1)$$

We can therefore compare the total variances in two populations with inbreeding coefficients f_1 and f_2 respectively. The difference between the two will be

$$(f_1 - f_2)2uvd^2 \left\{ 1 - \frac{h^2}{d^2} - \frac{2h}{d} + u \left[\frac{4h}{d} + \frac{2h^2}{d^2} (2 - f_1 - f_2) \right] - 2u^2 \frac{h^2}{d^2} (2 - f_1 - f_2) \right\}. \quad (2)$$

The situation of most interest to us is one in which f_1 is quite close to one and f_2 in the region of 0.15–0.25 so that $f_1 - f_2 > 0$. The population with higher inbreeding will therefore have greater total variance provided

$$1 - \frac{h^2}{d^2} - \frac{2h}{d} + u \left[\frac{4h}{d} + \frac{2h^2}{d^2} (2 - f_1 - f_2) \right] - 2u^2 \frac{h^2}{d^2} (2 - f_1 - f_2) > 0. \quad (3)$$

In analysing this quadratic equation for *u*, we note first that (3) is always true if $0 < \frac{h}{d} < \sqrt{2} - 1 \approx 0.414$, so that in these cases, for all gene frequencies *u*, the inbreeder will have greater total variance.

As *h/d* increase, (3) indicates for which gene frequencies the inbreeder will have greater total variance. Thus if $h/d = 1$, (3) is true for $u > 0.38$; while if $h/d = 2$, the requirement is $u > 0.65$. As *h/d* increases, *u* must also increase to validate (3). The situation is represented graphically in fig. 7. Note that when f_1 is close to one (as we suspect is the case in *T. longissimum*) and f_2 is relatively small (probably near 0.2 in *T. speltoides*) the situation is almost the same as that when $f_1 = 1$ and $f_2 = 0$, except for the factor

FIG. 7.—The expected total population variance for a given d as a function of dominant gene frequency for the absolute selfing situation ($f=1$) and for complete random mating ($f=0$). The function is described in the figure for three dominance ratio values: (A) $\frac{h}{d} = 0$, no dominance; (B) $\frac{h}{d} = 1$, complete dominance; (C) $\frac{h}{d} = \sqrt{2}$, over dominance.

$(f_1 - f_2)$. As f_1 and f_2 approach one another the difference between the systems vanishes.

If $h < 0$, then instead of analysing (3) as a function of u , we treat it as a function of v and, using $|h|$ instead of h , the above analysis gets a comparable form, with v the frequency of the dominant allele.

Qualitatively then, when the dominant allele is in high enough frequency (how high will be determined by how dominant it is), the inbreeding population will have a greater total variance than the outcrosser. Alternatively, if the total variance in the selfer is higher than in the outcrosser, the dominant allele is probably the more frequent.

(ii) *Within-family variances*

The theoretical treatment of the within-family variance is more difficult than the treatment given above for the total variance. For most calculations we use the theory derived by Hillel *et al.* (1972), without repeating the detailed derivations presented there. The basic problem we are confronted with is whether it is correct to infer from high within family variances a high heterozygote frequency.

First, consider the within-family variance for a single-locus situation as in the previous section, but with outcrossing only, so that $f = 0$. In this case the within family variance can be shown (using the same notation as above) to be

$$V = \beta\{3/4(d^2 + h^2) - h[\beta h/2 + 3(u-v)d/2]\} \quad (4)$$

where $\beta = 2uv$ is the heterozygote frequency. Obviously, if $h = 0$, V is proportional to β . However, when $h \neq 0$ the dependence of the variance on the heterozygote frequency is confounded by the $(u-v)$ term in (4). The dependence of the variance on β is shown in fig. 8. It is seen that relatively high variance can occur either for low or high heterozygote frequencies. For example, when $h/d = 1$, with $d^2 = 100$, the same value $V = 60$ is obtained at $\beta = 0.25$ and $\beta = 0.5$. One cannot, therefore, equate high heterozygosity with high variance.

The above remarks indicate that it is unwise to extrapolate from within-family variances to heterozygote frequencies. However, we may ask directly whether simple models can predict cases in which the within-family variance in a predominantly selfing species can be greater than in an outcrosser. Obviously, with pure selfing (at equilibrium) there is no within family variance. We chose inbreeding coefficients of $f = 0.9$ for the selfer and $f = 0.1$ for the outcrosser and substitute these into the formula of equation 2, table 4 of Hillel *et al.* (1972) to obtain variances V_1 and V_2 , respectively. Following the arithmetic manipulations the difference between the two variances is

$$\begin{aligned} V_1 - V_2 = uv\{-1.238d^2 - 1.142h^2 + 1.484dh\} \\ + u^2v^2[1.214h^2 - 2.428dh] \\ + 0.067uv(u-v)dh \end{aligned} \quad (5)$$

which can never be positive. It appears, therefore, that for the values of f we believe to be relevant to our cases, the selfer cannot have a higher within-family variance than the outcrosser, when selection is assumed to be absent

Can heterozygote advantage alter the conclusion from (5) and produce more variance in the selfer than in the outcrosser? First, without considering variances, let us compare two populations, one a pure selfer, in which the genotypes AA , Aa , aa have fitnesses $x : 1 : x$, respectively, and the other a pure outcrosser in which the fitnesses are $y : 1 : y$. Obviously, $x < 1/2$ is a prerequisite for polymorphism in the selfer (Allard *et al.*, 1967; Karlin, 1968).

FIG. 8.—Within-family variance v , as a function of heterozygote frequency. u = gene frequency of A . AA , Aa and aa contribute d , h , $-d$, respectively. (A) $h = 0$, (B) $h = d$, (C) $h = -d$.

If $x < 1/3$ and $y > x/(1-2x)$ there are more heterozygotes at equilibrium in the selfer than in the outcrosser. For example, if $x = 0.3$ then y must be greater than 0.75, while if $x = 0.2$, y must be greater than 0.33. Under these stringent selection conditions, therefore, more heterozygotes can occur in the selfer.

We now ask if, under the same selection conditions as in the previous paragraph but with $x < 1/2$ so that the selfer is in polymorphic equilibrium, the within-family variance for a character whose values are d , h and $-d$ as

before, can be greater in the selfer. It is not difficult to show that under these conditions the mean within-family variance for the selfer is

$$V_1 = \frac{x(1-2x)d^2}{(1+x)(1-x)} + \frac{x(1-2x)h^2}{(1+x)^2(1-x)} \quad (6)$$

and for the outcrosser

$$V_2 = \frac{y(1+2y)}{(1+y)^3} d^2 + \frac{y}{(1+y)^2} h^2. \quad (7)$$

Hence $V_1 - V_2 > 0$ when

$$\frac{h^2}{d^2} \left[\frac{x(1-2x)}{(1+x)^2(1-x)} - \frac{y}{(1+y)^2} \right] + \left[\frac{x(1-2x)}{(1+x)(1-x)} - \frac{y(1+2y)}{(1+y)^3} \right] > 0. \quad (8)$$

Numerical examination of (8) suffices to show that the inequality is true for moderate (h/d) values only when x and y are small, with y smaller than x . When $h = 0$ and $x = y$ in the range 0.15 through 0.35, (8) holds. The general conclusion is that selection in favour of heterozygotes is required to be extremely strong and in most cases it must be even stronger in the outcrosser than the selfer.

5. DISCUSSION

For the 36 quantitative characters investigated here it has been demonstrated that a great amount of variability exists in the selfing populations. In fact, there are higher total variances, higher variances between populations, and higher within-family variances in the selfer *T. longissimum* than in the outcrosser *T. speltooides*.

With reference to the statistical analysis made, we can discount that the F values are artifacts of scaling since most correlations between means and within-family variances were found to be insignificant (table 7). It cannot be argued that the variances we observe are due to environmental factors characteristic to the populations of the two species, because all the plants were grown in the same experimental field. The high correlations between the means of the S_0 and S_1 generations (table 7) further support a genetic interpretation of the results. Of course, this is not to say that genotype-environment interactions do not exist.

Population 3 of *T. longissimum* is a notable exception to the general trend of the results. This population is located (see table 1, fig. 1) on the edge of a desert area. The climate is harsh but very consistent. The population size is estimated to be no larger than 500 plants, the smallest of all of our populations. The plants were less vigorous than those from other sites. It is possible that the consistency of the environment has determined the short-term strategy of high homozygosity with long-term variability being provided by the infrequent outcrossing events. Population 7 comes from the area with the next lowest rainfall to population 3 (see table 1), yet has a high within-family variability, particularly for flowering time. In our experience of the past few years the climate in this area has been very variable. If this is a genuine characteristic of the environment it may have mediated the production and maintenance of this variability.

There is no difficulty in explaining the greater differences between populations of *T. longissimum* than between populations of *T. speltooides*.

Presumably, it is due to the low probability of a successful gene flow in *T. longissimum*, with each isolated population adapted to the specific conditions in its locality. Table 1 details the wide range of environments in which the populations of *T. longissimum* are found. The environments of the populations of *T. speltoides*, on the other hand, do not differ greatly from one another.

The theoretical arguments for a character controlled by a single locus (Section 4) produced the conclusion that when the dominant allele is in a sufficiently high frequency, the inbreeder will have a greater total variance, the cut-off point depending on the degree of dominance. Our attempts to develop a corresponding theory to explain the finding that the within-family variances are higher in the selfer than in the outbreeder, can be regarded as unsuccessful unless one accepts the possibility of extremely high heterozygote advantage in both *T. longissimum* and *T. speltoides*. Had there existed such strong selection, substantial differences would have been expected between the means of the S_0 and S_1 generations. These were not observed, so the theory does not appear to cope adequately with the existence of high within-family variances. Further experimental and theoretical studies are planned in the hope of elucidating what lies behind this surprising result.

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