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NOTES AND COMMENTS

MATING SYSTEMS AND POPULATION STRUCTURE IN TWO CLOSELY RELATED SPECIES OF THE WHEAT GROUP II. ENVIRONMENTAL FACTORS AND POPULATION STRUCTURE*

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SUMMARY

Correlations between environmental factors and means and variances of 36 quantitative characters were calculated for seven populations of a selfing species, *Triticum longissimum*, and five populations of the closely related outcrossing species *T. speltoides*. In *T. longissimum* more characters were correlated with environmental factors than in *T. speltoides*. This was attributed to the high interpopulation differences in the means and environmental conditions among *T. longissimum* populations, presumably mediated by effective isolation between these selfing populations. Between the *T. speltoides* populations there are small differences in the population structure or local environmental conditions. This could be due to gene flow between populations. In *T. longissimum*, correlations between growth characteristics and environmental conditions suggest that selection for more economical growth and for smaller units has been mediated by harsher conditions. In those *T. longissimum* populations where the annual fluctuations are smaller the variances within families are also smaller. On theoretical grounds this would be associated with decreased heterozygosity.

1. INTRODUCTION

Triticum speltoides (= *Aegilops speltoides*) and *T. longissimum* (= *Ae. longissima*) are closely related diploid species of the wheat group native to the Near East. The former is primarily an outcrosser while the latter is predominantly a selfer. Hillel, Feldman and Simchen (1973*a*) have recently analysed the relevance of this difference between the mating systems to differences in population structure, by comparing seven wild populations of *T. longissimum* with five wild populations of *T. speltoides*. The comparison was made with respect to 36 quantitative characters in terms of the between population variances, within population variances and within family variances.

In attempting to establish possible agents contributing to natural selection in these populations, we were looking for phenomena which can be regarded as long- and/or short-term adaptations to the prevailing environments. The present paper is concerned with the population structure of the two species mentioned above as reflections of certain ecological characteristics of the populations. The analysis will be made in terms of correlations between statistics measured from a common experimental field

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and some of the environmental factors prevailing at the original sites where the seeds were collected. In particular, for the characters analysed by Hillel *et al.* (1973*a*), we examine how population means and variances are correlated with three environmental factors; namely, distance from the Mediterranean coast, elevation and annual rainfall. From these we shall try to understand the relationship between the mating system and the environmental factors, and their joint contribution to the structure of the populations and to the species' diversity.

2. Materials and methods

Seven populations of *T. longissimum* and five of *T. speltoides* were sampled from various sites in Israel. The approximate sites and prevailing environmental conditions for the 12 populations were presented in table 1 and fig. 1 of Hillel *et al.* (1973*a*).

In the summer of 1968 seeds were taken from 40 to 50 plants from each of the wild populations. Each of these wild plants was used to establish a family consisting of three plants which were grown in experimental plots at the Hebrew University during the winter and spring of 1969. From these, in the summer of 1969, 10 families (30 plants total) were randomly selected and bagged for selfing. From each of these 30 plants four progeny plants were randomly selected. Two plants were randomly allocated to each of the two blocks and these were grown in the winter and spring of 1970. This generation we call S_1. In addition, 10 families were randomly selected from each wild population in the summer of 1969. Four progeny plants were taken from each family and were randomly allocated, two to each of the two experimental blocks. This generation was denoted S_0. The S_0 and S_1 plants were completely randomised in each of the two blocks.

Thirty-six measurements were made on each plant during the experiment. A detailed description of the characters on which the measurements were made is presented in Hillel *et al.* (1972*a*). The characters are listed in tables 1 and 2.

3. Results

The three components of the environment of the wild populations we consider are presented in table 1 of Hillel *et al.* (1973*a*). Clearly there exist correlations between these as, for example, average winter rainfall decreases as distance from the coast increases. It can be seen from that table that the differences between the climatic conditions experienced by the populations of *T. speltoides* are much narrower than between the populations of *T. longissimum.*

Correlation coefficients between environmental factors and population means in generations S_0 and S_1 were calculated separately for each of the two species and tested for significant deviations from zero. Their significance is summarised in table 1. The general picture is that for most characters the population means of *T. longissimum* in generations S_0 and S_1 under the experimental conditions are highly correlated with the environment (especially average annual rainfall) of the original sites from which the populations were sampled (see also fig. 1). For the *T. speltoides* populations, on the other hand, the number of characters that are correlated with the

TABLE 1

Significance of correlations between environmental factors and population means in generations S_0 and S_1

Characters			*T. longissimum*						*T. speltoides*					
			S_0			S_1			S_0			S_1		
No.	Description	Serial flowering (or heading) order	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3
1		1st	—	—	*	—	—	**	—	—	—	—	—	—
2	Heading time	2nd	—	—	**	—	—	**	—	—	—	—	—	—
3		3rd	—	—	**	—	—	**	—	—	—	—	—	—
4	Range between 1st and 3rd heading time		—	—	—	—	—	—	—	—	—	—	—	—
5		1st	N	N	N	N	N	N	—	—	—	—	—	—
6	Flowering time	2nd	N	N	N	N	N	N	—	—	—	—	—	—
7		3rd	N	N	N	N	N	N	—	—	—	—	—	—
8	Range between 1st and 3rd flowering time		N	N	N	N	N	N	—	—	—	*	—	—
9		1st	N	N	N	N	N	N	—	—	—	*	—	—
10	Range between heading and flowering time	2nd	N	N	N	N	N	N	—	—	—	*	—	—
11		3rd	N	N	N	N	N	N	—	—	—	*	—	—
12		1st	$\overline{**}$	$\overline{*}$	***	$\overline{**}$	$\overline{*}$	***	—	—	—	—	—	—
13	Total tiller height at flowering time	2nd	$\overline{**}$	$\overline{*}$	***	$\overline{**}$	$\overline{*}$	***	—	$\overline{*}$	—	—	—	—
14		3rd	$\overline{**}$	$\overline{*}$	***	$\overline{***}$	$\overline{*}$	***	—	—	—	—	—	—
15		1st	$\overline{**}$	$\overline{*}$	***	$\overline{**}$	—	**	—	—	—	—	—	—
16	Tiller height (without spike) at flowering time	2nd	$\overline{**}$	—	***	$\overline{**}$	—	**	—	—	—	—	—	—
17		3rd	$\overline{**}$	—	***	$\overline{**}$	—	**	—	—	—	—	—	—

TABLE —*continue*

Characters			*T. longissimum*						*T. speltoides*					
			S_0			S_1			S_0			S_1		
No.	Description	Serial flowering (or heading) order	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3
18		1st	—	—	—	—	$\bar{*}$	—	—	—	—	—	—	—
19	Spike length at flowering time	2nd	—	—	—	—	—	—	—	—	—	—	—	—
20		3rd	$\bar{*}$	$\bar{*}$	—	—	$\bar{*}$	—	—	—	—	—	—	—
21	Erectness		—	—	—	—	—	—	—	—	—	—	—	—
22	Dryness		**	—	$\bar{***}$	$\bar{**}$	—	$\bar{***}$	—	—	—	—	—	—
23	Difficulty in spike emergence		—	—	—	—	—	*	—	—	$\bar{*}$	—	—	$\bar{**}$
24	Colour		—	—	—	$\bar{*}$	—	*	—	—	—	—	—	—
25		1st	—	—	*	$\bar{*}$	$\bar{*}$	*	—	$\bar{*}$	—	—	—	—
26	Total tiller height at harvesting time	2nd	$\bar{*}$	$\bar{*}$	*	$\bar{*}$	$\bar{*}$	*	—	$\bar{*}$	—	—	—	—
27		3rd	$\bar{*}$	$\bar{*}$	*	—	—	*	—	$\bar{*}$	—	—	—	—
28		1st	$\bar{*}$	—	**	$\bar{*}$	$\bar{*}$	**	—	$\bar{**}$	—	—	—	—
29	Tiller height (without spike) at harvesting time	2nd	$\bar{*}$	$\bar{*}$	**	$\bar{*}$	$\bar{*}$	**	—	$\bar{*}$	—	—	—	—
30		3rd	—	—	—	$\bar{*}$	—	**	—	$\bar{*}$	—	—	—	—
31		1st	$\bar{*}$	$\bar{*}$	$\bar{*}$	—	$\bar{*}$	—	—	$\bar{**}$	—	—	$\bar{*}$	—
32	No. of spikelets	2nd	—	—	—	—	—	—	—	$\bar{*}$	—	—	$\bar{**}$	—
33		3rd	—	—	—	—	—	—	—	—	—	—	$\bar{**}$	—
34		1st	—	—	—	—	$\bar{*}$	—	—	—	—	—	—	—
35	Spike's dry weight	2nd	—	$\bar{*}$	—	—	$\bar{*}$	—	—	—	—	—	—	—
36		3rd	—	—	—	—	$\bar{*}$	—	—	—	—	—	—	—

N Population 3 of *T. longissimum* was not measured for flowering time.
* Positive significant correlation $0{\cdot}01 < P \leqslant 0{\cdot}05$.
$\bar{*}$ Negative significant correlation $0{\cdot}01 < P \leqslant 0{\cdot}05$.
** Positive significant correlation $0{\cdot}001 < P \leqslant 0{\cdot}01$.
*** Positive significant correlation $P \leqslant 0{\cdot}001$.
E_1 Distance from the coast.
E_2 Elevation.
E_3 Annual rainfall.

TABLE 2

Significance of correlations between environmental factors and variances

Characters			*T. longissimum*									*T. speltoides*								
			Total variance (S_0)			Within family variance (S_0)			Within family variance (S_1)			Total variance (S_0)			Within family variance (S_0)			Within family variance (S_1)		
No.	Description	Serial flowering (or heading) order	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3
1		1st	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	$\bar{*}$
2	Heading time	2nd	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	$\bar{*}$
3		3rd	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*	—	—	$\bar{*}$
4	Range between 1st and 3rd heading time		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5		1st	N	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—
6	Flowering time	2nd	N	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—		—
7		3rd	N	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—
8	Range between 1st and 3rd flowering time		N	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—
9		1st	N	N	N	N	N	N	N	N	N	—	$\bar{*}$	—	—	—	—	—	—	—
10	Range between heading and flowering time	2nd	N	N	N	N	N	N	N	N	N	—	—	—	*	—	—	—	—	$\bar{*}$
11		3rd	N	N	N	N	N	N	N	N	N	—	—	—	*	—	—	—	—	$\bar{**}$
12		1st	—	—	—	—	—	—	—	$\bar{*}$	—	—	—	—	—	—	—	—	—	—
13	Total tiller height at flowering time	2nd	—	—	—	—	—	—	$\bar{*}$	—	—	—	—	—	*	—	—	—	—	—
14		3rd	—	—	—	—	—	—	$\bar{*}$	$\bar{*}$	—	—	—	—	—	—	—	—	—	—

TABLE 2—*continued*

Characters			*T. longissimum*									*T. speltoides*								
			Total variance (S_0)			Within family variance (S_1)			Within family variance (S_1)			Total variance (S_0)			Within family variance (S_0)			Within family variance (S_1)		
No.	Description	Serial flowering (or heading) order	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3
15	Tiller height (without spike) at flowering time	1st	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16		2nd	—	$\bar{*}$	—	—	—	—	$\bar{*}$	—	—	—	—	—	*	—	—	—	—	—
17		3rd	—	—	—	$\bar{*}$	$\bar{*}$	*	—	—	—	$\bar{*}$	—	—	—	—	*	—	—	—
18	Spike length at flowering time	1st	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19		2nd	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20		3rd	—	—	—	—	—	—	—	—	—	—	$\bar{*}$	—	—	—	—	—	—	—
21	Erectness		$\bar{*}$	$\bar{**}$	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
22	Dryness		—	—	—	—	—	—	$\bar{*}$	$\bar{*}$	**	—	—	—	—	—	—	—	—	—	—
23	Difficulty in spike emergence		—	—	—	—	—	—	—	—	*	—	—	$\bar{*}$	—	—	$\bar{**}$	—	—	$\bar{**}$
24	Colour		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
25	Total tiller height at harvesting time	1st	—	—	—	—	—	—	$\bar{*}$	—	—	—	*	—	—	—	—	—	—	—
26		2nd	—	$\bar{*}$	—	—	$\bar{*}$	—	$\bar{*}$	—	*	—	—	—	—	—	—	—	—	—
27		3rd	—	—	—	—	—	—	$\bar{*}$	—	**	—	*	—	—	—	—	—	—	—
28	Tiller height (without spike) at harvesting time	1st	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
29		2nd	—	—	—	—	$\bar{*}$	—	—	—	—	—	—	—	—	—	—	—	—	—
30		3rd	—	—	—	—	—	—	$\bar{**}$	$\bar{*}$	**	—	**	—	*	—	—	—	—	—

TABLE 2—*continued*

Characters			*T. longissimum*									*T. speltoides*								
			Total variance (S_0)			Within family variance (S_0)			Within family variance (S_1)			Total variance (S_0)			Within family variance (S_0)			Within family variance (S_1)		
No.	Description	Serial flowering (or heading) order	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3
31		1st	—	—	—	—	—	—	—	$\bar{*}$	—	—	—	—	—	—	—	—	—	—
32	No. of spikelets	2nd	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
33		3rd	—	—	—	—	—	—	$*$	$\bar{*}\bar{*}$	—	—	—	—	—	—	—	—	—	—
34		1st	—	—	—	—	—	—	$**$	$\bar{*}\bar{*}\bar{*}$	—	—	—	$**$	—	—	—	—	—	—
35	Spike's dry weight	2nd	—	$\bar{*}$	—	—	$\bar{*}$	—	—	$\bar{*}$	—	—	—	—	—	—	—	—	—	—
36		3rd	—	—	—	—	—	—	$\bar{*}$	$\bar{*}\bar{*}\bar{*}$	—	—	—	$*$	—	—	$*$	—	$\bar{*}$	—

N Population 3 of *T. longissimum* was not measured for flowering time.
* Positive significant correlation $0{\cdot}01 < P \leqslant 0{\cdot}05$.
$\bar{*}$ Negative significant correlation $0{\cdot}01 < P \leqslant 0{\cdot}05$.
** Positive significant correlation $0{\cdot}001 < P \leqslant 0{\cdot}01$.
*** Positive significant correlation $P \leqslant 0{\cdot}001$.
E_1 Distance from the coast.
E_2 Elevation.
E_3 Annual rainfall.

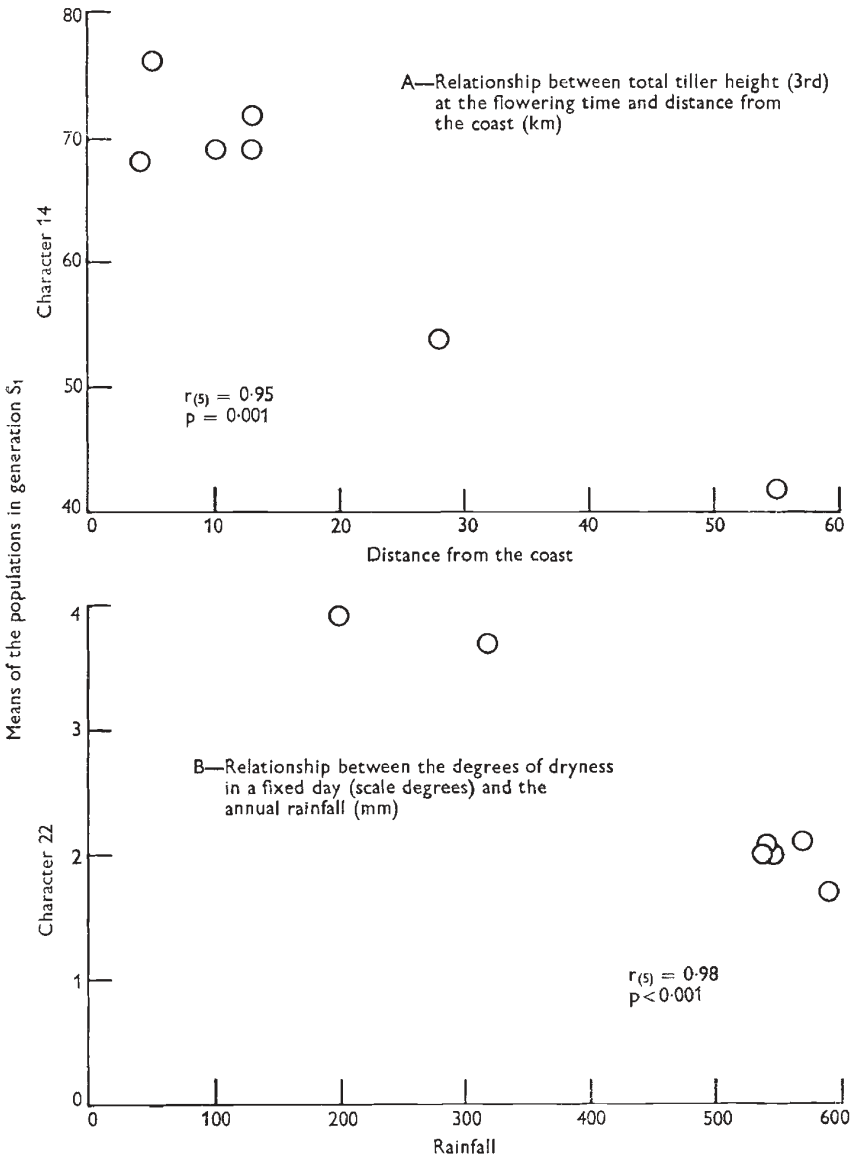

FIG. 1.—Relationship between population means of *T. longissimum* in generation S_1 and environmental variables.

environmental factors is smaller and the degree of significance is lower. Thus in *T. longissimum*, 18 out of 29 characters which were measured in generation S_0 are highly correlated with the average annual rainfall while in *T. speltoides* only one character out of 36 showed such a correlation. Moreover, where the correlated characters in *T. longissimum* appear to be the same in generations S_0 and S_1 this accord is not evident in the *T. speltoides* populations.

Correlation coefficients were computed between each of the three

environmental factors and the variances characterising the populations, namely the total population variances, the mean variances within S_0 families in generation S_0 and the mean variances within S_1 families in generation S_1 (see also Hillel, Feldman and Simchen, 1973*a*, *b*). The levels of significance of these correlations are shown in table 2. Three of the most extreme cases are demonstrated in fig. 2.

From tables 5 and 6 of Hillel *et al.* (1973*a*) and table 2 and fig. 2 of the present paper, all of which are concerned with variances and their correlations with environmental variables, the following principal conclusions may be drawn. Only for a few characters are the variances in *T. speltoides* correlated with the environmental variables. Most correlations between the environmental variables and either the total population variance or the mean variances within S_0 families in S_0 generation are insignificant. For *T. longissimum*, 11 out of 29 characters show significant correlations between the mean variances with S_1 families and the distance of the population from the coast. For elevation and annual rainfall the corresponding number of characters were ten and five, respectively.

4. Discussion

In this paper we deal with correlations between environmental variables that prevail in the original sites of our populations and genetic characteristics of samples from these populations that were revealed in a controlled experiment, removed from the original sites. The values of the correlation coefficients are expected to be zero if there are no differences between either the genetic means or the environmental characteristics of the populations. Thus, provided there are non genotype-environment interactions, we are justified in concluding that a non-zero correlation is truly due to the relationship between the genotypic means of the populations and the wild environments. The same will hold for correlations between genetic variances and environmental variables of the original sites.

It is apparent from the data that the relatively small differences between the climatic conditions experienced by the populations of *T. speltoides* has been insufficient to produce differences in the means and variances of these populations. Presumably, *T. speltoides* is subject to some amount of gene flow between populations and this could explain its relative uniformity. Karlin and McGregor (1972) have shown that, theoretically, fairly small amounts of migration are sufficient to maintain effectively mixed populations. Such mixing would preclude the formation of new isolates and colonisation of new habitats. However, when gene flow is extremely low, Karlin and McGregor found that evolutionary processes are more rapid. This could explain the wide range of environments occupied by *T. longissimum* for which effective gene flow is prevented or limited to very low levels.

Since the expected level of gene flow is so small, the theory developed by Karlin and McGregor (1972) could explain the existence of limited genetic variability within populations while allowing for the adaptation of the different populations to their special environments. For example, where conditions are bad, as in the cases of populations 3 and 7, the plants seem to have developed economical growth and economical production of dispersal units such as smaller plant size, shorter life-cycle (*i.e.* early flowering and early maturation) and spikes with fewer and lighter spikelets. For

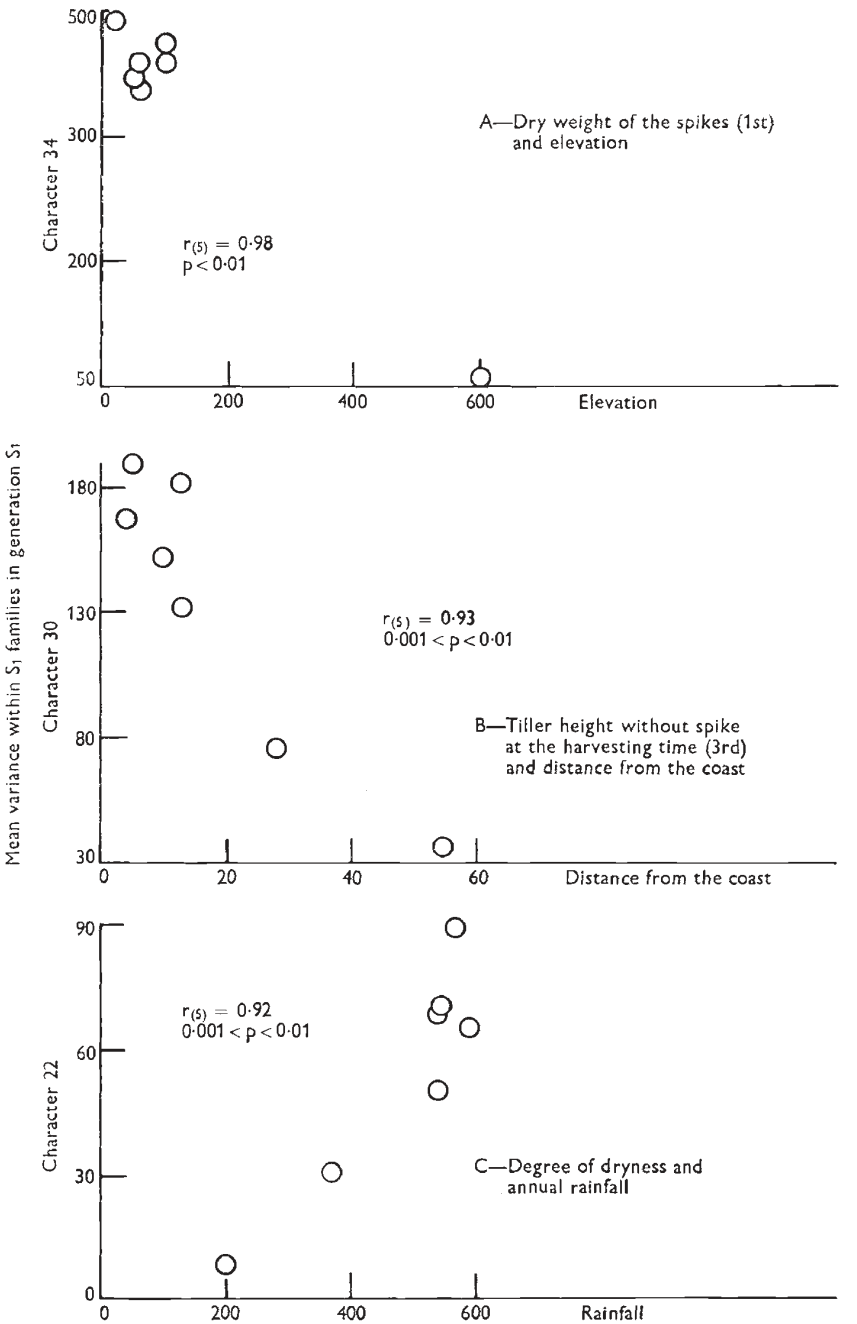

FIG. 2.—Relationship between variances within S_1 families and environmental factors in *T. longissimum* populations.

T. longissimum we therefore expected genetic differences between those populations experiencing small annual environmental fluctuation and those in areas of dramatic change from year to year. Thus, population 3, at the

edge of the desert, experiences relatively minor climatic fluctuations (within the general range of " bad "). It has smaller variances within S_1 families and this is taken to imply that it has less genetic variability. On the other hand, where annual fluctuations are more dramatic, such as in the coastal plain or Northern Negev, one would predict the existence of a reservoir of genetic variability. Population 7 from the Northern Negev which has very high variances within S_1 families (especially for flowering time) could be such a population.

Several examples of closely related species or populations within a species exhibiting adaptation to microhabitat have been documented (see *e.g.* Schoener, 1967; Jain and Marshall, 1967; Wallace and Vetukhiv, 1955). Jain and Marshall (*loc. cit.*) pointed out with reference to *Avena fatua* and *Avena barbata* that adaptations might manifest itself through obvious genetic variability, or through phenotype plasticity with less genetic variability. The theoretical models of Levins (1962) and Levins and MacArthur (1966) would predict greater variability in a more heterogenous environment such as that experienced by population 7. Experimental verification of this theory in terms of genetic variation as measured by electrophoretic mobility has only recently begun to be made.

G. B. Johnson (private communication of unpublished results) has found in comparing three alpine and montane species of the butterfly Colias by electrophoretic variation in enzymes, that populations in areas of greatest environmental fluctuation have the greatest degree of polymorphism. Powell (1971) in a laboratory situation with *Drosophila willistoni* found that those populations maintained in heterogeneous enviroments were characterised by greater average heterozygosity than populations in more constant environments. It is possible, therefore, that electrophoretic analysis of enzymes in samples from our wheat populations will enable us to determine the extent to which the variation we observe is genetic and to describe more exactly the selective effects apparent in our data.

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