THE GENETICS OF FLOWERING TIME IN RAPHANUS SATIVUS L. III. EARLY X LATE CROSSES, F_1 AND F_2 GENERATIONS.

AHSAN A. VAHIDY* AND RICHARD W. HARTMANN

Department of Horticulture, University of Hawaii, Honolulu, Hawaii, U.S.A.

Abstract

Crossing experiments between early flowering and late flowering lines were conducted in the greenhouse. For this purpose, 10 Early and 10 Late plants were divided into two sets (each set consisting of 5 Early and 5 Late plants). The crosses were made between Early and Late plants in all the possible combinations (including reciprocals) within each set. No significant differences between the crosses and their reciprocals were found for the time of flowering. The data of both the F_1 and F_2 plantings were adjusted by comparing with check plants to make the data of these plantings comparable to that of the original parental planting. Frequency distributions of the F_1 and F_2 showed no dominance for the time of flowering and indicated that there probably are many genes controlling this character. The heritability for the time of flowering was 34.90 percent as calculated from the variances of F_1 and F_2 generations.

Introduction

The pertinent literature on the genetics of flowering time in *Raphanus sativus* L. has been reviewed in an earlier paper of this series (Vahidy & Hartmann, 1971). The present study was conducted with certain Early and Late flowering plants of *R. sativus* ev. 'Chinese Daikon' to study the inheritance of flowering time in F_1 and F_2 generations.

Materials and Methods

Crosses between early flowering lines and late flowering lines were made in the greenhouse in the spring of 1968. Twentyfive Early and 25 Late lines were sown in the greenhouse and, of these, 10 Early and 10 Late lines were selected for making crosses. The pedigrees of these lines are given in Table 1. Seeds were sown in jiffy pots, 6 seeds per jiffy pot, and 2 jiffy pots per line. There was a difference of 3 weeks in sowing time of Early and Late lines, so that both may bloom at the same time. Two weeks after sowing the plants were thinned to one plant per jiffy pot and were transferred to two gallon cans. Fertilizer (8: 12: 14) was applied to both Early and Late plants at the rate of two teaspoons per can on 16, 30 and 40 days after sowing. Plants were watered once or twice a day as required.

Five Early and five Late flowering plants that bloomed approximately at the same time constituted Set I. In the same way set II contained 5 different Early

^{*} Present address: Department of Genetics, University of Karachi, Karachi-32, Pakistan. Journal series No. 1591 of the Hawaii Agricultural Experiment Station.

	Table	1.	Pedigrees	of	\mathbf{P}_{1}	and	\mathbf{P}_2	plants.
--	-------	----	-----------	----	------------------	-----	----------------	---------

MINISTER STREET, STREE	ary of the second of the particular contract of the second	
	E-I	U ^a -100-E ^b -5-1-1
	E-II	U-100-E-5-1-2
	E-III	U-100-E-5-3-1
	E-IV	C ^c -25-L ^b -8-E-2-4-1
	E-V	C-26-L-8-2-E-1-2-2
Set I:	L-I	C-31-L-3-3-5-3-1
	L-II	C-26-L-1-6-3-3-1
	L-III	C-30-L-5-3-1-1-1
	L-IV	C-31-L-3-3-4-3-1
	L-V	C-31-L-3-3-5-1-1
	E-VI	U-75-E-5-2-1
	E-VII	U-75-E-5-2·2
	E-VIII	C-25-L-11-E-4-1-1
	E-IX	C-26-L-8-2-E-1-2-1
Set II:	E-X	C-25-L-7-E-2-1-1
	L-VI	C-30-L-5-3-1·3-1
	L-VII	C-26-L-7-1-1-1
	L-VIII	C-30-L-5-3-1-1-2
	L-IX	C-30-L-5-3-5-1-1
	L-X	C-31-L-3-3-5-3-1
MINESTER STATE OF THE STATE OF		

^aNot treated with colchicine.

and 5 different Late flowering plants that bloomed approximately at the same time. Within Set all the possible crosses (including reciprocal crosses and selfs) between Early's and Late's were made.

One day before the crosses were made all the open flowers were discarded. Newly opened buds and large unopened buds were carefully emasculated with forceps. Pollen was applied directly from newly opened flowers to the stigmas of emasculated

^bEarly or late selection in generations following the symbol.

^cColchicine treated.

flowers. Pollinated flowers were covered with small translucent paper bags closed with paper clips. Some emasculated, unpollinated flower buds were also covered similarly to check contamination. Paper bags were removed 4 to 5 days after pollination.

 F_1 seeds were sown in the late summer of 1968. For each individual cross (including reciprocals) two plants were raised. One replication was grown in two gallon cans and the other in gallon cans. The two replications were treated alike otherwise. The plants were transferred outside the greenhouse after 4 weeks. F_1 Plants belonging to different Sets were kept on separate benches. Selfed P and P seeds were also grown at the same time. The P_1 plants were destroyed by a heavey infestation of aphids, but the mean flowering day of the P_2 plants was 3 days less than in the original spring, 1968 planting. On this basis the data of the F_1 plants were transformed by adding 3 days to all the plants.

A number of F plants were destroyed by strong winds and heavy rain before blooming. As a result there were too many missing values to permit analysis described by Comstock & Robinson (1948). The data are therefore, presented as the mean flowering day of F₁ plants that had a common parent in the original crosses (Table 2). An individual plant is used twice in this table, once as a common female parent and a second time as a common male parent.

 F_2 seeds were obtained after open pollination of F_1 plants. F_2 plants were grown in the greenhouse during May to October, 1969. In order to make back crosses, the F_2 seeds were sown in two lots (four replications each), with one week between the two plantings. The late parents were sown about 3 weeks before the F_2 and the Early parents about two weeks after. Twenty Check seeds (no selection) were also sown with each late and early sowing. All the plants were grown in two gallon cans.

On the basis of the performance of the Check plants and the Early and Late parents, the data of the F₂ plants were transformed to make comparable to original parental and F₁ data in the following manner. The first Check planting (sown with Late parents) flowered from June 16 to July 10, with a mean flowering date of 50.55 days. The second Check planting (sown with Early parents) flowered from August 17 to September 18, with a mean of 77.77 days. However, rather than a continuous distribution as in other plantings, there was a gap of 12 days after the 72nd day, during which no plants flowered. Possibly this was caused by painting the glass of the greenhouse. Therefore, 12 days were subtracted from all the Check plants that flowered after the 72nd day and a new mean was calculated of 71.77 days. The mean of the two Check plantings was thus 61.16 days, very similar to the overall mean of all Check plantings of an earlier report (Vahidy & Hartmann 1972).

Table 2. Mean flowering day of F₁ plants^a.

Parent Plant	Used as	Female	Used as Male		
Parent Plant	Rep. I	Rep. II	Rep. I	Rep. II	
Set I:					
E-I	57.00	58.20	60.33	61.33	
E-II	55.60	57.00	60.00	62.66	
E-III	61.50	65.00	60.50	63.00	
E-IV	63.00	58.00	64.00	64.00	
E-V	58.50	62.50	54.50	55.33	
L-I	58.33	64.00	62.25	59.33	
L-II	61.60	68.00	57.40	60.00	
L-III	59.60	60.00	57.33	60.00	
L-IV	55.75	57.33	49.33	58.00	
L-V	63.75	62.40	60.50	72.50	
Set II:					
E-VI	59.40	61.75	61.50	64.50	
E-VII	55.00	61.00	56.50	59.50	
E-VIII	65.50	69.33	62.25	62.66	
E-IX	63.25	72.00	60.66	61.00	
E-X	62.66	65.66	60.50	61.00	
L-VI	69.33	75.00	60.00	62.33	
L-VII	67.50	65.75	59.60	69.00	
L-VIII	59.00	55.75	63.00	66.00	
L-IX	66.50	63.00	54.33	52.66	
L-X	59.25	56.50	63.66	60.50	

^aEach figure is calculated from the mean of 1 to 5 plants.

The F_2 flowering dates were, therefore, corrected in the following manner. Those which bloomed up to July 10 (when the first Check bloomed) had 41 days added (61.16—50.55—approximately 11). Those which flowered from July 11 to July 26 had 5 days added. Those which flowered from July 27 to August 16 were left unchanged. Those which flowered from August 17 (the day the first plant of the second Check planting bloomed) to September 9 (the day when the 12 days gap period was over) had 11 days substracted (71.77—61.16—approximately 11). Those which flowered after September 10 had 23 days substracted (12+11). The F_2 data were analyzed after subjecting to these corrections.

Results and Discussion

The means, variances, standard deviations, and coefficients of variation of flowering time in P_1 , P_2 , F_1 and F_2 are given in Table 3. The estimates of heritabilities of flowering time, calculated from the variances of F_1 and F_2 are also given in this table. The average heritability of flowering time in the F_2 was found to be 34.90 percent. The frequency distributions of P_1 , P_2 , F_1 and F_2 are given in Figure 1.

The F_1 was grown in two replications and included all reciprocal crosses as well. The effects of these two factors are given in Table 4. The effect of the replications was highly significant, most likely due to the effect of the two different sizes of cans used for the two replications. There were no significant differences in the mean flowering time between reciprocal crosses, therefore, these were combined for all subsequent analyses. Two comparisons, described in Table 4, were made from the data given in Table 2 which gives the mean flowering day of the F_1 plants that had either a male common parent or a female common parent.

The variances as well as the coefficients of variation were much lower in P_1 and P_2 than in the F_1 generation. The reason for this is that the parental plants used for the crosses did not represent the full range of blooming dates for the parental lines. There was a deliberate selection of plants that bloomed more or less at the same time to constitute each parental group. This was true for both parents in both Sets. For this reason, the estimation of environmental variance was based only on the F_1 data, rather than the mean of P_1 , P_2 and F_1 data. The results of the crossing experiments showed no dominance for the time of flowering, and are not in accordance with the results of a previous worker, Frost (1923). He has reported contradictory results from the crosses of early and late lines of Raphanus sativus and R. raphanistrum. From the one set of experiments he concluded that the time of flowering in radish is controlled by a "recessive lateness gene", while the results of another planting reported in the same study showed it to be controlled by a "dominant lateness gene". Probably the contradictory results were due to the lack of a proper control in his plantings.

Table 3. Mean, variance, standard deviation, and coefficient of variation of flowering time in P_1 , P_2 , F_1 and F_2 ; and estimation of heritability.

		Set I	Set II	Combined
P ₁ :				
	n	5	5	10
	Mean	44.20	47.80	46.00
	Variance	4.70	5.20	8.00
	St. deviation	2.17	2.28	2.83
	C.V. (%)	4.90	4.76	6.15
P₂:				
	n	5	5	10
	Mean	84.00	83.80	83.90
	Variance	3.00	1.70	2.10
	St. deviation	1.73	1.30	1.45
	C.V. (%)	2.05	1.55	1.72
F ₁ : a				
	n	61	61	122
	Mean	62.83	64.93	63.88
	Variance	41.93	42.22	42.84
	St. deviation	6.48	6.50	6.55
	C.V. (%)	10.31	10.01	10.25
F ₂ : a				
	n	193	187	380
	Mean	64.70	63.09	63.91
	Variance	62.00	68.77	65.81
	St. deviation	7.88	8.29	8.11
	C.V. (%)	12.17	13.13	12.68
	Heritability (%)	32.37	38.60	34.90

^aTransformed data.

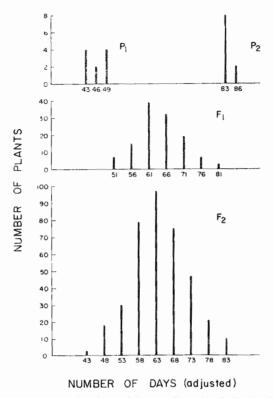


Fig. 1. Frequency distributions of days to flowering in P1, P2, F1 and F2.

However, the results of the present study are in accordance to those reported by Panetsos & Baker (1968). They found the hybrids of two species of radish to be almost intermediate between the parents in the duration of the period from germination to flowering.

The F_2 distribution (Figure 1) shows that there are probably many genes responsible for the time of flowering, though it seems rather difficult to make an estimation of the actual number of genes involved. Even though about 1/16 of the F_2 are equal to the parent, it seems likely that more than 2 pairs of genes are involved, since the response to selection was gradual, and an appreciable amount of variation was found even after six generations of selection (Vahidy & Hartmann, 1971). Penetsos & Baker (1968) have also concluded that flowering time in radish is polygenically controlled, though they recognized three distinct groups, with the ratios of 5: 10: 3 in the F_2 generation. Growing all generations under controlled conditions for environmental factors such as photoperiod, light intensity, temperature, etc. may very likely lead to a reliable estimate of the number of genes responsible for the time of flowering in radish.

Table 4. Effects of replication and reciprocal crosses on mean flowering day of F_1 progeny.

	Rep. I vs. Rep. II	Crosses vs. Reciprocal crosses
Mean differences	1.97	1.42
Variance of differences	6.02	26.82
St. dev. of differences	2.45	5.18
St. Error of differences	0.55	1.16
t-Value	3.58**	1.23 ^{n.s.}
t-Value	3.58**	1.23 ^{n.s.}

n.s. Nonsignificant.

Since the estimation of heritability of flowering time obtained in the present study was quite similar to the two methods described earlier (Vahidy & Hartmann 1971, 1972) it was concluded that three methods seem equally reliable.

Acknowledgment

The senior author is greatly indebted to the East-West Center, the faculty and the members of the department of Horticulrure, University of Hawaii for the financial aid, cooperation and help to conduct this research.

This work is a part of a dissertation approved for the award of the degree of Doctor of Philosophy at the University of Hawaii, Honolulu, U.S.A.

^{**}Significant at .01 level of probability.

References

- Comstock, R.E. and H.F. Robinson. 1948. The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. Biometrics 4: 254—266.
- Frost, H.B. 1923. Heterosis and dominance of size factors in *Raphanus*. Genetics, 8: 116-153.
- Panetsos, C.A. and H.G. Baker. 1968. The origin of variation in "Wild" *Raphanus sativus* (cruciferae) in California. Genetics, 38: 243-274.
- Vahidy, A.A. and R.W. Hartmann. 1971. The genetics of flowering time in *Raphanus sativus* L. I Bidirectional selection. Pak. J. Bot., 3: 1-10.
- Vahidy, A.A. and R.W. Hartmann. 1972. The genetics of flowering time in *Raphanus sativus* L. II Genetype-environment interaction. Pak. J. Bot., 4: 1-25.