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THE GENETICS OF FLOWERING TIME IN *RAPHANUS SATIVUS* L. I. BIDIRECTIONAL SELECTION

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Abstract

The genetics of flowering time in *Raphanus sativus* was studied through bidirectional selections. Individual plant selection, from the original open pollinated parent, was practiced for six generations for late flowering, and for four generations for early flowering. Realized heritabilities of mean flowering time were computed using the formula for genetic advance, $Gs = k \times St. Dev. \times h.^2$. The average realized heritability in the first four generations of selection was 37.42 percent. The assumptions on which these estimations were based and the limitations of the results are described and discussed. The estimation of realized heritability in more advanced generations was somewhat lower, about 33 percent. From the results of selection in the opposite direction it was concluded that an appreciable amount of genetic variability was present even after four generations of selection. Since planting time had a great effect on the mean flowering day, transformation of data was necessary to make comparisons between plantings at different times. The assumptions for such a transformation are discussed.

Introduction

There are several environmental factors that affect flowering in radish. Garner and Allard (1920, 1923) observed that radish is a long day plant with flowers being formed only during long photoperiods. These results were later confirmed by other workers (Sinskaja, 1962; Banga and Smeets, 1956; Sulgin, 1964; Krjuckov, 1963). It has been reported by Banga and Van Bennekom (1962) that flowering in radish is accelerated at higher temperatures and no flowering occurs at a temperature of 8°c. However, flower formation was induced in Japanese radish by low temperature (Eguchi *et al.*, 1963). Strong light intensity is reported to reduce the effect of long photoperiods as far as flowering in radish is concerned (Banga and Van Bennekom, 1962).

There is little work done on the genetics of flowering time in radish. Frost (1923) found that in three out of four crosses between early and late lines of the cultivated species of radish, *Raphanus sativus*, the hybrids flowered "nearly or quite as early as the earlier selfed lines and the general average was earlier." More or less similar results were obtained with crosses of wild species, *Raphanus raphanistrum*, as well as with crosses involving the wild X cultivated species. However, from the results of another planting reported in the same study, he concluded that the time of flowering was controlled by a dominant lateness gene. Probably the contradictory results were due to the lack of a proper control. This was especially needed here because he grew the parent and the offspring at different times.

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Panetsos and Baker (1968) found little variation in the period from germination to flowering in both *R. sativus* and *R. raphanistrum*. F_1 plants bloomed (both in summer and winter) earlier than those of *R. raphanistrum*. Three groups were identified among the F_2 plants, early, medium, and late in the ratio of 5:10:3.

The present study was conducted with the cultivar 'Chinese half long' grown in Hawaii. There it is known as Daikon and is the fourth largest vegetable crop by total acreage in the state of Hawaii (Collier *et al*, 1967).

Materials and Methods

The type of radish known in Hawaii as Chinese Daikon is grown from seed saved by the farmers from each crop. Such seed was obtained in 1964 and grown in the greenhouse. Seedlings were treated with 1.0,0.2, and 0.1 percent concentrations of colchicine.

For the present study seed of selected colchicine treated plants together with seed of untreated plants were grown in the field for selection for late flowering. Each plot was a row 25 feet long, spaced 4 feet apart. Seeds were hand sown and thinned 3 or 4 weeks later about one foot apart. Furrow irrigation was supplied when necessary. Fertilizers were applied according to the recommendation for the particular location. Weeding was either by hand or by the use of recommended herbicides.

Flowering date was recorded as the day when floral buds were just visible. Data were collected every 2 to 4 days.

Selected plants were covered with net cloth after pod set to avoid damage by birds. At maturity the pods were harvested and dried either under the sun or indoors at room temperature. Individual plant selection from open pollinated plants was used.

Plantings were conducted in the fields at the University of Hawaii, Manoa campus and at the Poamoho and Waimanalo Experimental Farms. Poamoho Experimental Farm is located about 30 miles North of the University campus, at 700 feet above sea level with a wahiawa soil type, which is a low humic latosol soil. Waimanalo Experimental Farm is situated about 20 miles East of the campus, at 50 feet above sea level with a Waimanalo soil type, which is a grey hydromorphic soil.

In the summer of 1966 a planting was made consisting of untreated seeds and colchicine treated seeds which had been selected for late flowering for 0,1, and 2 generations. Size of stomata, guard cells and pollen grains were studied to attempt to identify tetraploids. However, no differences between the check and the treated (selected or unselected) plants were found.

At this time selection was started for earliness in flowering, and selection for lateness was continued. The data of these selection experiments were used to compute the realized heritability of mean flowering time, using the following formula:

$$Gs = k \times \text{St. Dev.} \times h^2$$

where Gs = genetic advance under selection
k = constant for particular selection pressure
St. Dev. = phenotypic standard deviation, and
h^2 = realized heritability.

After four generations of selection for late flowering an experiment was planned to test whether genetic variability still existed in these lines. For this purpose, selection in the opposite direction (i.e., for earliness) was initiated in 25 breeding lines that had been selected for late flowering for four generations. Selection for late flowering was also continued.

Data from the fourth and fifth generations of selection for lateness and the first generation for earliness have been used to estimate realized heritabilities for the various lines. As the parental genecation and the offspring were grown at different times, the flowering dates of the parental generation were transformed to make them comparable to that of progeny. This transformation was based on the assumption that breeding lines number 13 and 18 are homozygous, since there was no response to selection in either direction in these lines. The original and transformed parental means, and the means of their early and late selected progeny are given in Table 1. The method of transformation is described in Table 2. For each transformed parental mean, the phenotypic standard deviation was calculated from the coefficient of variation of the transformed mean in the following manner:

Original mean = 79.02
Original standard deviation = 9.94
Original coefficient of variation = 9.94/79.02 x 100 = 12.59
Transformed mean = 59.11
Transformed standard deviation = (12.59 x 59.11) /100 = 7.44

Results and Discussion

The response to selection was gradual with no appreciable decrease of variability even after six generations. It was not possible to estimate the actual genetic advance due to selection in each generation because of the large effect of environment on the flowering time at different times of the year and the absence of a suitable check in all plantings. However, the early and late lines became more and more differentiated in each generation,

TABLE 1. Mean flowering days of parental, early selected and late selected lines.

Line No.	Original Parent[a]	Progeny Early Selection[b]	Progeny Late Selection[c]	Transformed Parent[d]
1.	90.31	54.12	68.82	67.08
2.	78.60	52.53	66.68	58.38
3.	78.60	62.30	75.16	58.38
4.	81.74	57.50	74.57	60.71
5.	81.74	57.31	67.25	60.71
6.	85.09	62.66	74.54	63.20
7.	88.30	50.23	68.50	65.58
8.	88.30	56.19	74.40	65.58
9.	88.30	52.34	77.78	65.58
10.	88.50	57.73	72.00	65.73
11.	90.37	66.31	69.79	67.12
12.	83.50	57.25	62.89	62.02
13.	82.34	62.00	60.16	61.16
14.	90.70	62.30	72.45	67.37
15.	74.75	53.00	68.17	55.52
16.	84.42	45.81	64.33	62.70
17.	84.42	66.00	72.19	62.70
18.	91.52	67.40	68.73	67.97
19.	91.80	57.42	69.03	68.18
20	91.80	66.45	71.80	68.18
21.	85.34	61.80	66.39	63.18
22.	81.00	57.60	62.60	60.16
23.	85.20	63.95	69.61	63.28
24.	85.20	62.73	70.09	63.28
25.	80.31	51.45	62.60	59.65

[a]4th generation of late selection. Poamoho – Fall, 1967 Planting.

[b]Selection in opposite direction. Poamoho—Summer, 1968 Planting.

[c]5th generation of late selection. Poamoho—Summer, 1968 Planting.

[d]Transformation is applied to make the figures of parental lines comparable to those of progeny lines. See Table 2 for procedure.

TABLE 2. Transformation of parental lines in Table 1.

	Fall-1967 Planting	Summer-1968 Planting		
Line No. [a]	Original parental line	Early selection	Late selection	Means of offspring
13	82.34	62.00	60.16	61.08
18	91.52	67.40	68.73	68.06
Total	173.86	129.40	128.89	129.14
Mean	86.93	64.70	64.44	64.57

Tranformation: 86.93 days to flowering of Fall—1967 planting is equal to 64.57 days to flowering of Summer—1968 planting. The data of original parental line of Table 1 is transformed on this scale.

[a]These are considered homozygous lines on the basis of their performance. See Table 1.

until at the end of the study, there was very little overlapping in the frequency distributions of the Early and Late lines (Figures 1 and 2). At this time Early lines had been selected for four generations and the Late lines for six generations. The unselected Check lines had a distribution that was somewhat in between the Early and Late lines.

The data were utilized to estimate realized heritabilities of mean flowering time at different stages of selection. These estimates, for the plantings where parental and offspring generations were grown at the same time, are given in Table 3. The average

TABLE 3. Realized heritabilities of mean flowering time from the plantings where parents and offspring were grown at same time.

Generation of selection					Mean flowering day		Realized
Parent	Offspring	Location	Season & Year	Line No.	Parent	Offspring	Heritability %
1st Late	2nd Late	Manoa Campus	Summer '66	25	52.54	60.33	46.06
1st Late	2nd Late	Manoa Campus	Summer '66	26	51.90	58.43	42.59
2nd Late	3rd Late	Poamoho	Spring '67	25	54.10	57.51	29.83
3rd Late	4th Late	Poamoho	Fall '67	25	69.85	76.16	38.43
3rd Late	4th Late	Greenhouse	Fall '67	25	81.06	82.00	30.22

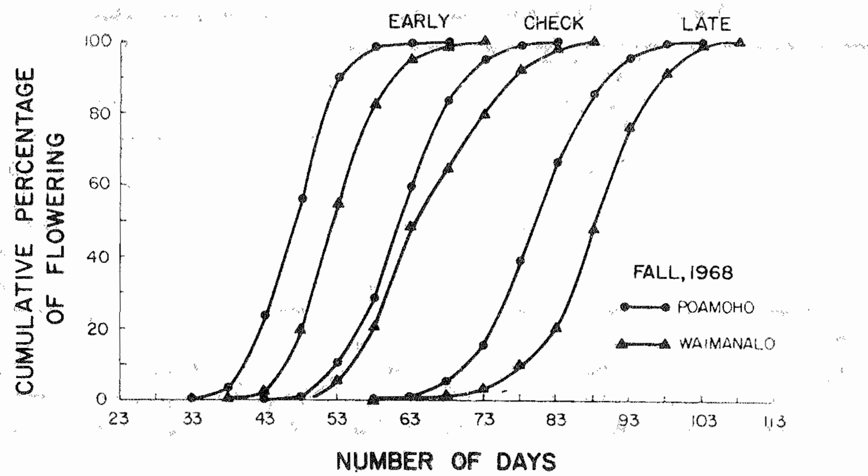

Figure 1. Cumulative percentage of flowering for the Early, check, and Late populations in the plantings of fall, 1968.

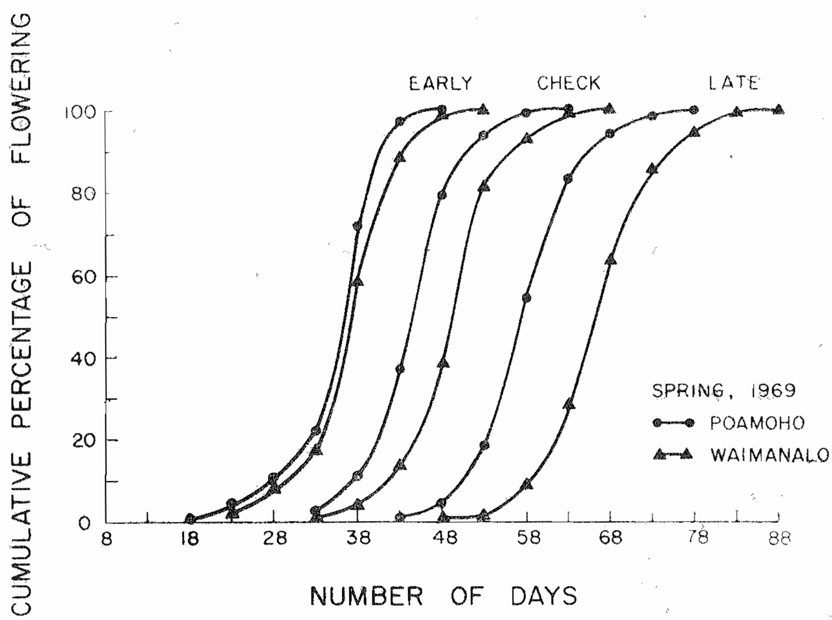

Figure 2 Cumulative percentage of flowering for the Early, check, and Late populations in the two plantings of spring, 1969.

realized heritability of mean flowering time was 37.42 percent. These estimates were based on the assumption that the mean performance of parents and their half sibs is same. This assumption was necessary because the offsprings were grown with the half sibs of their parents, not with their actual parents. Inclusion of the half sibs of the parents in the offspring generation could be made within one planting. The environmental changes caused erratic changes in the time of flowering. As a result comparisons were rather difficult to make if the parents and their offspring were in different plantings.

One of the basic assumptions for the analysis of variance is that the treatments (in this case, varieties) all have the same variances. If the treatments have significantly different variances and are, therefore, heterogeneous, then the F-test is not valid. Thus, it is important to test for heterogeneity of variances when the treatments have markedly different means. In the present studies there was a possibility of heterogeneity of variances since selection made the means of Early and Late lines more and more different. Because of this possible heterogeneity, the coefficient of variation rather than the variance was used to compare lines with different means, such as when calculating the realized heritabilities.

TABLE 4. Effects of selection in opposite direction and continued selection for lateness after four generations of late selection.

	4th vs. 5th generation of late selection	4th generation of late vs. selection in opposite direction
Mean differences	5.88	4.77
Variance of differences	22.49	32.61
St. dev. of differences	4.74	5.71
St. Error of differences	0.94	1.14
t—value	6.25**	4.18**

**Significant at .01 level of probability.

After four generations of selection for late flowering, two planned comparisons were made, namely the fourth generation of late selection was compared with an additional generation of late selection and with one generation of selection in opposite direction. The progeny were grown in the Summer of 1968, while parents were grown in the Fall of 1967. Both the early and late selections bloomed in a shorter time than the parents since radish is a long day plant and flowers earlier in summer than in fall. The flowering dates of the parents were therefore transformed as described in Table 2. The results of these comparisons, using the transformed parental data, are given in Table 4. Realized heritabilities were also estimated for various groups of these same lines and are given in Table 5. Each group of lines can be traced back to a single plant.

The estimates of heritabilities of mean flowering times in Table 5 were obtained after eliminating part of the environmental component of variance, that was due to the different planting times, from the total environmental variance. Thus these estimates may actually be biased upwards somewhat.

TABLE 5. Realized heritabilities of mean flowering time from the plantings where parents and offspring were grown at different times.

Generation of selection			Mean flowering day		Realized
Parent[a]	Offspring[b]	Line No.	Parent[c]	Offspring	Heritability %
4th Late	5th Late	30	63.39	70.76	46.86
4th Late	5th Late	31	64.85	70.20	34.51
4th Late	5th Late	33	63.38	66.39	31.41
4th Late	5th Late	42	61.72	66.22	33.84
4th Late	5th Late	44	59.65	62.60	20.48
4th Late	1st Early[d]	30	63.39	56.90	41.45
4th Late	1st Early	31	64.85	60.32	32.23
4th Late	1st Early	33	63.38	61.80	16.49
4th Late	1st Early	42	61.72	60.47	17.45
4th Late	1st Early	44	59.65	51.45	48.46

[a]Grown at Poamoho-Fall, 1967.

[b]Grown at Poamoho-Summer, 1968.

[c]Transformed values to make comparable with offspring. Method of transformation in Table 2.

[d]Selection in opposite direction.

However, the magnitude of realized heritabilities calculated in this manner was similar to the magnitude of the heritability calculated when both parents and offspring were grown at the same time (Table 3). From the results shown in Table 5 it may be concluded that the lines 33 and 42 have lost most of the genes for earliness, while line 44 has lost most of the genes for lateness. Also that lines 30 and 31 still have genes for both earliness and lateness which are not fixed. The results also show that an appreciable amount of genetic variance for flowering time is still available in these lines that have already been selected for four generations.

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References

Banga, O. and J. L. Van Bennekom. 1962. Breeding radish for winter production under glass. Euphytica, 11: 311-326.

Banga, O. and L. Smeets. 1956. Some effects of the photoperiod on growth and pithiness of radishes. Euphytica, 5: 196-204.

Collier, W.L., J. R. Davidson and T. Pee. 1967. Analysis of Daikon production on the Island of Hawaii. Agricultural Economics Report No. 75. Hawaii Agr. Exp. Sta. pp. 15.

Eguchi, T., T. Matsumura and T. Koyama. 1963. The effect of low temperature on flower and seed formation in Japanese radish and Chinese cabbage. Proc. Amer. Soc. Hort. Sci., 82: 322-331.

Frost, H.B. 1923. Heterosis and dominance of size factors in Raphanus. Genetics, 8:116-153.

Garner, W. W. and H. A. Allard. 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. J. Agr. Res., 18: 553—606.

Garner, W.W. and H. A. Allard. 1923. Further studies in photoperiodism, the response of day and night. J. Agr. Res., 23: 871—877.

Krjuckov, A.V. 1963. The use of certain environmental conditions in the selection of radishes resistant to the tendency to bolting. (Russian) Dokl. mosk. sel'.-hoz. Akad. K.A. Timirjazeva. 83:235-240. in Hort. Abst., 34:714.

Panetsos, C.A. and H.G. Baker. 1968. The origin of variation in "wild" *Raphanus sativus* (Cruciferae) in California. Genetics, 38: 243-274.

Sinskaja, E. 1962. On the nature and conditions of the formation of esculent roots. Bull. Appl. Bot. and Pl. Br., 16: 26-35.

Sulgin, I.A. 1964. On the effect of visible and infra-red radiation on the development of radishes. (Russian) Fiziol. Rast. 11: 398-408. in Hort. Abst., 34:714.