A GENETIC FACTOR FOR THE ANNUAL HABIT IN BEETS AND LINKAGE RELATIONSHIP[1]

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INTRODUCTION

Practically all the cultivated varieties of *Beta vulgaris* L., including the sugar beet, show wide genetic variability in respect to the annual and biennial growth habit. Beets that are biennial form vegetative foliar rosettes during the first season of growth. After a period of necessary low-temperature exposure the crown buds of such vegetative beets develop aerial stems bearing spikelike inflorescences. In the annual type this stem development takes place during the first season. These annual types are commonly termed "bolters." Their occurrence is widespread and has been reported from practically all regions of the beet culture in the United States and Europe.

A review of literature indicates that a divergence of opinion exists as to the mode of inheritance of the annual character in beets. As early as 1876, Rimpau (*13*)[3] cited evidence that annual habit is dominant. In a controlled cross between the annual wild beet (*Beta patula* Ait.) and pollen from relatively biennial commercial stock, all the hybrid progeny proved to be annuals. Dudok van Heel (*3*) concluded that bolting factors are recessive. However, this conclusion was not supported by critical breeding data. Vilmorin (*14*) noted marked strain differences in bolting, but from the crosses made he was not able to define the mode of inheritance. Munerati (*10*), in 1931, contributed the first significant advance on the genetics of the bolting character. He crossed several strains which in previous tests had proved to be uniformly annual and biennial, respectively. Some of the biennials used in these crosses were selections from commercial stock, and the annuals were apparently also established from economic sugar-beet varieties. All the F_1 plants were decidedly annual, although showing a somewhat later time of blooming than the annual parent. In summing up Munerati's data which are restricted to reciprocal F_2 progenies, the observed numbers of 3,502 annuals and 1,155 biennials agree closely with the expected 3 : 1 ratio. Munerati concluded that the annual tendency is controlled by a simple Mendelian factor.

The results on the inheritance of the annual character presented in this paper were derived from crosses of one of Munerati's annual strains with several relatively biennial types selected by the writer. Aside from an extension of the simple genetical analysis of the annual habit, the chief contribution relates to a linkage between the factor for annual habit and a factor that chiefly affects hypocotyl and crown

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[2] The writer wishes to express his appreciation to F. V. Owen, geneticist, and Eubanks Carsner, senior pathologist, Division of Sugar Plant Investigations, for suggestions and criticism during the progress of this work and in connection with the preparation of the manuscript.

[3] Reference is made by number (italic) to Literature Cited, p. 510.

color. A foliage venation character resembling that of the common plantain (*Plantago major* L.) was also introduced in some of the crosses and gave an opportunity for a study of three contrasting characters.

RELATION OF ANNUAL HABIT TO BREEDING PROBLEMS

The removal of strong bolters in newly selected disease-resistant stocks constitutes a major breeding problem. The need for nonbolting beet varieties suitable for early planting under California conditions is shown by the results of bolting tests conducted by Carsner [4] with two lots of seed grown from the U. S. 1 variety and separated on the basis of time of maturity of the seed. Those plants on which the seed matured early were harvested June 7, 1932. This selection was given the designation V. Selection W, the later maturing lot, was harvested July 8. In a bolting test at Spreckles, Calif., with seed planted January 3, 1933, the final counts on September 6 gave the following bolting percentages: V, 77; W, 23; and the commercial brand Elite Braune, 6. The average weight in pounds per beet at harvest was: V, 1.14; W, 2.23; and Elite Braune, 2.14. In sugar percentage also selection V was the lowest. This evidence shows that in extreme cases bolting results in large losses in yield of sugar.

Results obtained by Esau (*4*) indicated that in the European variety Old Type, grown in central California, the occurrence of a relatively high percentage of bolters may have had very little influence on the final yield. It might be assumed that in this commercial brand selection had removed many of the rapid and hence most undesirable bolting types. The breeding problem now is to combine the nonbolting tendency exemplified by the best European varieties with specific disease resistance to meet conditions where the crop is grown. A demonstration of the heritable basis of the annual habit and the linkage relations to other characters would be helpful in such practical breeding procedures.

MATERIAL

ANNUAL AND BIENNIAL PARENTAL STRAINS

Annual Strain

During 1931 two beet strains [5] were tested for bolting. One of these proved to be uniformly annual, even in plantings made as late as June 25 at Salt Lake City, Utah. Figure 1 shows the annual strain in comparison with relatively biennial strains. In subsequent crosses the annual strain proved to be homozygous for both of the simple Mendelian characters—red hypocotyl-crown color and normal pinnate venation—with which the writer has worked extensively.

Biennial Strains

The biennials used for crosses are representative of similar types found in economic varieties. A brief history of these biennial strains follows:

[4] Carsner, E. Unpublished data of Division of Sugar Plant Investigations, Bureau of Plant Industry U. S. Department of Agriculture.

[5] Received from Dr. O. Munerati, Rovigo, Italy, to whom grateful acknowledgment is made.

Strains 12c21 and 042.—Both of these strains were originally selected by Carsner (*1*) for high resistance to curly top. In 1931 the writer selected from 12c21 a group of eight stecklings that were relatively nonbolting in habit. Further tests of the seed increase from these stecklings proved that the selection was a strong biennial type producing no annuals. This strain was also homozygous for both red hypocotyl color and normal venation. The original stock of 042 contained an appreciable number of bolting types. In an early planting of 1930 at Salt Lake City the 042 strain produced no bolters, but other related strains bolted as high as 50 percent. This indicates the absence of annual types in the 042 strain. This strain has yellow hypocotyl color and its leaf venation is normal.

Plantain strain.—This strain traces back to a selection from commercial Kleinwanzleben stock made by D. A. Pack, formerly associate agronomist, Division of Sugar Plant Investigations. It bred true for

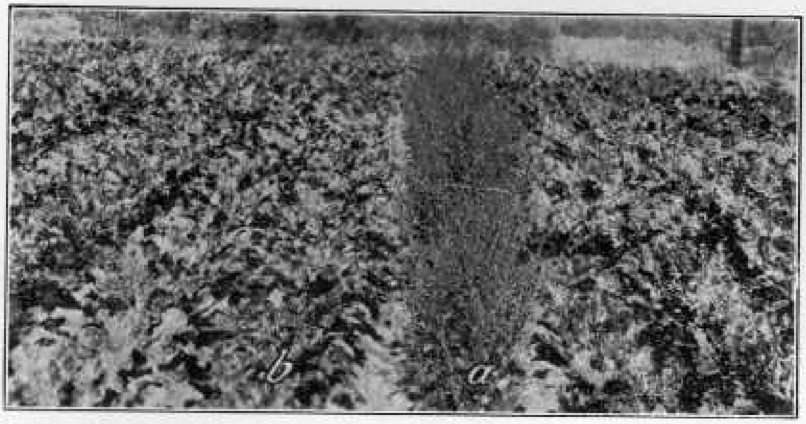

FIGURE 1.—Munerati's annual strain (*a*) in bloom, compared with his biennial type (*b*, in the single row to the left of *a*) and with other biennial strains. Planted at Salt Lake City, Utah, March 24, and photographed June 19, 1931.

a foliage type marked by semiparallel veins. The foliage venation of the strain under consideration shows prominent lateral veins that are more or less free to the base of the leaf blade, and in this respect it resembles the ribbed condition of the foliage of the common plantain, *Plantago major* (fig. 2). This selection will be designated in this paper as the plantain strain. Reselections have been extensively tested for a number of years and have shown no annuals. This type carried the recessive yellow hypocotyl-crown color.

HYPOCOTYL-CROWN COLOR CHARACTER

The red and yellow hypocotyl-crown color character, which has been mentioned under the description of the annual and biennial parental strains, produces sharply contrasted types. Keller (*8*) describes the *R* plants as having a rose or pale-red color in seedling hypocotyls. The bases of stems and petioles also may show this rose or red color. In large vegetative beets the central bud clearly shows the pigment. The writer has also been able to detect this color in most types in small buds located in the axils of leaf petioles and seedstalks. This is a means of classifying plants in the bolting stage, in which the color intensity may be reduced.

The yellow type (*r*) lacks anthocyan pigment. The hypocotyls are green, with more or less yellow pigment. The intensity of this yellow pigmentation is apparently correlated with exposure to sunlight.

Nuckols (*11*) notes that in young sugar-beet seedlings the color of the red hypocotyl types may vary from a carmine red to light shades of pink. In the seedlings lacking anthocyan pigment the yellow

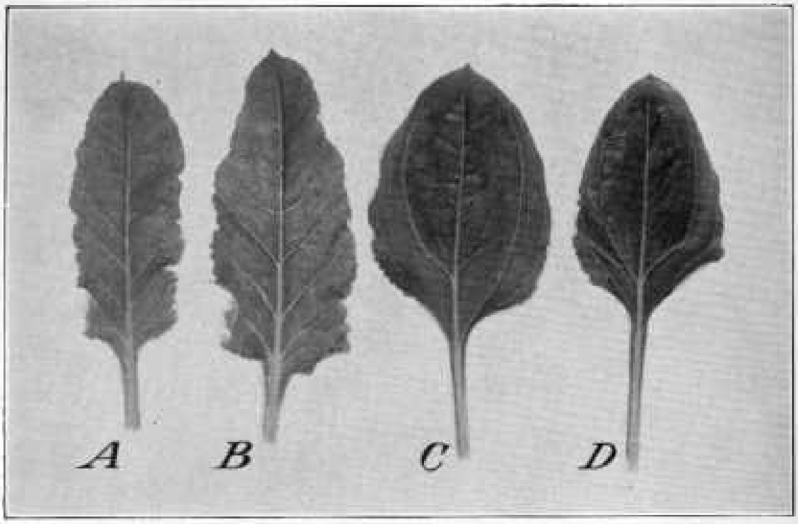

FIGURE 2.—Two leaves (*A*, *B*) with normal pinnate venation (*Pl*), and two leaves (*C*, *D*) with semiparallel venation (*pl*) typical of the plantain beet strain. Foliage taken from sib plants in backcross progeny 08 (*pl* × *Plpl*), February 1932.

coloration varies from deep orange to light shades that appear almost white. In a test of 37 varieties Nuckols found that the red and yellow color classes were apparently equal in both root yield and sugar content.

CROSSES

The following crosses and their reciprocals were made:

Cross 1, annual × 12c21.
Cross 2, annual × 042.
Cross 3, annual × plantain strain.

METHODS

CROSSING TECHNIQUE

The types crossed were highly self-sterile. Therefore the methods of distance isolation and bagging proved to be satisfactory for crossing. In the crosses made by the writer, the percentage of contamination with outside strains was very low. The bagging technique was similar to that used in corn breeding. For crosses a simple exchange of bags of the two parents yielded a satisfactory amount of seed. Since self-sterility is not complete under all conditions, the presence of selfed individuals needs to be considered. In crosses such as *rr* × *RR*, the color character shows the presence of selfs having the *r* plant as seed parent and certifies the red plants as crosses. The reciprocal combination does not furnish this information immediately, and a further breeding test is required. In the combination *rr* × *Rr* a large excess of yellow types may be indicative of considerable selfing, and likewise in the *Rr* × *rr* cross an excess of reds may be due to selfs. Such marked deviations, however, occur rarely under conditions of strong self-sterility.

FIELD TESTS

Crosses between the annual type × 12c21, 042, and the plantain strain, respectively, were made in 1932. In 1933, F_1, backcross, and F_2, progenies, as well as parental strains, were tested for annual habit. This material, sown on March 23, was transplanted to the field during the last week of April. The backcross and F_2 plants were either definitely annual or biennial in character, with the exception of four plants that turned vegetative after the initiation of a seedstalk. This material was classified for bolting on July 5, July 20, and November 11. The last two counts showed close agreement. A field planting of backcross progeny 3492 (F_1 × plantain strain) was made May 31. A count made July 10, only 40 days after planting, showed a good separation into annual and biennial types.

On April 23 and 24, 1934, several progenies and parental strains were sown in small 3-inch pots. Seedlings which had been singled were marked, but in the subsequent field test transplants and undisturbed seedlings showed no difference in the percentage of bolters. Approximately 1,000 of these potted plants were transplanted to the field on May 22 and spaced uniformly from 6 to 8 inches in the row. The material was classified on July 9 and 30. Between these two dates only one plant in all the progenies changed from the vegetative to the flowering state.

On April 26, 1934, several F_2 lots and parental strains were field-sown. The plants were thinned at random to 4 to 6 inches apart in the row. A maximum of bolting was apparently reached on July 22. A previous count on July 2, especially in progenies 3427 and 3432, showed a very large excess of vegetatives. The slow rate of bolting may be partly attributed to a severe infection of curly top to which the plants were exposed. The same F_2 lots were grown under conditions of reduced disease or in the absence of curly top, and in both cases the agreement between the expected and observed annual to biennial ratio was satisfactory.

In both the 1933 and 1934 field tests, check plantings were made of the three parental biennials, 042, 12c21, and plantain strain, respectively, and likewise of the annual type. Out of a total of 320 plants from the biennial strains tested, all remained vegetative. All of the annual parental strain, a total of 241 plants, bolted early. All 84 F_1 plants from crosses 1 and 2 proved to be annual in habit.

GREENHOUSE TESTS

By means of controlled experiments it has been shown by Garner and Allard (*6*) and Chroboczek (*2*) that lengthened photoperiods and low-temperature exposure are conditions which, if applied in proper growth stages, increase bolting in beets. Under greenhouse conditions the manipulation of temperature and light serves a useful purpose in genetic studies of growth habit.

The parental strains and the F_1 and F_2 progenies were sown outdoors in flats on August 12, 1933. On September 12, transplants were set in a greenhouse bench and spaced 3 to 4 inches apart in the row. Rows were spaced 8 inches apart. The greenhouse temperatures over the essential period of the test are given in table 1. Shortly after the plants were set into the bench, additional light was furnished from 100-watt globes spaced 3 to 4 feet apart. From the middle of September to the middle of November these plants received an average of 8 hours of artificial light in addition to the regular daylight.

The separation between annuals and biennials was excellent. In cross 1 (annual × 12c21 biennial) a period of 60 days intervened between the appearance of the last F_2 annual and the beginning of seedstalk formation among the F_2 biennial segregates. In cross 2 (annual × 042 biennial) a period of 40 days separated the completion of bolting by the F_2 annuals and the initiation of seedstalks among the biennial segregates. In cross 3 (annual × biennial plantain strain) an average period of 35 days separated annuals and biennials. In this cross only 2 late and more or less intermediate bolters appeared in a total of 244 F_2 plants tested.

TABLE 1.—*Greenhouse temperatures for September to December 1933*

Month	Maximum	Minimum	Mean	Month	Maximum	Minimum	Mean
	° *F.*	° *F.*	° *F.*		° *F.*	° *F.*	° *F.*
September	90.2	52.4	71.3	November	76.7	48.8	62.8
October	83.6	43.7	63.6	December	73.7	43.8	68.8

In the 1933 greenhouse test, check plantings were made of the three biennial parental strains, 12c21, 042, and the plantain type. A total of 84 plants from the biennial strains remained vegetative during the entire period of the test. In contrast, 65 plants of the annual type all bolted very early.

On April 24, 1934, pot plantings of several backcross and F_2 progenies were made. Until June 21 the greenhouse plants received additional light daily from two 100-watt globes burning from 9 p. m. to 5:30 a. m. On June 21 all vegetative plants were transplanted to the field for further observation. Only 2 plants in a total of 111 classified previously as vegetatives produced seedstalks later in the field.

A small number of F_3 lines were planted October 16, 1934, in a cool greenhouse with additional light. Six red and nine yellow F_2 plants from cross 2, which had been classified in the 1933 greenhouse test as biennials, were backcrossed to yellow and biennial plants. This material was classified for bolting and color January 12, 1935.

EXPERIMENTAL RESULTS

DOMINANCE OF ANNUAL HABIT

Cross 3 (annual × biennial plantain strain) was made in 1932 by means of bagged branches on greenhouse plants. Only a small amount of F_1 seed was obtained. In a field planting of May 5 a stand of only seven plants resulted, but all were annual in habit, red in color, and normal in venation. A comparison of the blooming stage reached by the annual parent strain and the F_1 plants showed that while the annual was past full bloom three of the F_1 plants were in full bloom and four in late bud stages.

In the 1933 test, dominance of the annual habit was clearly indicated. Eighty-four F_1 plants were grown from crosses 1 and 2 (12e21 × annual and 042 × annual), respectively. It was apparent that the F_1 plants were somewhat slower in reaching the full-bloom stage than the annual type planted in the same plot. Twenty-eight plants of strain 042 and 20 plants of strain 12e21 remained vegetative. Figure 3 shows the relative development reached by the annual

FIGURE 3.—Dominance of annual habit. Rows *a* and *b*, annual and biennial 042 parental strains, respectively; row *c*, F_1 annual plants from cross 042 × annual. Transplanted in April and photographed July 5, 1933.

and biennial parental strains and their F_1 progeny from cross 2 (042 × annual).

The 1933 greenhouse test gave F_1 results in agreement with the field test. Sixty-two F_1 plants from crosses 1 and 2 were definitely annual in habit but slower in developing seedstalks than the annual parental strain. All greenhouse plantings of the biennial parental strains remained vegetative.

Dominance of the annual habit presents a problem, especially in relation to the comparative rates of seedstalk development of the annual parent, F_1 bolters, and the annual F_2 segregates. Munerati (*10*) has called attention to the fact that the annual parent develops a seedstalk more rapidly than either F_1 plants or annual F_2 segregates. The writer has gathered some preliminary data on this question also from material grown in the greenhouse. Spacing of plants in replicated rows was quite uniform. The measurement of seedstalk height was made when the plants of the annual parent strain were nearly all in or near the blooming stage.

The data in table 2 show that the annual strain, with a mean stalk height of 64.54 ± 2.14 cm, is significantly higher in rate of bolting than either F_1 or F_2 annuals. The coefficients of variability of annual and F_1 plants are practically equal. This indicates that with reference to the annual and biennial character the respective parental strains were uniform. However, it is expected that the parental strains could carry factors that would modify heights of inflorescence or time of blooming.

Several hypotheses may be advanced for the apparently incomplete dominance of the annual habit. The most common hypothesis would be that heterozygous *Bb* plants (*B* is the factor symbol for annual character and *b* for vegetative character) are slower in rate of seedstalk development than the homozygotes *BB*. Some F_2 data in table 2 show that this assumption does not explain all results. With some homozygous types present, one would expect the mean seedstalk height of the F_2 bolters (neglecting the vegetative segregates) to be greater than that for the F_1 annuals. However, this is not the case. In the two F_2 progenies 3430 and 3432, the seedstalk heights are 26.39 ± 1.16 and 22.08 ± 1.78 cm, respectively. The heights of the corresponding F_1 progenies are 33.87 ± 1.66 and 26.00 ± 1.45 cm, in both cases higher than those of the F_2 lots. It is also evident from the 12c21 × annual cross that F_1 and F_2 progenies are not significantly different in coefficient of variability. The F_2 progeny of the annual × 042 cross is significantly higher in variability than the F_1 progeny. However, reference to table 2 shows that a preponderance of the higher variability of the annual × 042 F_2 progeny comes from an increase of plants in the lower seedstalk heights. There is no definite indication from these data that *BB* plants have increased the average seedstalk heights to any great extent in the F_2 progenies.

A comparison of the rate of bolting of F_1 and F_2 plants needs further consideration. It is possible that F_1 plants possess on an average a greater number of favorable growth factors for height than F_2 plants. Therefore, F_1 plants may not reveal the net effect of the *Bb* factors on rate of seedstalk development. In comparison, the inbred F_2 plants may show a lower mean seedstalk height, owing to the presence of individuals with a reduced number of favorable growth factors. If a correction could be made for the opposing effects of these growth factors in F_1 and F_2, *BB* plants might prove to be faster than *Bb* plants in seedstalk development. Detailed examination of various hybrids in other plants has shown that in many instances dominance is not complete.

Considering the frequency distributions from all three F_2 progenies in table 2, it is clear that out of a total of 143 bolters not over 10 plants approximated the average seedstalk height of the annual parent (64.54 ± 2.14 cm) and that only 1 plant in the F_2 exceeded this. If *BB* F_2 plants were considerably faster in bolting than *Bb* annuals, the expectation would be that approximately one-third of the bolters in the F_2 would be near the mean seedstalk height of the annual parent.

TABLE 2.—*Distribution and variability of seedstalk height in crosses between annual and biennial types, greenhouse test, 1933*

Current no.	Strain or cross	Vegetative plants	Plants with seedstalk of indicated height												Total plants with seedstalk	Height of seedstalks		
			6 cm	14 cm	22 cm	30 cm	38 cm	46 cm	54 cm	62 cm	70 cm	78 cm	86 cm	94 cm		Mean [1]	σ	Coefficient of variability
		Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Cm*	*Cm*	
2240	Annual parental type	0	------	------	------	4	1	3	10	8	12	11	1	4	54	[2] 64.54±2.14	15.72±1.51	24.4±2.5
2248	F_1 (12c21 × annual)	0	------	1	2	7	9	2	------	------	------	------	------	------	21	33.87±1.66	7.59±1.17	22.4±3.6
2250	F_1 (042 × annual)	0	------	3	9	6	3	------	------	------	------	------	------	------	21	26.00±1.45	6.63±1.02	25.5±4.2
3427	F_2 (Plantain × annual)	13	5	12	5	10	7	8	4	2	------	1	------	------	54	30.52±2.33	17.09±1.64	56 ±6.9
3430	F_2 (annual × 12c21)	9	------	7	14	19	5	1	------	------	------	------	------	------	46	26.39±1.16	7.87± .82	29.8±3.4
3432	F_2 (annual × 042)	20	5	12	15	5	3	------	3	------	------	------	------	------	43	22.08±1.78	11.70±1.26	53.0±7.1

[1] The mean, standard deviation, and coefficient of variability were calculated from the ungrouped data.
[2] All errors given as standard errors. P. E.=±0.6745 × standard error.

There is no doubt that as far as initiation of seedstalks is concerned the annual habit is strongly dominant, for F_2 ratios restricted to the strains used in this study have always been 3 annual to 1 biennial. From the data presented it seems that *BB* and *Bb* types do not differ greatly in rate of seedstalk growth. It is possible that other factors for height or maturity exist which depress the rate of seedstalk development in both F_1 and F_2 while not inhibiting initiation of the reproductive phase.

INHERITANCE OF ANNUAL HABIT (CROSS 1)

Table 3 shows that the distribution of annual and biennial plants in F_2 progenies (12c21 × annual) from cross 1 is in very close agreement with the expected 3:1 ratio. It is also apparent that the

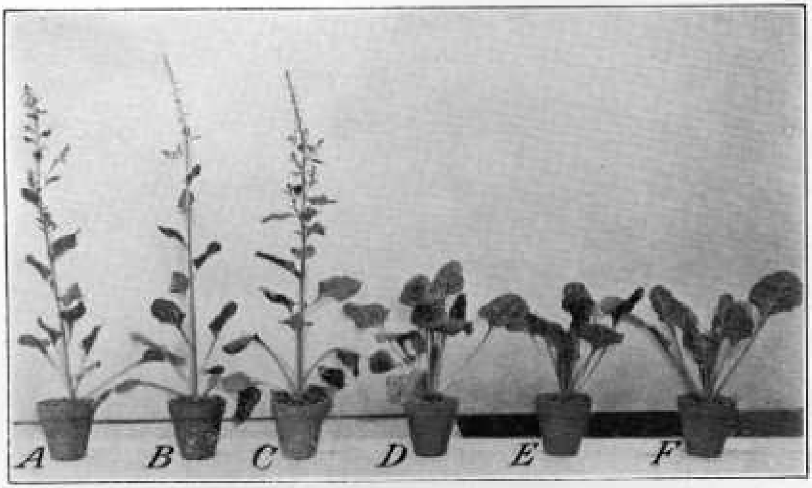

FIGURE 4.—Segregation for annual (*A–C*) and biennial (*D–F*) plants in F_2 progeny 3429 (12c21 biennial × annual), October 1933.

greenhouse lots, grown with an increased photoperiod, and the field-grown groups are practically equal in bolting percentage. Figure 4 shows annual and biennial segregates obtained from one of the F_2 progenies grown in the greenhouse.

Under greenhouse conditions the bolters in the F_2 progenies from cross 1 developed rapidly. On September 22, only 14 days after the plants were placed under light and 41 days after the seed was sown, 97 percent of all the bolters were evident. By October 18 only six more plants bore seedstalks. After that date and until December 16, when most of the plants were discarded, no more bolters appeared. The extreme vegetative nature of the F_2 biennial segregates is evident from the following test: After December 16, 10 vegetative segregates of each of the reciprocal F_2 progenies 3429 and 3430 were kept under light for further observation. On January 3, 1934, 77 days from the time the last six bolters appeared, only one plant was definitely starting a seedstalk.

TABLE 3.—*Segregation of annual and biennial habit in F_2 progeny, no. 3429 (12c21 × annual), and the reciprocal, no. 3430* [1]

Current no.	Date and location of test	Total plants	Biennial plants	Annual plants	
		Number	*Number*	*Number*	*Percent*
3429	1933, greenhouse	98	32	66	67.3
	1934, field	198	47	151	76.3
3430	1933, greenhouse	154	36	118	76.6
	1934, field	176	42	134	76.1
Total observed		626	157	469	74.9
Calculated, 3:1 ratio			156.5	469.5	
Deviation [2]			+.5	−.5	

[1] 3 stecklings each from the reciprocal F_1 lots were grown for F_2 seed in separate field isolations.
[2] $\frac{\text{Deviation}}{\text{Probable error}}=0.07$.

INDEPENDENT ASSORTMENT OF B AND Pl

In cross 3 (plantain strain × annual) the plants differed in leaf venation as well as in growth habit. One of the biennial strains, as previously indicated, was marked by foliage venation similar to that in the common plantain. The inheritance of the plantain venation character is explained on a simple Mendelian basis, with normal pinnate venation dominant. *R* and *Pl* are independently inherited. Therefore, *B* and *Pl* should likewise show independent inheritance. The results support this expectation.

The backcross data in table 4 are in very close agreement with the calculated 1 : 1 : 1 : 1 ratio. The F_2 results reported in table 5 are not in satisfactory agreement with the calculated 9 : 3 : 3 : 1 ratio. It is not a question of linkage, for the poor fit is associated with a large plus deviation of plantain types in the annual class. The deficiency of 13 biennials is not significant. The deviation of biennials is only 2.4 times the probable error. In table 5, according to Fisher's method (*5*), the observed and calculated frequencies of annuals and biennials are compared separately in the normal and plantain classes. The fit now is satisfactory, χ^2 reducing from 10.766 to 2.851. With two degrees of freedom, *P* lies between 0.2 and 0.3.

TABLE 4.—*Independent assortment of factors B (annual habit) and Pl (leaf venation) in backcrosses of type bpl × BbPlpl*

Types backcrossed	Current no.	Annual plants		Biennial plants		Total plants
		Normal	Plantain	Normal	Plantain	
		Number	*Number*	*Number*	*Number*	*Number*
bpl × *BbPlpl*	2311, 2312, 2314	31	45	35	35	146
Reciprocal	3492	71	53	68	67	259
Total observed		102	98	103	102	405
Calculated 1 : 1 : 1 : 1 ratio		101.25	101.25	101.25	101.25	
Deviation [1]		+.75	−3.25	+1.75	+.75	

[1] $\chi^2=0.146$; *P*=between 0.98 and 0.99.

TABLE 5.—*Independent assortment of factors B (annual habit) and Pl (leaf venation) in F_2 progenies from matings of the type BbPlpl inter se*

Current no.	Total plants	Annual plants		Biennial plants		Normal [1]		Plantain [1]	
		Normal [2]	Plantain [2]	Normal [2]	Plantain [2]	Annual plants	Biennial plants	Annual plants	Biennial plants
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
2383, 2385, 2386	96	50	22	17	7	50	17	22	7
3427	244	132	64	34	14	132	34	64	14
Total	340	182	86	51	21	182	51	86	21
Calculated		191.25	63.75	63.75	21.25	174.75	58.25	80.25	26.75
Deviation		−9.25	+22.25	−12.75	−.25	+7.25	−7.25	+5.75	−5.75

[1] Theoretical ratio, 3 : 1; $\chi^2=2.851$; P=between 0.2 and 0.3.
[2] Theoretical ratio, 9 : 3 : 3 : 1; $\chi^2=10.766$; P=between 0.01 and 0.02.

LINKAGE RELATIONS BETWEEN R AND B

BACKCROSS DATA

Cross 2 was made in 1932 in a field isolation between yellow biennial 042 strain × red annual, clone 59. Seed from the two plants was harvested separately. Seventy-five F_1 plants of both combinations were tested and all proved to be annual and red in hypocotyl color. Fifty-four of these F_1 plants came from the white biennial as seed parent and all showed the presence of the *R* marker, thus certifying the cross in that particular combination.

Cross 3 was originally made in 1932 between two greenhouse plants, yellow biennial plantain venation *rbpl* × red annual pinnate venation *RBPl*. The parental plants were self-sterile. The F_1 plants proved to be annual, and all the F_1 plants backcrossed to the double recessive were found to be heterozygous for *R* and *B*. Figure 5 shows the annual parent that entered into cross 3 and a representative plant from the biennial parental strain. The plantain leaf venation of the biennial strain is evident.

Table 6 gives a summary of data from seven backcross progenies. Seed was obtained by the bagging method. The results clearly indicate linkage in the coupling phase between *R* and *B*. Out of a total of 690 plants observed, 110, or 15.94 percent, were of the recombination classes *Rb* and *rB*. This direct value is practically equal to the 16.1±0.95 percent crossing over as calculated by Owen's (*12*) product-moment method. The cross-over value calculated from the total of cross 2 was 20.0±1.60 percent, the individual values ranging from 18.0 to 25.8 percent. In comparison, the cross-over value of 13.0±1.13 percent from cross 3 was considerably lower.

The total number of annuals and biennials, 342 and 348, respectively, is in very close agreement with the expected 1 : 1 ratio, showing a deviation of only ± 3. This comparison is made in table 7.

The total numbers of observed red and yellow hypocotyl types deviate from the calculated by only ±5. There is therefore no disturbance in the ratios which may be attributed to selfing of either parent in the backcrosses. In the backcross *rb* as female there is no excess of yellow types, and in the *RBrb* female there is no indication of an excess of red-hypocotyl plants. Figure 6 shows annual and

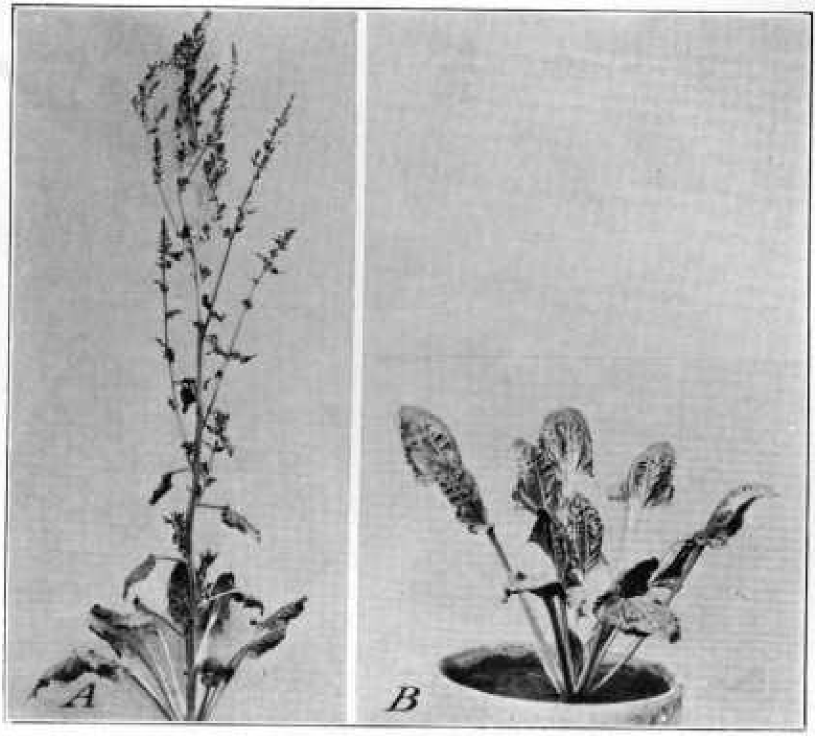

FIGURE 5.—Parental types used for cross 3 differ in three factors: (*A*) Red annual pinnate veins (*RBPl*) × (*B*) yellow biennial plantain veins (*rbpl*).

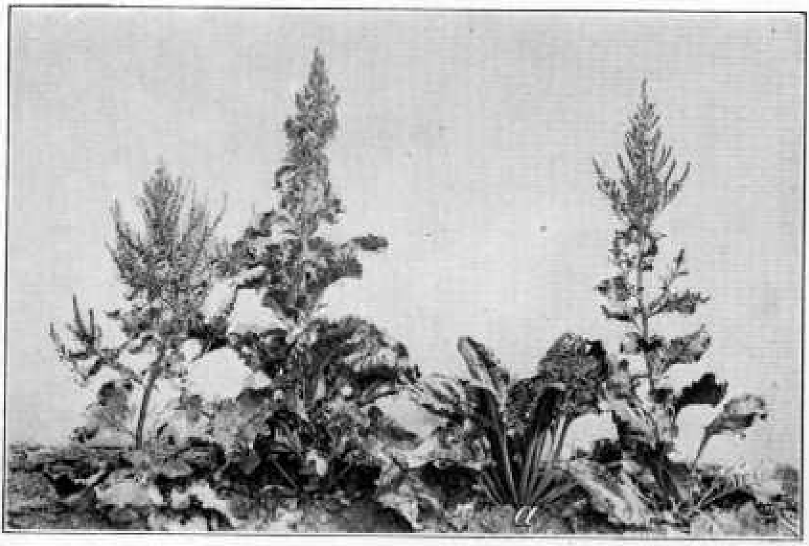

FIGURE 6.—Annual and vegetative segregates in backcross progeny 2311 (*rb*×*RBrb*). The vegetative plant (*a*) shows the plantain venation character. Photographed July 5, 1933.

vegetative segregates from backcross progeny no. 2311 (*rb* × *RBrb*). The vegetative plant happens to be of the plantain venation type, while the three bolters are normal in venation.

TABLE 6.—*Linkage in coupling phase between factors R (hypocotyl color) and B (annual habit) in backcross progenies of the type red annual F_1 (RBrb) × yellow biennial rb and reciprocal and in F_2 progenies of red annual F_1 plants of the type RBrb crossed inter se*

BACKCROSS PROGENIES

Cross no.	Type of mating	Current no.	Red hypocotyl: Annual plants	Red hypocotyl: Biennial plants	Yellow hypocotyl: Annual plants	Yellow hypocotyl: Biennial plants	Total plants	Cross-over value [1]
			Number	*Number*	*Number*	*Number*	*Number*	*Percent*
2	*rb*×*RBrb*	3498	58	14	13	58	143	
	do	3499	22	8	9	27	66	
	RBrb×*rb*	3530	30	3	11	34	78	
	Total		110	25	33	119	287	20.0±1.60
3	*RBrb*×*rb*	3492	111	17	14	117	259	
	rb×*RBrb*	2311, 2312, 2314	65	12	9	58	144	
	Total		176	29	23	175	403	13.0±1.13
2 and 3	Total		286	54	56	294	690	16.1± .95

F_2 PROGENIES

Cross no.	Type of mating	Current no.	Red hypocotyl: Annual plants	Red hypocotyl: Biennial plants	Yellow hypocotyl: Annual plants	Yellow hypocotyl: Biennial plants	Total plants	Cross-over value [1]
2	*RBrb*×*RBrb*	3432	549	72	62	163	846	16.66± .96
		3535	99	8	8	30	145	11.50±1.92
		3536	206	17	6	34	263	9.61±1.30
	Total		854	97	76	227	1,254	14.81± .74
3	do	3427	177	17	19	31	244	17.89±1.86
		2383, 2385, 2386	64	6	8	18	96	15.41±2.74
	Total		241	23	27	49	340	17.18±1.54
2 and 3	Total		1,095	120	103	276	1,594	15.29± .67

[1] The cross-over value for the backcrosses calculated according to Owen's (*12*) product-moment correlation. The cross-over value for the F_2 progenies and the probable errors for both backcross and F_2 distributions calculated from Immer's (*7*) tables.

F_2 DATA

Table 6 gives also a summary of the F_2 linkage data between *R* and *B* derived from crosses 2 and 3. Progenies 3432 and 3427 were obtained from field isolations of three and six F_1 stecklings, respectively. Both were grown in plots distant enough from other lots to preclude contamination. The remaining F_2 progenies were obtained from F_1 plants crossed inter se by the ordinary exchange of bags.

The cross-over values, as calculated by Immer's (*7*) tables, ranged from 9.61 to 17.89 percent. Out of a total of 1,594 F_2 plants, 223 were recombinations, giving a cross-over value of 15.29±0.67 percent. Eleven hundred and ninety-eight plants were annual in habit, and 396 remained vegetative. This is in very close agreement with the expected 3 annual to 1 biennial ratio. Table 7 shows an F_2 summary of the simple 3 : 1 ratios, including also data from cross 1 (12c21 biennial × annual clone 62). The close agreement is apparent.

TABLE 7.—*Summary of segregation of annual and biennial habit from backcross and F_2 progenies, respectively*

Progenies	Annual plants	Biennial plants	Total plants
Backcrosses:	*Number*	*Number*	*Number*
Total observed	342	348	690
Calculated, 1 : 1 ratio	345	345	690
Deviation	−3	+3	0
F_2 progenies:			
Total observed	1,667	553	2,220
Calculated, 3 : 1 ratio	1,665	555	2,220
Deviation	+2	−2	0

Progeny 3427 (table 6) was also grown in the field in 1934. A total of 635 F_2 plants were classified for color and annual habit. The distribution for bolting is shown in table 8.

The excess of 47 vegetatives, which was evident in both *R* and *r* color classes, varies significantly from expectation. The failure to bolt probably lies in the fact that these plants were exposed to an early infection of curly top. The parental strains that were combined in cross 3427 were known to be highly susceptible to this destructive virus disease. Under greenhouse conditions, excluding curly top infection, the same F_2 progeny gave a normal 3 : 1 distribution for growth habit. Under both conditions, the linkage between *R* and *B* is apparent. The cross-over value of the field-grown lot under discussion was 19.66 ± 1.21 percent, as compared with 17.89 ± 1.86 percent for the greenhouse material.

F_3 TEST OF VEGETATIVE F_2 PLANTS

In the 1933 greenhouse test, 20 plants were classified as vegetative segregates in an F_2 distribution of cross 2 (annual × 042). Fifteen of these vegetative segregates, six red and nine yellow in hypocotyl color, were backcrossed further with the 042 *rb* biennial parent strain. An average number of 52 plants per progeny was grown. Out of a total of 777 plants, only 6 bolters were found in 2 progenies. These bolters were of a decidedly slow type as compared with the annual check lot, most of which were in bloom on January 12, 1935. One of the six red F_2 plants proved to be homozygous for color (*R*). All of the whites bred true for color in F_3. The number of F_2 reds was too small to test the *R–B* linkage.

TABLE 8.—*Segregation of annual and biennial habit in F_2 progeny 3427* [1] *grown in the field in 1934*

Analysis of progeny 3427	Annual plants	Biennial plants	Total plants
	Number	*Number*	*Number*
Total observed	429	206	635
Calculated, 3 : 1 ratio	476	159	635
Deviation	−47	+47	0

[1] See table 6 for greenhouse data.

This F_3 test, with an admittedly small number of progenies, has essentially verified the classification of the F_2 plants in cross 2 as vegetatives. New crosses between annual and biennial types are available now into which a strong self-fertility factor has been introduced. This will greatly reduce the labor of securing an adequate number of F_3 progenies and should give a critical test of the *R–B* linkage.

DISCUSSION

Interest in bolting has recently been accentuated by earlier commercial planting. West of the Rocky Mountains early sowing is practiced as a means of increasing yields and especially for reducing losses from the curly-top disease. However, in early plantings beets may be exposed to conditions that tend to a marked increase in annual beets. It has been pointed out that bolting is a serious problem in California, where the occurrence of a high percentage of annuals may reduce yields. Bolters are also objectionable to the grower because their presence gives a poor appearance to beet fields. Other tangible objections are encountered in the factory process, since these annual beets, with their woody roots and high fiber or marc content, are difficult to slice. Frequently the presence of a high percentage of bolters results in a pulp of such woody quality that it is unsuitable for stock feed.

The bolting character is so highly sensitive to environmental factors that empirical and superficial selection may often be misleading. Such factors as temperature and light may induce a vegetative condition in beets that inherently possess strong bolting tendencies. For efficiency in commercial breeding operations it is important to recognize genetic factors such as that responsible for the annual habit. Up to the present time the breeding behavior of only a few beet characters has been demonstrated, but, with the great variability existing in sugar beets, genetic investigations should reveal new factors. The presence of a small number of chromosomes in sugar beets, reported by Kuzmina (*9*) to be nine bivalents, favors the charting of new factors.

The following brief summary of the results presented in this paper shows that the annual habit is dominant over the biennial type and that it is controlled by a single Mendelian factor. A total of 690 backcross plants ($Bb \times b$ and reciprocal) gave 342 annuals and 348 biennnials. A total of 2,220 F_2 plants, from matings of the type *Bb* inter se, showed 1,667 plants in the annual class and 553 biennials. Both the observed backcross and F_2 distributions are in very close agreement with the expected 1 : 1 and 3 : 1 ratios, respectively. The check plantings of annual and biennial parental strains grown under the same conditions as the backcross and F_2 progenies bred true for their respective habits. The results obtained on the inheritance of annual habit verify the conclusion reached by Munerati (*10*) that the annual tendency is controlled by a simple Mendelian factor.

It has been demonstrated that the F_1 plants and annual segregates from F_2 progenies are slower in rate of development of seedstalks than the annual parental strain. This apparently incomplete dominance of the annual habit, also noted earlier by Munerati (*10*), does not seem to be highly correlated with a heterozygous *Bb* constitution.

The hypothesis that modifying factors exert a partial inhibitory effect should be considered in any explanation of the slower rate of seedstalk development of F_1 and F_2 plants.

Keller (*8*) has established the first linkage group in beets. The cross-over value between the hypocotyl-color factor *R* and the basic-pigment factor *Y* was found to be approximately 7.5 percent. The present study has added the annual habit factor *B* to this first linkage group.

The data for the *R* and *B* linkage has been secured from two reciprocal crosses, 042×Munerati's annual, and plantain strain ×annual. Both of these crosses were of the coupling type *rb*×*RB*.

The summarized backcross data from both crosses (table 6) gave a distribution of 286 *RB*, 54 *Rb*, 56*rB*, and 294 *rb*, and a total of 690 plants. This is obviously in very poor agreement with the expectation on a basis of independent assortment of *R* and *B*. The cross-over value from the backcross data proved to be 16.1 ± 0.95 percent. The F_2 results, from a total of 1,594 plants, likewise indicate the *R–B* linkage, showing a cross-over value of 15.29 ± 0.67. Extreme cross-over values were found to be 9.61 ± 1.30 and 20.0 ± 1.60 percent. The approximate average cross-over value from all data is 15.5 percent.

In cross 3 (plantain strain × annual) the new factor *Pl*, with which the writer has worked extensively, was introduced. The *Plpl* factor pair determines dominant pinnate foliage venation versus a semiparallel venation resembling that found in ribbed leaves of the common plantain. *R* and *Pl* are inherited independently. Backcross data have indicated that *B* and *Pl* are also inherited independently. The agreement with the calculated 1 : 1 : 1 : 1 ratio was very close. F_2 data likewise support the independent relationship of *B* and *Pl*.

It is highly probable that the annual factor that the writer has described also operates to produce bolting in many cultivated sugar-beet varieties. The biennial plantain strain used in the present study was derived from commercial stock. The 12c21 and 042 selections with which the writer has worked are relatively biennial in habit and appear to be, so far as the bolting character is concerned, representative of similar types commonly present in sugar-beet stock derived from commercial varieties. The annual strain, as indicated earlier, is probably related to similar annual types which Munerati (*10*) has established from commonly cultivated varieties of sugar beets. It is of interest in this connection that, aside from the above-mentioned types, even more divergent forms such as table beets, mangels, and the wild beet (*Beta maritima* L.) intercross readily with sugar beets and appear to be closely related. If the possibility that these related forms have common ancestors is admitted, it follows that homologous genetic factors may exist which produce strikingly parallel variation. In more specific terms, wild beets, table beets, and sugar beets may carry a homologous bolting-factor pair such as *Bb*. The *R* and *B* linkage discussed in this paper offers one means of testing the hypothesis of an isomorphic bolting factor.

The divergent biennial strains that the writer has crossed with the annual type have given essentially identical genetic results as far as inheritance of annual habit and the *R* linkage is concerned. The apparent correspondence of the bolting character of the biennials used in this study with those commonly present in cultivated sugar-beet

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varieties gives ground for the belief that the genetic results of the present investigation may apply directly to the bolting character present in commercial sugar-beet varieties.

SUMMARY

Annual versus biennial habit (*Bb*) in *Beta vulgaris* is explained on a simple Mendelian basis. The observed numbers of annual and biennial beets in backcross and F_2 distributions were found to agree closely with the expected 1 : 1 and 3 : 1 ratios, respectively. The single-factor basis for the annual character in beets confirms Munerati's results.

Annual habit is dominant. Annuals in both F_1 and F_2 progenies were slower in average seedstalk development than the plants from the annual parental strain. This indicated that dominance, although shifting strongly toward the annual side, may not be complete. The difference between *BB* and *Bb* plants in rate of seedstalk development does not appear to be very great. Other factors may exist which partly inhibit seedstalk growth of F_1 and F_2 annuals, while not suppressing the initiation of the reproductive phase.

The *B* factor assorts independently with *Pl*, the factor connected with the plantain leaf venation character. A definite linkage of *B* was noted with the common hypocotyl-crown color factor *R*. The cross-over value from all data approximates 15.5 percent. This places the factor *B* in the *R–Y* linkage group determined by Keller (*8*).

The biennials used in this study apparently correspond in their bolting character with similar types commonly present in cultivated sugar-beet varieties. It is therefore probable that the genetic results of the present investigation may find direct application to the bolting character present in commercial sugar-beet varieties.

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