INHERITANCE OF STEM-BRANCHING IN *PISUM*

Thesis for the Degree of M. S.

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Robert Louis Andersen

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ABSTRACT

INHERITANCE OF

STEM-BRANCHING IN *PISUM*

by Robert Louis Andersen

In the process of developing a winter hardy culinary pea for Michigan it has been determined that the habit of plant growth necessary to accomplish over wintering is a rosette of spreading branches with short internodes, lying prostrate on the ground.

Jade and Early Perfection, which are early, upright, green seeded, culinary types, and Austrian Winter, which is a winter hardy field pea, were used as parents in an experiment designed to study the inheritance of stem-branching.

The data suggest that the character is conditioned by two factor pairs which act in an additive, independent manner. They are designated $\underline{Ti_1ti_1Ti_2ti_2}$.

INHERITANCE OF

STEM-BRANCHING IN *PISUM*

By

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DEDICATION

To my family, who have endured.

TABLE OF CONTENTS

INTRODUCTION

The garden pea is one of the earliest of all annual vegetable crops in the northern temperate regions. However, if earlier types of any crop can be developed there are often cultural, processing, and marketing advantages to be enjoyed. Several Russian, English, and American plant scientists are presently engaged in projects and associated experiments to obtain earlier culinary peas by developing strains that have the ability to initiate growth in the autumn, over winter, and then in the spring resume growth utilizing the living root system and crown that remains (5, 7, 9). The workers in all three countries have been successful in developing types which will over winter. Holland and Frost (6) have also demonstrated a maturity date and quality advantage with their material in England.

It was first noted by Khirchinski (7) in Russia and later by Markarian and Andersen (9) in the United States that the habit of plant growth in the autumn that is necessary to accomplish over wintering in the more severe winters of these areas is a rosette of spreading branches with short internodes lying prostrate on the ground, as contrasted to the upright, standing habit of growth exhibited by spring planted types (fig. 1). Markarian and Andersen (9) have made a cross between _Pisum sativum_, var. Early Perfection, which is a cultivated garden pea that has an upright and usually single stemmed habit of growth, and _Pisum sativum_, sub. _arvense_, var., Austrian Winter which is a winter hardy field pea. The latter has

FIGURE I

A. Jade (P_1) after 80 days.
Note that apical dominance
is evident but two secondary
branches are present.
Also note flower.

B. F_1 (P_1 x P_2) after 80 days.
Note the robust stems but
the lack of apical domin-
ance.

C. AW 62-14 (P_2) after 80 days.
Note habit of growth is
prostrate, multi-stemmed,
small leaved, and short
interned. Again apical
dominance is lacking.

the prostrate habit of growth when fall planted. In subsequent generations both parental types evolved, as well as, a range of intermediate types (Fig. II). This lead to the obvious conclusion that branching and the other associated morphological characters of prostrate growth, small leaves, and short internodes are heritable characters and probably correlated to hardiness.

That different varieties of spring seeded peas can show differences in their ability to branch out is a comparatively well known fact amongst pea breeders. The only work that has been reported on the inheritance of branching in *Pisum* was done by Lamprecht (8) in which he reported the character is controlled by polymeric genes which he designated *fr* and *fru*. Since different lines, which presumably had the same genetic composition at the two branching loci, showed variation in their ability to branch he concluded that the environment and the remainder of the genetic constitution of any one line may cause it to differ in degree of stem-branching from other lines which are identical to it at the branching loci. The gene *fru* resulted from x-radiation.

FIGURE II

A. F_2 Segregate after 80 days which approaches P_1 in upright habit of growth.

B. F_2 Segregate after 80 days which approaches F_1 in habit of growth.

C. F_2 Segregate after 80 days which approaches P_2 in habit of growth.

OBJECTIVE

The objective of this experiment was to attempt to determine the mode of inheritance of stem-branching as expressed subsequent to fall planting in the winter hardy material developed by Markarian and Andersen.

MATERIALS

In 1960 a hybridization program was started at the Michigan Agricultural Experiment Station to determine if winter hardiness of the Austrian Winter variety of field pea could be incorporated into the culinary pea variety Early Perfection.

F_3 bulked seed (20,000) were planted September 1, 1961. All of the plants which subsequently over wintered were multi-stemmed. Fifteen single plant selections were made in June of 1962 and the F_4 seed of these plants was retained along with over 200,000 bulked F_4 seed from other unselected plants that over wintered. It was felt that some of the plant and seed types had sufficiently good commercial qualities to warrant continuation of the program.

One of the fifteen F_3 plants that was selected (designated AW 62-14) had five stem-branches, each of which bore twelve or more pods. AW 62-14 (P_2) was chosen as the multi-stemmed parent for this study. Jade (P_1), which is an early, large, green seeded, freezing type, was chosen as the other parent because it had shown no winter hardiness and no tendency to develop stem-branches in the fall planting made in 1961.

F_4 plants of AW 62-14 were first allowed to self pollinate naturally in the greenhouse to obtain F_5 seed. The percentage of homozygosity in the F_5 of a self pollinated crop like peas is 95 per cent when the number of indepently inherited gene pairs is one. (Allard, p. 55). Therefore, it was decided that the seed produced by the F_4 plants would be screened for commercial type and that five lines should be selected as the multi-stemmed parents

for this study since it could not be certain that the genes conditioning branching were in a homozygous condition.

METHODS

The study included the parental lines, the F_1, F_2, and the first backcross generation to each parent. All hybridizations, to obtain F_1 and backcross populations, were accomplished in the greenhouse during the winter of 1963-1964. Hybridizations were made without bagging the flowers. However, since the stigmas were exposed during emasculation, the greenhouses that were used were fumigated on a weekly basis to prevent an infestation of greenhouse insects. Some flowers of the parental plants were allowed to self pollinate naturally, as were some on F_1 plants which were grown for the purpose of producing F_2 and backcross hybrid seeds.

The seed was planted at the Michigan State University Horticulture Farm on September 7, 1964, in an extremely level and uniform plot that had been fallowed during the summer of 1964. A spacing of four inches between seeds was used to allow easy observation of the stem-branching habit. The only weed control measure was to carefully hoe a small patch of Convolvulus arvensis that appeared after about two weeks. Approximately one inch of irrigation was applied by sprinkler system on the day after planting. Subsequently, frequent light rains kept a plentiful moisture supply present. Counts to determine the number of stem-branches per plant were taken on October 20 through 25, 1964, when plants were of the approximate size shown in Figure I and II. All visible branches over approximately one half inch long were counted. These data are shown in Table I. Ultimately only

Table 1. Frequency Distribution of Stem-Branches Per Plant for Different Generations of Pea Plants

Generation	No. of Plants	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	$\bar{X}$	
Jade (P_1)	147	28	60	59	—	—	—	—	—	—	2.18	0.74
AW 62-14 (P_2)	141	—	—	1	4	34	84	18	—	—	5.81	0.71
F_1 (P_1 x P_2)	78	—	—	1	7	34	31	5	—	—	5.41	0.80
F_1 (P_2 x P_1)	106	—	—	8	33	43	20	2	—	—	4.76	0.93
F_2 (P_1 x P_2)	277	1	23	76	92	57	21	6	1	—	3.99	1.19
F_2 (P_2 x P_1)	194	—	9	44	50	55	25	8	3	—	4.41	1.29
F_2 (Pooled)	471	1	32	120	142	112	46	14	4	—	4.10	1.41
BC to P_1 P_1 x (P_1 x P_2)	112	7	29	47	24	5	—	—	—	—	2.92	0.95
BC to P_2 P_2 x (P_1 x P_2)	102	—	—	6	20	49	26	1	—	—	4.98	0.73

1 1.5, 2.5, 3.5, etc. are upper class limits.

2 0.5 - 1.5 = no branch on stem, 1.5 - 2.5 = one stem-branch a. s. o.

Line Two was chosen for analysis because it showed the least total variance and was therefore thought to be derived from the most homozygous F_5 line of the five that were chosen originally.

The experimental design used for this material is adequate to illustrate the method of analysis and give a preliminary suggestion of the number of genes conditioning the branching character, but a more extensive genetic design is desirable as a basis for final genetic conclusions. Adequate design would include randomization, replication, a more highly inbred P_2, and reciprocal backcrosses.

The data used in the computations involve the actual number of stem-branches observed for each plant in the parent, F_1, F_2, and backcross generations grown in the same year (September through November 1964). The estimate of genetic differences in this cross was based on a comparison of the observed and hypothetical means and a chi square test of "goodness of fit" of the observed frequency distributions of the segregating populations to theoretical frequency distributions calculated using the hypothetical means and an estimate of the environmental variance.

THEORETICAL GENETIC HYPOTHESIS

It is now necessary to develop a genetic hypothesis against which the obtained frequency distribution may be tested.

Frequency distributions expressed in percentages

First, the observed frequency distributions are converted to percentages. For example, the Jade parent has 28 plants in the one branch class. The percentage is then computed: $\frac{28}{147} \times 100 = 19.04$

Table 2. Frequency distributions of obtained data of parent, backcross populations of a Jade x AW 62-14 cross expressed as percentages.[1]

Population	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	Total Plants
	Frequency Distribution in Percentages Upper Limit of Class								
Jade (P_1)	19.04	40.82	40.14	—	—	—	—	—	147
AW 62-14 (P_2)	—	—	0.71	2.84	24.11	59.57	12.77	—	141
F_2 (P_1 x P_2)	0.36	8.30	24.73	33.21	20.58	7.58	2.17	0.36	277
F_2 (P_2 x P_1)	—	4.64	22.68	25.77	28.35	12.89	4.18	1.55	194
F_2 (Pooled)	0.02	4.67	25.47	30.15	23.78	9.77	2.97	0.85	471
BC to P_1	6.25	25.89	41.96	21.43	4.46	—	—	—	112
BC to P_2	—	—	5.88	19.61	48.04	25.49	0.98	—	102

[1] Brackets indicate classes grouped in formulation of theoretical genetic hypothesis.

per cent, and so on, in a similar manner, for the other percentage values. These data are complied in Table II.

Examination of the F_2 frequency distribution expressed in percentages indicates a single mode that falls between the modes of the parental generations. The simplest genetic hypothesis which could be based on this fact would be that a single factor pair expressing no dominance is causing this situation. One reciprocal F_2 generation (P_2 x P_1) would appear to approximate a 25%:50%:25% proportion if the 3 and under classes are added to obtain 27.32 per cent, the 4 and 5 classes are similarly grouped to obtain 54.12 per cent, and the 6 and above classes are grouped to give 18.62 per cent. Calculations accomplished in a similar manner on the reciprocal F_2 (P_1 x P_2) are inconsistant with this hypothesis, however. Inspection of the backcross generations reveals that a single factor hypothesis would appear to also be invalid in these segregating populations because it is impossible to derive a 1:1 ratio from them.

This indicates at least two factor pairs condition the branching character in the F_2. Since the frequency distribution of the F_2 generations have been shown to have intermediate modes between those of the two parents, the simplest two factor hypothesis that would be consistant with this fact would be that of additivity because the F_2 mode (and mean) of a character conditioned by 2 additive factor pairs should fall intermediate to those of the parents.

The percentages of the total frequency distribution theoretically should form five classes in the F_2, viz., 6.25 per cent _aabb_, 25.00 per cent _aaBb_, _Aabb_, 37.50 per cent _AaBb_, _AAbb_, _aaBB_, 25.00 per cent _AABb_, _AaBB_, and 6.25 per cent _AABB_ (Table III). Grouping by adding

Table 3. Complete genetic hypothesis expressed as percentages and ratios; including hypothetical means for F_2 and backcross populations.

Genotype Groups	Proportion of F_2 Population Percent	Ratio	$\bar{X}$
1) aabb	6.25	1	2.180
2) aaBb, Aabb	25.00	4	3.090
3) AaBb, AAbb, aaBB	37.50	6	3.995
4) AABb, AaBB	25.00	4	4.900
5) AABB	6.25	1	5.810
	Proportion of Backcross Population to Jade		
6) aabb	25.00	1	2.180
7) Aabb, aaBb	50.00	2	3.090
8) AaBb	25.00	1	3.995
	Proportion of Backcross Population to AW62-14		
9) AaBb	25.00	1	3.995
10) AABb, AaBB	50.00	2	4.900
11) AABB	25.00	1	5.810

observed percentages in the F_2 (P_1 x P_2) as follows: classes one and two combined total 8.66 per cent, class three 24.73 per cent, class four 33.21 per cent, class five 20.58 per cent and class six and above combined total 10.11 per cent; it can readily be seen that an additive scheme is approximated. The same grouping in the reciprocal F_2 (P_2 x P_1) shows inconsistancy with this hypothesis. However, similar grouping of the pooled F_2 again yields an approximation of the 1:4:6:4:1 ratio. Again, as in the case of the one gene hypothesis, examination of the back-cross data should yield support of this hypothesis if any is available. A 25%:50%:25% proportion is expected in backcross generations in an additive 2 factor scheme. If the observed percentages of the frequency distribution of the backcross to F_1 are grouped and added it yields: classes one and two 32.14 per cent, class three 41.96 per cent, and classes four and five 25.89 per cent. Grouping and adding the back-cross to AW 62-14 it yields: classes three and four 25.49 per cent, class five 48.04 per cent, and classes six and seven conbined total 26.47 per cent. The fact that three segregating populations out of four seem to support the hypothesis of branching being conditioned by 2 factor pairs, plus the fact that pooling the data from the F_2 reciprocals also yields an approximation of the expected ratio constitutes the basis for examining this possibility further.

METHOD OF ANALYSIS

Before this genetic hypothesis can be tested, one must compute the means for the genotype groups (Table III). The designation of Jade as <u>aabb</u> and of AW 62-14 as <u>AABB</u> is done solely as an expedient

to facilitate clarity and ease of discussion. The plus (capital letter) values are assigned to AW 62-14 because it can be noted that partial dominance is expressed by the means of the F_1 and F_2 populations in the direction of this, the multi-stemmed, parent. Further discussion of this fact will follow in the Discussion.

Assuming additivity, the mean of the heterozygous F_1 genotype and both of the other genotypes with exactly two plus alleles is calculated by taking the average of the two parental means. This gives the mid point, or in this case, the hypothetical mean of Genotype Group 3. In a similar manner, the hypothetical means of Genotype Groups 2 and 4 are calculated respectively as follows: $\frac{2.18 + 3.995}{2} = 3.09$ and $\frac{3.995 + 5.810}{2} = 4.900$.

"t" tests are then performed to determine if these hypothetical means correspond to those of the observed segregating F_2 and backcross generations. The data from these tests can be found in Table IV. The "t" tests for the F_2 ($P_1 \times P_2$) and the pooled F_2 show there is no significant differences between the observed means of 3.99 and 4.10, respectively, when they are compared with the calculated mean of 3.995 at the 5 per cent level of signifigance. The F_2 ($P_2 \times P_1$) shows significant difference between the observed mean of 4.41 and the calculated mean 3.995. The "t" tests for the backcrosses to P_1 and P_2 show there is no significant difference between the observed means of 2.92 and 4.98 when they are compared with their respective hypothetical means of 3.09 and 4.90.

The final analysis of interest that can be completed using these data is to estimate the number of gene pairs acting. This is accomplished

Table 4. "t" test comparing observed and hypothetical means for segregating populations[1].

Population	Obs. $\bar{X}$	Hyp. μ	Obs. S^2	Hyp.[2] σ^2	t	$t_{.025}$
F_2 ($P_1 \times P_2$)	3.990	3.995	1.416	1.117	0.05	± 1.960
F_2 ($P_2 \times P_1$)	4.410	3.995	1.660	1.117	3.45*	± 1.960
F_2 (Pooled)	4.100	3.995	2.000	1.117	1.31	± 1.960
BC to P_1	2.920	3.090	0.903	0.935	1.30	± 1.980
BC to P_2	4.980	4.900	0.533	0.935	0.66	± 1.980

* Signifigant at the 5 percent level

1. $t = \dfrac{\bar{X} - \bar{X}_2}{sp\sqrt{\frac{1}{N_1}+\frac{1}{N_2}}}$ where sp^2 is the pooled estimate of the ^{2} given by $sp^2 = \dfrac{(N_1-1)\ S_1^{\ 2}+(N_2-1)\ S_2^{\ 2}}{N_1+N_2-2}$

and the degrees of freedom $= N_1 + N_2 - 2$
taken from Dixon and Massey (2)

2. $\sigma_G^{\ 2} = \dfrac{\sum f\ (\text{midrange} - \text{class center})^2}{N}$

3. $\sigma_E^{\ 2} = \dfrac{\sigma_G^{\ 2} - \sigma_G^{\ 2}\ H}{H}$

$\sigma^2 = \sigma_G^{\ 2} + \sigma_E^{\ 2}$

These formulas are taken from Allard (1) and were used to calculate the hypothetical variance.

by determining if the observed frequency distributions of the segregating populations will fit an estimated theoretical frequency distribution constructed by applying the observed environmental variance 0.525 to the hypothetical means of the various genotypes. This is the best available estimate of the environmental variance expected for each genotype (10). The theoretical values are calculated by the method suggested by Powers, et.al. (11). Table V contains an example of this method.

Calculations were accomplished in the manner described below. The upper class limit is subtracted from the mean of the particular genotype being considered. This difference is then divided by the standard deviation ($\sqrt{0.525}$). The quotient is the value t which is used to enter the Table of Areas, Ordinates, and Derivatives of the Normal Curve of Error (4). The values of the area under the curve from the ordinate at t = 0 to the ordinate for the values of t can thus be read in the area column.

Calculation of t values and deriving of the area located under the particular class interval for the aabb genotype of the F_2 (Pooled) data would be as follows: the upper class limit of the first class is 1.5. It is subtracted from 2.18, the genotypes' hypothetical mean, 2.18 - 1.50 = 0.68. Dividing 0.68 by 0.725 yields the value t. Reading from the table of areas we find the corresponding area to be 0.3264. This value must be subtracted from 0.5000 to arrive at the area under the curve to the left of 1.5, which is the ordinate of interest. In this case the area under the 1.5 class is thus calculated to be

Table 5. Example of calculation of number of gene pairs conditioning branching of peas in F_2 (Pooled) population.

Genotype	S_E^2	S_E	$\bar{X}$	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	%	N
aabb	.525	.725	2.18	17.36	49.64	29.36	3.37	0.07	--	--	--	--	100	
2 aaBb	.525	.725	3.09	2.86	38.94	101.34	51.62	5.16	0.08	--	--	--	200	
aaBB	.525	.725	3.99	0.03	1.94	22.85	50.98	22.32	1.85	0.03	--	--	100	
2 Aabb	.525	.725	3.99	2.86	38.94	101.34	51.62	5.16	0.08	--	--	--	200	
4 AaBb	.525	.725	3.99	0.12	7.76	91.40	203.92	89.28	7.40	0.12	--	--	400	
2 AABb	.525	.725	4.90	--	0.10	5.26	52.88	101.10	37.96	2.66	0.04	--	200	
AAbb	.525	.725	3.99	0.03	1.94	22.85	50.98	22.32	1.85	0.03	--	--	100	
2 AaBB	.525	.725	4.90	--	0.10	5.26	52.88	101.10	37.96	2.66	0.04	--	200	
AABB	.525	.725	5.81	--	--	0.07	3.44	29.85	49.53	16.12	0.98	0.01	100	
Total				23.26	139.36	379.93	521.69	376.69	136.71	21.62	1.06	0.01	1600	
T/16				1.45	8.71	23.75	32.61	23.52	8.54	1.35	0.07	0.0007	100	
Calc.				6.83	41.02	111.86	153.59	110.78	40.22	6.36	0.33	0.003		471
Combined Calc.				47.85		111.86	153.59	110.78		46.91				471
Obs.				1	32	110	142	112	46	14	4			471
Comb Obs.				33		110	142	112		64				471
df.				14.85		1.86	11.59	1.22		17.09				
d^2				220.52		3.46	134.32	1.49		292.07				
d^2/Calc.				4.61		0.03	0.87	0.01		6.23*				

* $X^2 = 6.23$ P = 0.05 - 0.01

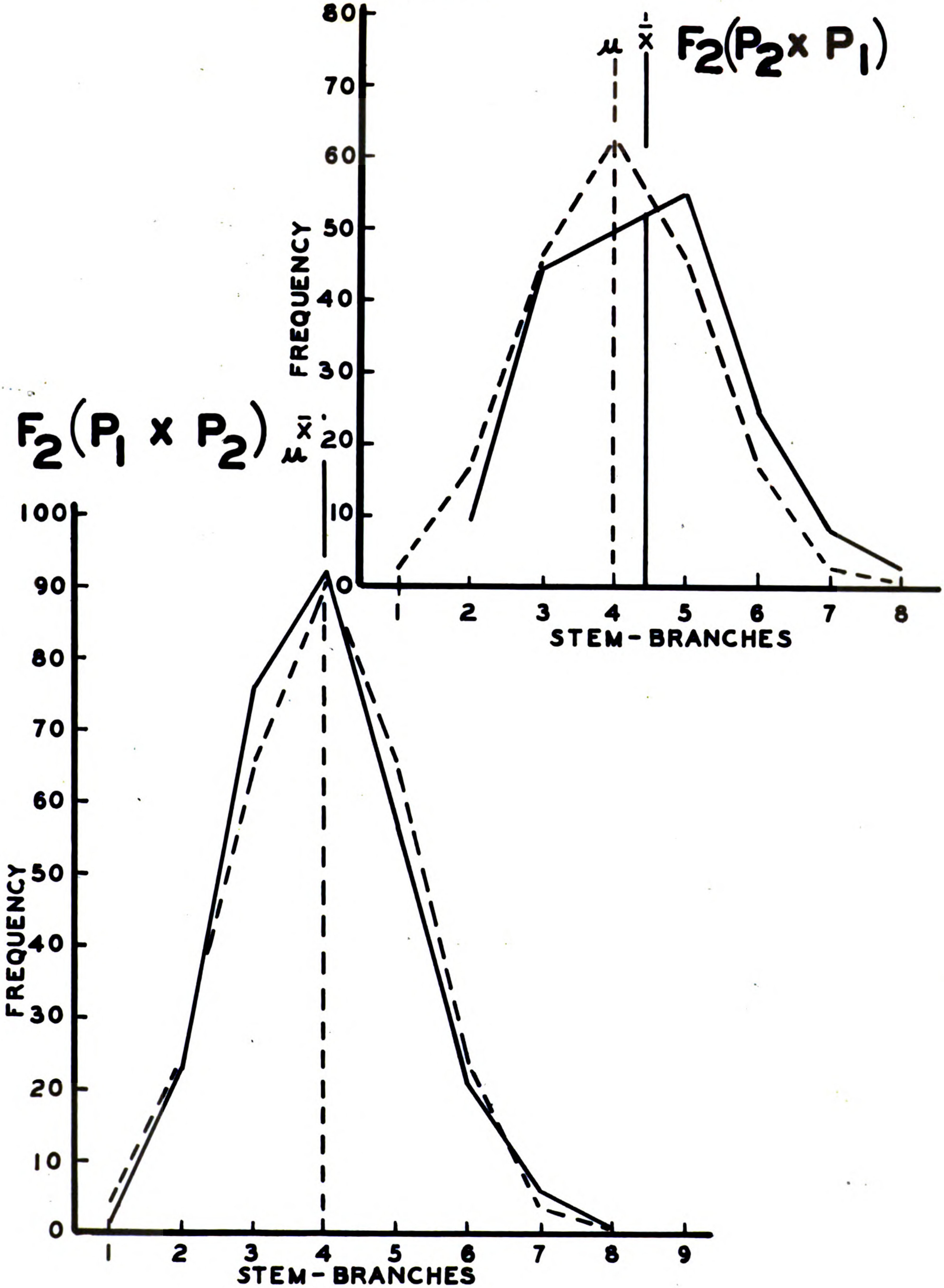
0.5000 - 0.3464 = 0.1736. The next upper class limit is similarly subtracted and the difference again divided by the standard deviation, $\frac{2.5 - 2.18}{0.725} = \frac{0.32}{0.725} = 0.44$. The area corresponding to 0.44 as obtained from the table is 0.1700. In this case the area 0.1700 is added to the area 0.3264 which was obtained previously. This is necessary because 0.1700 represents the area from the ordinate at $\underline{t} = 0$ to the ordinate value 2.5, and similarly 0.3464 represents the area from the ordinate at $\underline{t} = 0$ to the ordinate value 1.5. The difference between the next upper class limit and the mean is 3.5 - 2.18 = 1.32. When it is divided by the standard deviation of 0.725 the resulting $\underline{t}$ value is 1.82. The area 0.4656 corresponding to 1.82 is again obtained from the table. In this case it is necessary to find the difference between this value and the area value 0.1700 which was previously determined because 0.4656 represents the total area from the ordinate $\underline{t} = 0$ to the ordinate 3.5 and it is only desired to know the area between the ordinates 2.5 and 3.5. This is repeated for the remaining upper class limits until a value of zero is obtained for the area under a subsequent class. This step by step process is accomplished for each genotype. The total area under each class interval is then obtained and converted to per cent. The theoretical number of individuals that should lie within this class interval is then obtained by multiplying the percentage of individuals lying within a class interval times N. Similar calculations are accomplished for the F_2 (P_1 x P_2), F_2 (P_2 x P_1), BC to P_1, and BC to P_2. Figure III and Figure IV show the comparison of these theoretical frequency distributions to the observed frequency distributions.

FIGURE III

Upper Graph shows the observed frequency distribution of the F_2 (P_2 x P_1) population in solid line as compared to the theoretical computed frequency distribution in intermittent line. A "poor fit" is obtained when these 2 distributions are compared by chi square test.

Lower Graph shows the observed frequency distribtuion of the F_2 (P_1 x P_2) population in solid line as compared to the theoretical computed frequency distribution in intermittent line. A "good fit" is obtained when these 2 distributions are compared by chi square test.

FIGURE III



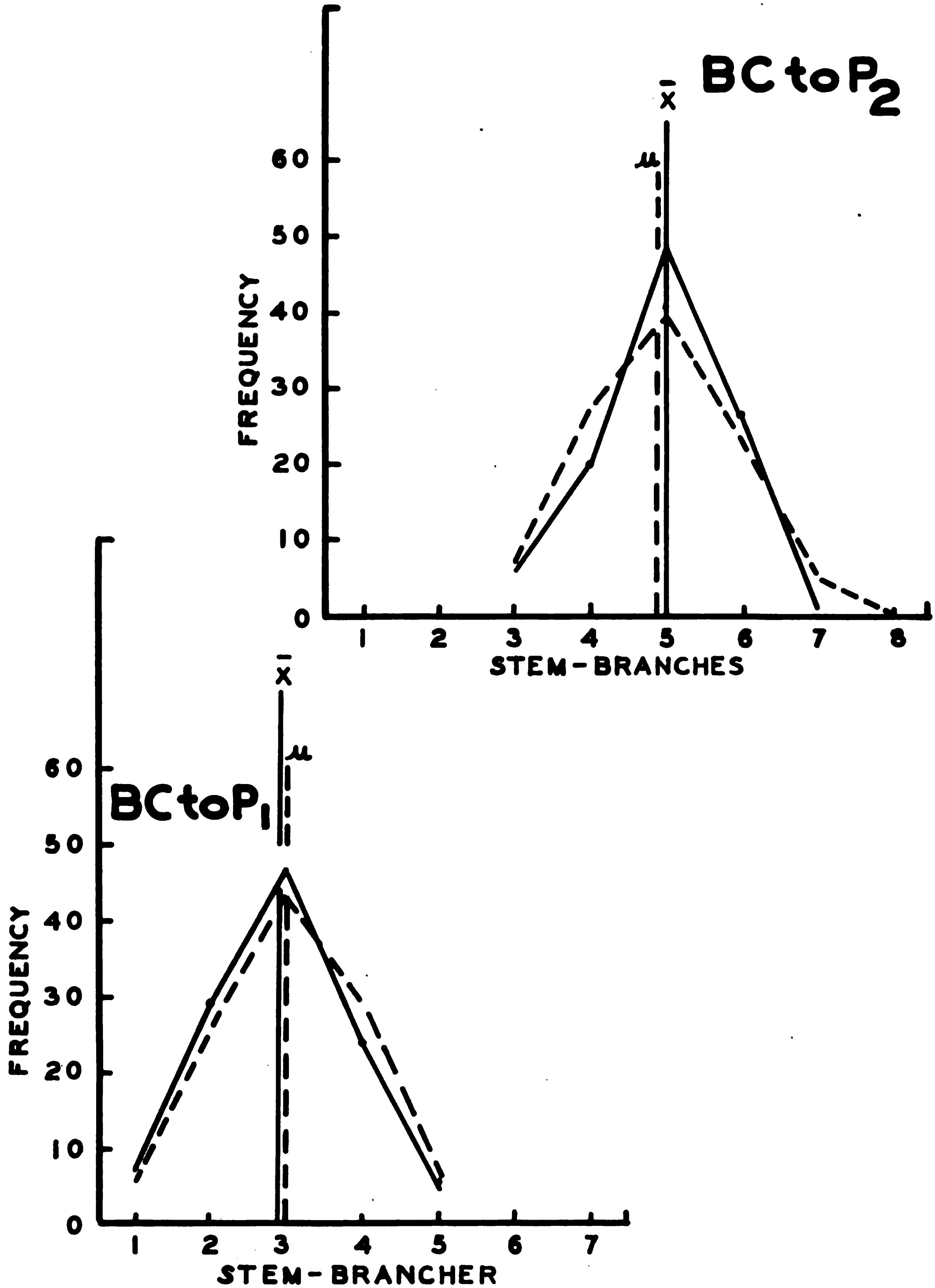
F2(P2 x P1)
μ
x̄
FREQUENCY
0
10
20
30
40
50
60
70
80
1
2
3
4
5
6
7
8
STEM-BRANCHES
F2(P1 x P2)
μ
x̄
FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5
6
7
8
9
STEM-BRANCHES

FIGURE IV

Upper Graph shows the observed frequency distribution of the BC to P_2 population in solid line as compared to the theoretical computed frequency distribution in intermittent line. A "good fit" is obtained when these 2 distributions are compared by chi square test.

Lower Graph shows the observed frequency distribution of the BC to P_1 population in solid line as compared to the theoretical computed frequency distribution in intermittent line. A "good fit" is obtained when these 2 distributions are compared by chi square test.

FIGURE IV


BC to P_2
$\bar{x}$
μ
60
50
40
30
20
10
0
FREQUENCY
1 2 3 4 5 6 7 8
STEM-BRANCHES
$\bar{x}$
μ
BC to P_1
60
50
40
30
20
10
0
FREQUENCY
1 2 3 4 5 6 7
STEM-BRANCHER

Chi Square Test for Homogeneity

It is now desirable to test for homogeneity of agreement between the data of the original observed F_2 frequency distributions and those of the theoretical F_2's and backcrosses calculated in the manner explained in the last paragraph. The tail classes of the distributions are grouped. A chi square (x^2) test approximation for homogeneity is used in order to determine "goodness of fit" of the various observed and theoretical frequency distributions as suggested by Fisher (3). Table VI shows the chi square tests for the segregating generations. An acceptable fit is obtained in all instances except the F_2 (P_2 x P_1).

Table 6. Chi square test for homogeneity of data for observed and theoretical F_2 and backcross frequency distributions.

Population	Class	Obs.	Calc.	O-C	$O-C^2/C$	df	P
F_2 ($P_1 \times P_2$)	2.5	24	28.15	4.15	0.61		
	3.5	76	65.79	10.21	1.58		
	4.5	92	90.33	2.79	0.03		
	5.5	57	65.15	8.15	1.02		
	6.5	28	27.59	0.41	0.01		
					3.25	4	0.50-0.30
F_2 ($P_2 \times P_1$)	2.5	9	19.71	10.71	5.82		
	3.5	44	46.08	2.08	0.09		
	4.5	50	63.26	13.26	2.78		
	5.5	55	45.63	9.37	1.92		
	6.5	36	19.33	16.67	14.38		
					24.99	4	$<0.01^{**}$
F_2 (Pooled)	2.5	33	47.85	14.85	4.61		
	3.5	110	111.86	1.86	0.03		
	4.5	142	153.59	11.59	0.87		
	5.5	112	110.78	1.22	0.01		
	6.5	64	46.91	17.09	6.23		
					11.75	4	0.02-0.01
BC to P_1	2.5	7	5.67	1.33	0.31		
	3.5	29	25.34	3.66	0.53		
	4.5	47	43.05	3.95	0.36		
	5.5	24	29.67	5.67	1.08		
	6.5	5	8.26	3.26	1.29		
					3.57	4	0.50-0.30
BC to P_2	3.5	6	7.79	1.79	0.41		
	4.5	20	27.37	7.37	1.98		
	5.5	49	39.09	9.91	2.51		
	6.5	27	27.85	0.85	0.03		
					4.93	3	0.20-0.10

DISCUSSION AND SUMMARY

Inheritance of the number of stem-branches in autumn planted peas was studied in reciprocal crosses and selfing of hybrids between Jade and AW 62-14, an early garden pea and a winter hardy F_5 breeding line, respectively. The results suggest that the character studied was controlled by two major gene pairs. Segregation was discernible in the F_2 and backcross populations which suggested additive genetic inheritance. The "t" tests calculated to test the hypothesis that the observed means and the hypothetical means (midpoints) were equal showed no significant difference existed between these values except in the case of the F_2 (P_2 x P_1) population. The fact that this population showed significant difference is probably of little concern in view of the good aggreement shown by the other three segregating populations, viz., F_2 (P_1 x P_2), BC to Jade, and BC to AW 62-14; and also, taking into account the fact that the pooled F_2 data showed insignificance when it was used in testing the same hypothesis.

Calculations to determine the number of gene pairs conditioning branching in this material indicate that two factor pairs with equal independent effects are involved. The analysis used to determine this result was based on the observed frequency distributions of segregating generations as compared by chi square test approximation for homogeneity to a theoretical frequency distribution calculated by using the method suggested by Powers, et.al. (11). The fact that the F_2 (P_2 x P_1) again was different than the other segregating

generations leads to the explanation that there was apparently some experimental error in counting this population or that some biological condition which is unaccounted for may have caused this discrepancy.

It can readily be determined from Table I that the F_1 means of 5.41 and 4.46 are not equal to 3.99, which is the hypothetical mean calculated to represent the F_1 genotype. This fact seems to be inconsistant with the hypothesis of additivity. It is proposed that the partial dominance expressed by the F_1 means is caused by heterosis. This proposition is supported by the definition of the term "heterosis" suggested by Schull (12) which encompasses cases where the hybrid may show vigor over the mean of the parents. The fact that the F_2 populations show a decreased amount of deviation from the hypothetical mean is in good agreement with this suggestion of heterosis because the number of individuals of the same genotype as the F_1 are reduced by 75 per cent in the F_2 in a dihybrid situation.

CONCLUSIONS

The results of this study of inheritance of stem-branching in *Pisum* fit a dihybrid model with equal and additive value assigned to each contributing gene. Two factor pairs are therefore concluded to independently condition the character.

Heterosis appears to be expressed by the F_1 populations. Vigor which causes the mean number of stem-branches in the F_1 populations to surpass the mean of the two parents is expressed.

DESIGNATION OF GENE PAIRS

Since the results of this study indicate two as yet unreported gene pairs it is imperative that they be designated appropriately. In the text of this thesis the symbols AaBb were used. These genes are now redesignated $Ti_1ti_1Ti_2ti_2$. The symbol Ti refers to the term "tillering." It probably best describes the prostrate group of stem-branches observed in autumn plantings of winter hardy peas. The small lettered symbols ti_1 and ti_2 represent the genes which are neutral in their effect on tillering. The capital lettered symbols Ti_1 and Ti_2 represent the factors which actually contribute to this additive, independent scheme of genetic inheritance.

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