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Title: THE INHERITANCE OF AXILLARY HEADING IN CABBAGE, BRASSICA OLERACEA VAR. CAPITATA L. AND ITS RESPONSE TO PLANT SPACING, FERTILIZER AND TRANSPLANTING

Abstract approved: Dr. J. R. Baggett

Development of axillary heads below the main head is undesirable in commercial cabbage which is to be mechanically harvested. To determine the factors controlling the development of axillary heads, genetic and cultural effects were studied.

Crosses were made between inbred lines of widely differing tendencies for axillary heading. Both a scoring system and quantitive measurement were used to determine the degrees of axillary head development in genetic populations. F_1 progenies from the crosses of low scoring and high scoring parents had low axillary heading scores identical to or slightly higher than the low parents and less than the mid-parents. Some segregating F_2 populations showed genetic ratios close to 3 low : 1 high, but other F_2 populations deviated from 3:1 ratios usually because of an excess number of

plants with low axillary heading. Frequency distributions for all F_2 populations for both scoring and quantitive data were similar and generally supported a hypothesis that axillary heading is controlled by a single recessive gene. Segregation in the backcrosses of F_1 progenies with high and low scoring parents did not consistently give the 1:1 or 1:0 ratios expected for a single major gene hypothesis. Deviation from expected 1:1 ratios were usually the result of an excess number of plants with low axillary heading. F_3 population derived from single F_2 plants showed considerably less than expected tendency to segregate plants with high axillary heading. Estimates were high for broad sense and very low for narrow sense heritability. There was no association between the yield of main and axillary heads. Maternal effects were significant in three backcross populations and in some F_2 comparisons but others were non-significant and were not considered of importance.

The effect of plant size and vigor on the development of axillary heads were studied by using two different plant spacings, with and without the application of fertilizer. Both wider spacings and fertilizer application increased the size of main heads and greatly increased the proportion of axillary heads. Spacing had a greater effect than fertilization.

There were highly significant differences in axillary head development between transplanted and direct-seeded plants.

Transplanting greatly decreased the occurrence of axillary heads.

The behavior of F_1 progenies, deviations from expected genetic ratios in the F_2, backcross, and F_3 populations, and the responses to cultural treatment, indicated that axillary head development was not only controlled by a single recessive gene but also modified by minor genes and environmental factors.

The Inheritance of Axillary Heading in Cabbage, *Brassica oleracea* var. *capitata* L. and its Response to Plant Spacing, Fertilizer and Transplanting

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INTRODUCTION

Cabbage is by far the most important member of the genus Brassica, and is one of the most widely grown vegetable crops. In western Europe cabbage production involves 80,000 to 100,000 hectares. In East European countries the total acreage of vegetables is about two million hectares of which probably at least thirty percent is cabbage. Even in warm countries cabbage is grown on a fairly large scale. Reports from the United State Department of Agriculture show that cabbage is ranked eighth in farm value of the vegetable crops grown for fresh market in United States. It occupies about 43,830 hectares (108,260 acres) for fresh market and about 4,500 hectares (10,950 acres) for processing. Total value of this crop grown in the U. S. is over 70 million dollars a year.

The cabbage plant is biennial, producing in the first year the edible part, a large terminal bud called the head, which is surrounded by an open rosette of leaves. The stem, which is short, thick and fleshy has axillary buds in the leaf axils both inside and below the edible head. The degree of development of axillary buds during the first year varies among varieties and in some cases these buds develop into small heads resembling those of Brussel sprouts. In the second year, after exposure to low temperature, an elongating stem emerges from the head followed by the development of flowers on the terminal and axillary buds. The flowers have four sepals and petals and a superior ovary typical of Cruciferae. The fruit is silique, a long and slender pod.

As with most other vegetable crops, the hand labor requirement for harvest in the production of cabbage is relatively high. Mechanical harvesters have been under development since about 1966 and have been generally successful. Ideally, a mechanical harvester should be able to harvest both fresh-market and sauerkraut crops. This means that the harvester should be able to cut a head with several attached wrapper leaves for fresh market used, or a head with no wrapper leaves attached for processing.

The physical characteristics of cabbage plants as related to mechanical harvest have been studied by a few researchers. Stem diameter and stem length of two parts of the cabbage plant, namely the part between the soil level and the lower leaves, and the distance between the lower leaves and the desired cutting level, are of particular importance for proper function of mechanical harvesters (Parsons and Rehkugler, 1966 and Wright and Splinter, 1966).

The presence of basal sprouts or axillary heads below the main head can be detrimental to efficient harvesting. Not only do they cause problems in mechanical harvesting but also alter the head shape at the base. The axillary buds are sometimes present inside the main head causing variation in color and texture.

Though axillary heading has been considered desirable for garden use, and seed catalogs have even listed "cut and come again" varieties, they are considered a defect in breeding cabbage for commercial use.

No research has so far been carried out to determine the inheritance of axillary head development. The following objectives were undertaken in this study:

1. Determine genetic factors controlling axillary head development.
2. Determine the effects of certain cultural practices on development of axillary heads.

REVIEW OF LITERATURE

Axillary Buds of Cabbage

Very little research has been reported on the axillary buds of cabbage. Nieuwhof (1969) found that removal or abortion of growing points in cabbage plant caused axillary buds to sprout. Walkof (1964) made a three-way cross, 'Early Vienna' X'Golden Acre' crossed with 'Golden Acre No. 84,' which resulted in three good quality strains. After the primary head was harvested, the plants produced, from axillary buds, a crop of secondary heads resembling the heads of Brussel sprouts in size, appearance and flavor.

Genetics of Morphological Characteristics, Yield and Earliness of Cabbage

Head shape of cabbage, in general, is controlled by many factors with no definite dominance. Crosses between extreme flat-headed and long-headed lines showed an intermediate shape. There are some dominant factors for flatness with complementary or multiple modifying factors for round head. Transgressive segregation for flat-head shape was also observed (Pearson, 1934). Chiang (1966) reported that the polar diameter and equatorial diameter of the head were under control of both dominant and additive genes. Narrow sense heritability estimate for polar diameter was high, 68.94%, so the process of selection would be effective in either direction. The relatively low heritability estimate for equatorial diameter, 10.60%, suggested that additive genetic variation constituted only a small portion of the phenotypic variation. Swarup and Sharma (1965) found that head shape was intermediate in the F_1 but that it was inherited additively. Heritability estimate for head shape by Dickson and Carruth (1967) was 0.51.

No dominance was shown in the inheritance of penetration of core into the head (Pearson, 1934). However, Dickson and Carruth (1967) reported that core length in cabbage is controlled by two incompletely dominant genes for short core with an additive effect for shorter core from each dominant allele. Short core was correlated with round head and long core with flat head. The narrow sense heritability estimate for core length was 0.70. Chiang (1969) has shown that the length of the inner core is inherited mainly in an additive manner, with a heritability 34.56% and only one group of genes involved.

Complete dominance with a slight gene interaction and heterosis for earliness were reported by Swarup et al. (1963). Absence of heterosis for the number of days to maturity was observed by Swarup and Sharma (1965). Chiang (1969) implied that the number of days to maturity was inherited largely in an additive way. The maturity of F_1's were close to their mid-parents. Both positive and negative heteroses were observed. The heritability for this trait was 82.68% Nieuwhof (1963) found that the F_1 of intervarietal crosses showed heterosis for earliness expressed as more rapid head formation.

Positive heterosis for yield was found by Nieuwhof (1963) in early spring cabbage and by Swarup et al. (1963), Swarup and Sharma (1965) and Angeles (1966). Diallel analysis revealed complete dominance in the case of number of marketable heads and net weight of heads, while overdominance was involved in yield inheritance (Swarup et al., 1963). Chiang (1969) found that dominant genes are important in determining cabbage yield.

Physical measurements and yield data were recorded from small and large plants, and from small, medium, large and ungraded seeds of King Cole, Market Topper and Marion Market. Results indicated that variation could be more readily accounted for by genetic than by environmental factors (Halsey et al., 1970).

Crosses of an early-splitting inbred derived from Golden Acre and a late-splitting inbred from Baby Head indicated that head splitting is controlled by at least three gene pairs. Gene action for number of days to splitting after maturity was mostly additive, but partial dominance for early splitting was detected. The narrow sense heritability estimate was 47.47% (Chiang, 1972).

Number of leaves beneath the terminal head is probably governed by modifying factors. The dominant tendency is toward few leaves (Pearson, 1938). Chiang (1969) reported that the number of wrapper leaves was largely under environmental control.

Nitrogen Fertilization

Cabbage is a heavy feeder, especially of nitrogen. The amount and type of fertilizer used varies in different areas, depending upon soil and climatic conditions (Thompson and Kelly, 1957). Positive yield responses of cabbage to rates of nitrogen as high as 184 pounds per acre have been reported (Haworth, 1962; Haworth, Cleaver and Bray, 1967; and Khokhar, Singh, and Parshad, 1970). The uptake of potassium, phosphorus, magnesium and calcium by cabbage plants increased with increases in the rate of nitrogenous fertilizers (Haworth et al., 1967). Miller, Splinter and Wright (1969) reported that there was no advantage of using more than 60 pounds of nitrogen per acre for cabbage yield.

Volk, Bell and McCubbin (1947) found that the nitrogen level in sandy soil in Florida was the most important factor influencing cabbage yields. When nitrate level in soil dropped below 15 pounds per acre, the yield was reduced, Ram and Sharma (1969) reported that an application 60 kg N/acre was better than 20, 40, and 80 kg. nitrogen per acre for plant height, stem girth, number of leaves, head diameter, compactness, ascorbic acid content and yield per acre.

Consistent increases in yield were obtained with up to 300 pounds nitrogen per acre, but at the higher rates the effects were small and varied with the season (Webber and Williams, 1969). On sod-podzolic soil in the Moscow region, yields of cabbage were raised mainly by nitrogen at 90 to 135 kg/ha (Borisova, 1971). However, increasing the rate of nitrogen fertilization resulted in more burst heads under certain conditions (Vittum and Harvey, 1952).

The influence of time of nitrogenous fertilizer applications on seed production of cabbage and chinese cabbage was reported by Eguchi (1960). Nitrogen fertilizer side dressed at the bolting stage was effective in increasing the number of secondary branches, flowers and fruits. The application of nitrogen at the flowering stage resulting in a high percentage of fruit set. Yield of seed was high in plots where nitrogen fertilizer was applied at bolting time.

Plant Spacing

Maximum yield was obtained at a spacing of 1800 square cm per plant for most varieties which have different size of heads. Varieties of cabbage with large heads can be grown successfully for fresh market size if they are spaced properly to reduce head size (Oyer, 1959).

There is a definite relationship between head weight and plant spacing. As the plant spacing was increased the head weight was also increased (Halsey et al., 1967; Shumaker, 1970; Flones, 1970; Bowers and Mulkey, 1967; Spivey et al., 1963 and Vittum and Peck, 1954). Prohorov (1964) reported that closer spacing increased the total yield per unit area but reduced the weight and quality of the individual cabbage heads.

In a trial of conical-headed varieties grown under irrigation, maximum head size was obtained with a spacing of 35-40 cm in 75 cm rows, while ball-headed varieties under non irrigated condition attained maximum head size with a 90 cm spacing. Close spacing resulting in higher yield per acre, though with greater variability in head size. Varying the fertilization had no apparent effect on head size (Davey, 1965).

Plants at closer spacing have required a rather longer time to reach maturity with more variation in head size than those the wider spacings (Hodnett and Campbell, 1963 and Betzema and Commandeur, 1966). Prohorov (1964) found that the rate of maturation of the late varieties was less affected by the spacings employed.

Variations in leaf stem length, stem and head diameter due to different spacings between plants were reported by Halsey et al. (1968).

Nitrogen-Spacing

Vittum and Peck (1956) reported that the gross yield per acre was increased considerably by nitrogen fertilization but most of this gain was offset by a large increase in burst heads. In such condition, close spacing of plants in the row reduced the percentage of burst heads and greatly reduced the average head weight.

Khakhar and Arora (1968) suggested that a spacing 20 cm. apart in 60 cm row with application of 75 kg N/ha at transplanting and a month later, would be the best practice for Golden Acre.

Betzema and Commandeur (1968) found that rates of nitrogen fertilization and spacings had an effect on two disorders in stored cabbages, namely grey speckling and internal discoloration. When no nitrogen was applied with close spacing almost no discoloration occurred but the yield was markedly lower than at higher fertilizer levels.

Direct Seeding - Transplanting

Volkov (1964) reported that in late varieties the yield and the quality of direct-seeded cabbage were equal to those of transplanted controls. Deeper planting in the transplanted plots gave more uniformity of head alignment (Hensel *et al.*, 1969). The most uniform plants, as measured by variance of head weights were produced by transplanting to shallow or medium depths. Greater yields were usually produced by plants designated as large at transplanting. There was no important uniformity difference between plant sizes (Miller _et al._, 1969).

Direct-seeded cabbage showed increased in earliness, yield and average head weights (Shumaker, 1970 and Tulupora, 1965).

Different ages of seedlings at transplanting had no effect on yield and quality but had an effect on time to maturity (Valdya and Patil, 1965). The earlier the transplanting time, the earlier was the harvest and the greater was the early yield (Kanema,. 1964). More recently Whitwell (1972) reported that large transplants of cauliflower matured earlier than small transplants.

MATERIALS AND METHODS

Genetic Studies

General Procedure

The experiments were conducted at the Vegetable Research Farm, Corvallis, Oregon from 1971 to 1973. Prior to planting experimental materials each year, a band of 600 kgs/ha of 8-24-8 fertilizer was applied. Cabbage seeds were planted in rows 90 cm (3 ft.) apart by a belt planter. Seedlings were thinned to 45 cm (18 inches) apart in the row. Irrigation and insecticide were applied to maintain good growth. Weed control was obtained by hand and mechanical weeding and pre-plant incorporated application of trifluralin.

Seeds for these studies were produced in the greenhouse from plants selected in the field. Plants were dug and then vernalized at 4.4 ^{o}C (40 ^{o}F) for about 10 weeks for flowering induction. The vernalized plants were then grown in the greenhouse at approximately 15.6 ^{o}C (60 ^{o}F) night temperature and 21.1 ^{o}C (70 ^{o}F) day temperature. Self- and cross-pollinations were made by hand during the bud stage to avoid uncontrolled crosses and to overcome self-incompatibility. Seeds from individual plants were massed in each cross before sowing in the field except in the F_3 generation of the cross W7 (C88-6-1-3 X R51-2-1-2), where seeds from individual plants were sown separately.

At maturity the individual plants in each population were scored for axillary head development. Then a suitable varied number of plants in each population were saved for studying their progenies.

A scoring system was used to estimate the axillary heading in the individual plants, ranging from score 1 for no axillary heading to score 5 for extreme axillary heading. Figures 1 and 2 show axillary heading in parental lines scored 1 and 5.

Beside scoring, all of the plants from the crosses W11 (C78-4-10-2 X R52-4-1) and W12 (R56 X 'Badger10') were harvested to obtain the weights of main heads and axillary heads. Percent weight of axillary heads was based on the weight of main heads:

$$\% \text{ axillary head} = \frac{\text{Axillary head weight}}{\text{Main head weight}} \times 100$$

Correlation between main head and axillary head weights was determined from F_2 populations of the crosses W11 and W12.

Chi-square and confidence interval tests were used to determine goodness of fit in genetic ratios of the F_2 and backcross populations.

A broad sense heritability estimate was determined for axillary heads. The variability among F_2 plants within a cross was taken as a measure of both genetic (Vg) and environmental variance (Ve), whereas the geometric mean of the variability of the parental lines was used to estimate environmental variance. Calculations were as follows (Empig, Lantican and Escuro, 1970):

$$Hb = \frac{V_{F_2} - (V_{P}1 \cdot V_{P}2)^{1/2}}{V_{F_2}} \times 100$$

This formula is operational only under the assumption that the environmental variance and genetic X environmental interaction are equal in the F_2 and parent populations.

A narrow sense heritability estimate for this trait was obtained from the variances of three segregating populations, the F_2 and the summed backcrosses to each parent. The heritability was calculated as follows (Warner, 1952):

$$Hn = \frac{(1/2)D}{V_{F_2}}$$

where $(1/2)D$ = the additive genetic component of F_2

and V_{F_2} = total within variance of F_2

and $(1/2)D$ = $2(V_{F_2}) - (V_{B_1} - V_{B_2})$

where V_{B_1} and V_{B_2} are the total within variance of the backcrosses of the F_1 to the respective parents.

The formula is based on the conventional assumptions that additivity of genic effects, locus to locus (no epistasis) and independence of genotype and environmental variances are fulfilled. Also the effects of the environmental components of variance of the F_2 and of two backcrosses are of comparable magnitude.

Plant Materials

The crosses used to study the genetic factors controlling axillary head development were as follows, showing the axillary head scores for parent lines:

Identification symbol	Parentages Female	Score	Male	Score
W1	R69	5.0	R51-2-2-2	1.0
W2	R69	5.0	R51-3-2-4	1.0
W3	R69	5.0	R51-3-5-6	1.0
W4	C82-3-3-1	5.0	R51-3-2-5	1.0
W5	C82-3-3-1	5.0	R51-2-1-2	1.0
W6	C88-6-1-3	5.0	R51-1-1-3	1.0
W7	C88-6-1-3	5.0	R51-2-1-2	1.0
W8	C88-6-1-3	5.0	R51-2-2-3	1.0
W9*	R56	5.0	R52-4-1	1.5
W10*	C70-2-1-6	5.0	R52-4-1	1.5
W11*	C78-4-10-2	5.0	R52-4-2	1.5
W12*	R56	5.0	Badger 10	1.0+
W13*	C70-2-1-6	5.0	Badger 10	1.0+
W14*	C78-4-10-2	5.0	Badger 10	1.0+
W15*	C70-2-1-6	5.0	Bonanza inbred	2.0
W16	R56	5.0	C78-4-10-2	5.0

*Reciprocal crosses made

In addition, F_1 generations of 30 additional crosses were scored for axillary heads but were not followed further. These crosses are listed in the results, Table 1.

All cabbage lines used, except 'Badger 10' and the 'Bonanza' inbred are selections from the Oregon State University breeding program for club root resistance. The 'Badger 10' and 'Bonanza' inbred lines were obtained from Dessert Seed Company. The more recent parentages of the O. S. U. lines used were as follows:

Line	selfed Generation	Parentages
R52-4-1	F_8	(C27 X Danish Ballhead)F_2 X Babyhead
R56	F_6	(C28 X Babyhead)F_{4a} X Babyhead
R69	F_6	(C28 X Babyhead)F_{4b} X Unidentified line
C70-2-1-6	F_6	(C28 X Babyhead)F_{5a} X King Cole
C78-4-10-2	F_6	(C28 X Babyhead)F_{5b} X King Cole
C88-3-3-1	F_6	(C28 X Babyhead)F_{5c} X King Cole
C88-6-1-3	F_6	(C28 X Babyhead)F_{5d} X King Cole

The R51 sub lines are inbred lines derived from a club root susceptible line of obscure origin.

Differences in axillary head development between low and high scored lines are presented in Figure 1, and Figure 2 show the extreme axillary heading lines: C78-4-10-2 and C88-6-1-3.

Chronology of Genetic Tests

First year, 1971: (1) Scoring of 8 F_1's, W1-W8; single plants saved

(2) Selection of additional lines for crossing program

Second year, 1972: (1) Selfing W1-W8 F_1's in greenhouse, F_2 generation scored in field

(2) Single plant selection in F_2 population of W7 saved for F_3 tests

(3) Crossing between additional lines in greenhouse; F_1 generation of W9-W46 scored in field; plants from W9-W16 saved for F_2 seeds

Third year, 1973: (1) Selfing F_2 plants of W7 in greenhouse; F_3 generation scored in field

(2) Selfing F_1 plants of W9-W16 in greenhouse; F_2 generation scored in field

(3) Backcrosses of W9-W16 F_1's to parents in greenhouse; backcross progenies scored in field

(4) F_2 seeds of W11 and W12 obtained in greenhouse; F_2 populations tested in field by both scoring and by weighing main heads and axillary heads.

Cultural Experiments

Spacing and Fertilization Effects

'Bonanza,' an open-pollinated commercial cabbage cultivar was planted on May 23, 1972, to study the effects of fertilizer addition and different spacings on the development of axillary heads. The experimental design was a randomized block in factorial arrangement with six replications. Plant spacings in the row were 40 and 80 cm, with all rows 90 cm apart. Two levels of fertilization were used: (1) no application and (2) 600 kgs/ha of 8-24-8 fertilizer in a band application, with an additional 50 kgs/ha of NH_4NO_3 applied as a side dress on July 28. At maturity, 10 plants in each plot were harvested to measure the yields of main and axillary heads.

A second replicated experiment was conducted in summer 1973. In this case seeds of an inbred line with a high tendency for axillary heads, C78-4-10-2 were space planted in a randomized block design with six replications on May 16, 1973. Rates of fertilizer and method of application were the same as in the previous year except the spacings were changed due to the smaller plant size of the inbred line. Thirty and sixty cm were used as narrow and wide spacings. Ten plants from each plot were harvested for main and axillary head weights.

Transplanting Effects

On July 10, 1972, 300-500 seedlings each of the F_2's W1 (R69 X R51-2-2-2), W2 (R69 X R51-3-2-4), W3 (R69 X R51-3-5-6), W4 (C82-3-3-1 X R51-3-2-5), W5 (C82-3-3-1 X R51-2-1-2), W6 (C88-6-1-3 X R51-1-1-3), W7 (C88-6-1-3 X R51-2-1-2) and W8 (C88-6-1-3 X R51-2-2-3) were transplanted at 45 cm spacing in the row and 90 cm between rows. These seedlings were obtained by thinning direct-seeded populations planted for genetic data. The individual plants were scored for axillary heads at maturity. A chi-square test was used to determine the differences in the scores of axillary heads in the direct- seeded and transplanted populations.

In 1973, inbred lines C88-6-1-3, C78-4-10-2 and R56, which give high development of axillary heads, were selected to study the effect of transplanting on axillary head expression. The seeds of these three lines were planted on June 6, and a portion of the seedlings was transplanted on July 16. At maturity, weights of main and axillary heads were determined for 20 plants from both direct-seeded and transplanted plots. A T-test was used to determine the significance of differences between the effects of direct seeding and transplanting on the development of axillary heads.

(a)

(b)

(c)

Figure 1. Two parental lines differing in degree of axillary head development, left: C88-6-1-3 (scored 5), right: R51-2-1-2 (scored 1).

Figure 2. Extreme axillary heading lines: C78-4-10-2 (left) and C88-6-1-3 (right).

EXPERIMENTAL RESULTS

Genetic Studies

Inheritance

The F_1 generation from many parental combinations generally showed varying degrees of dominance for a lack of axillary head development, but some exceptions were observed. Table 1 shows that some crosses between extremely low and high scoring lines resulted in F_1 progenies with axillary head scores identical to that of the low parents (W1-W8). In W9-W15, W21, W45 and W46 axillary heading was higher than that of the low parents, but less than the mid-parent level. The F_1 of W17 scored at the mid-parent level, and W18 F_1 tended toward the high scoring parent, C75-5-2-2. In crosses between two low scoring parents; W28, W31, W33, W34, and W36 the F_1's showed low scores for axillary heading. Crosses between low and intermediate, or intermediate and intermediate lines, gave intermediate F_1 progenies. Most of the crosses listed in Table 1, W17 and beyond, were not studied further.

Data from Table 6 also show that means of axillary head weight, percent axillary weight and scores from the F_1 of W12 were higher than the mean of the low parent. In the F_1 of W11, shown in Table 4, axillary head weight and percent axillary head weight were less than

Table 1. Average scores[1] for axillary heading of F_1 progenies and their parents.

Identification symbol	Parentages				Score	
	Female	Score	Male	Score	F_1	Reciprocal F_1
W1*	R69	5.0	R51-2-2-2	1.0	1.0	-
W2*	R69	5.0	R51-3-2-4	1.0	1.0	-
W3*	R69	5.0	R51-3-5-6	1.0	1.0	-
W4*	C82-3-3-1	5.0	R51-3-2-5	1.0	1.0	-
W5*	C82-3-3-1	5.0	R51-2-1-2	1.0	1.0	-
W6*	C88-6-1-3	5.0	R51-1-1-3	1.0	1.0	-
W7***	C88-6-1-3	5.0	R51-2-1-2	1.0	1.0	-
W8*	C88-6-1-3	5.0	R51-2-2-3	1.0	1.0	-
W9*	R56	5.0	R52-4-1	1.5	2.5	2.5
W10*	C70-2-1-6	3.0	R52-4-1	1.5	2.0	2.0
W11**	C78-4-10-2	5.0	R52-4-1	1.5	1.5	2.0
W12**	R56	5.0	'Badger10'	1.0+	2.0	2.0
W13*	C70-2-1-6	3.0	'Badger10'	1.0+	2.0	2.0
W14*	C78-4-10-2	5.0	'Badger10'	1.0+	2.0	2.0
W15*	C70-2-1-6	3.0	'Bonanza' inb.	2.0	2.0	2.0
W16*	R56	5.0	C78-410-2	5.0	5.0	-
W17	'Badger10'	1.0+	C43-2-1-2	5.0	3.0	-
W18	'Badger10'	1.0+	C75-5-2-2	5.0	4.0	-
W19	'Badger10'	1.0+	R54	3.5	2.5	2.0
W20	'Badger10'	1.0+	C82-3-2-1	2.0	2.0	2.0
W21	R51-3-2-5	1.0	C88-6-1-1	5.0	2.0	2.0
W22	R52-4-1	1.5	R54	3.5	3.0	3.0
W23	R54	3.5	C73-1-2-1	3.0	3.5	-
W24	R56	5.0	C73-1-2-1	3.0	3.0	-
W25	C78-4-10-2	5.0	C73-1-2-1	3.0	3.0	-
W26	C82-3-2-1	2.0	C70-2-1-6	3.0	2.0	2.0
W27	C82-3-2-1	2.0	C73-1-2-1	3.0	2.0	-
W28	C82-3-2-1	2.0	C82-3-2-4	2.0	2.0	2.0
W29	C82-3-2-1	2.0	C82-3-4-3	2.5	2.0	2.0
W30	C82-3-2-1	2.0	'Bonanza' inb.	2.0	1.5	1.5
W31	C82-3-2-4	2.0	R52-4-1	1.5	2.0	2.0
W32	C82-3-2-4	2.0	C70-2-1-6	3.0	2.0	2.0
W33	C82-3-2-4	2.0	C73-1-2-1	3.0	2.0	2.0
W34	C82-3-2-4	2.0	'Bonanza' inb.	2.0	1.5	1.5
W35	C82-3-3-2	3.0	R51-1-1-4	1.0	1.5	-
W36	C82-3-4-1	2.0	R51-3-2-5	1.0	1.5	-
W37	C82-3-4-3	2.5	R52-4-1	1.5	2.0	-
W38	C82-3-4-3	2.5	C70-2-1-6	3.0	2.0	2.0
W39	C82-3-4-3	2.5	C73-1-2-1	3.0	2.0	-
W40	C82-3-4-3	2.5	C82-3-2-4	2.0	3.0	3.0
W41	C82-3-4-3	2.5	'Bonanza' inb.	2.0	2.0	2.0
W42	'Bonanza' inb.	2.0	C70-2-1-6	3.0	3.0	2.0
W43	'Bonanza' inb.	2.0	C73-1-2-1	3.0	2.5	-
W44	'Bonanza' inb.	2.0	C82-3-2-4	2.0	1.5	2.5
W45	C88-10-1-3	5.0	R51-3-5-3	1.0	2.0	-
W46	C88-6-1-1	5.0	R51-3-2-5	1.0	2.0	-

* Studied through F_2 generation

** Studied both scoring and quantitative measurement

*** Studied through F_3 generation

[1]Scores 1-5 for low - high axillary heading

the mean for the low parent, R52-4-1. Figure 3 and 4 show the distribution of F_1 progenies in weights and percent axillary head weight.

F_2 scoring data are presented in Table 2, and frequency distribution for crosses W11 and W12 is shown in Figure 5. When scores were separated into low (scores 1 and 2) and high (3, 4 and 5) groups, all segregating F_2 populations, W1-W15, had larger numbers of plants with low axillary head scores than with high scores. Data the F_2 populations of W1, W4, W8, W9, W10, W10R, W11, W12, W12R, W13R, and W15R fit a 3 low : 1 high ratio. There were some low scoring segregates in W16, the cross between high scoring lines, so the confidence interval test rejected a 0:1 ratio of low to high scores. Only two backcrosses obtained from crosses between F_1 generations and high scoring parents fit a 1:1 ratio. Some backcrosses gave good fits to a ratio of 1 low : 0 high. These are backcrosses of W10 to R52-4-1, W11 to 'Badger10,' W12 to 'Badger10,' and W14 to 'Badger10.' Deviations from the expected ratios were not consistent in the F_2, with excess in either the high or low category, depending on the crosses involved. Backcross deviations all involved an excess number of low scoring plants when 1:1 ratios were expected. But when 1:0 was expected, there were always some high scoring plants, as might be expected from the F_1 data of many crosses (Table 1).

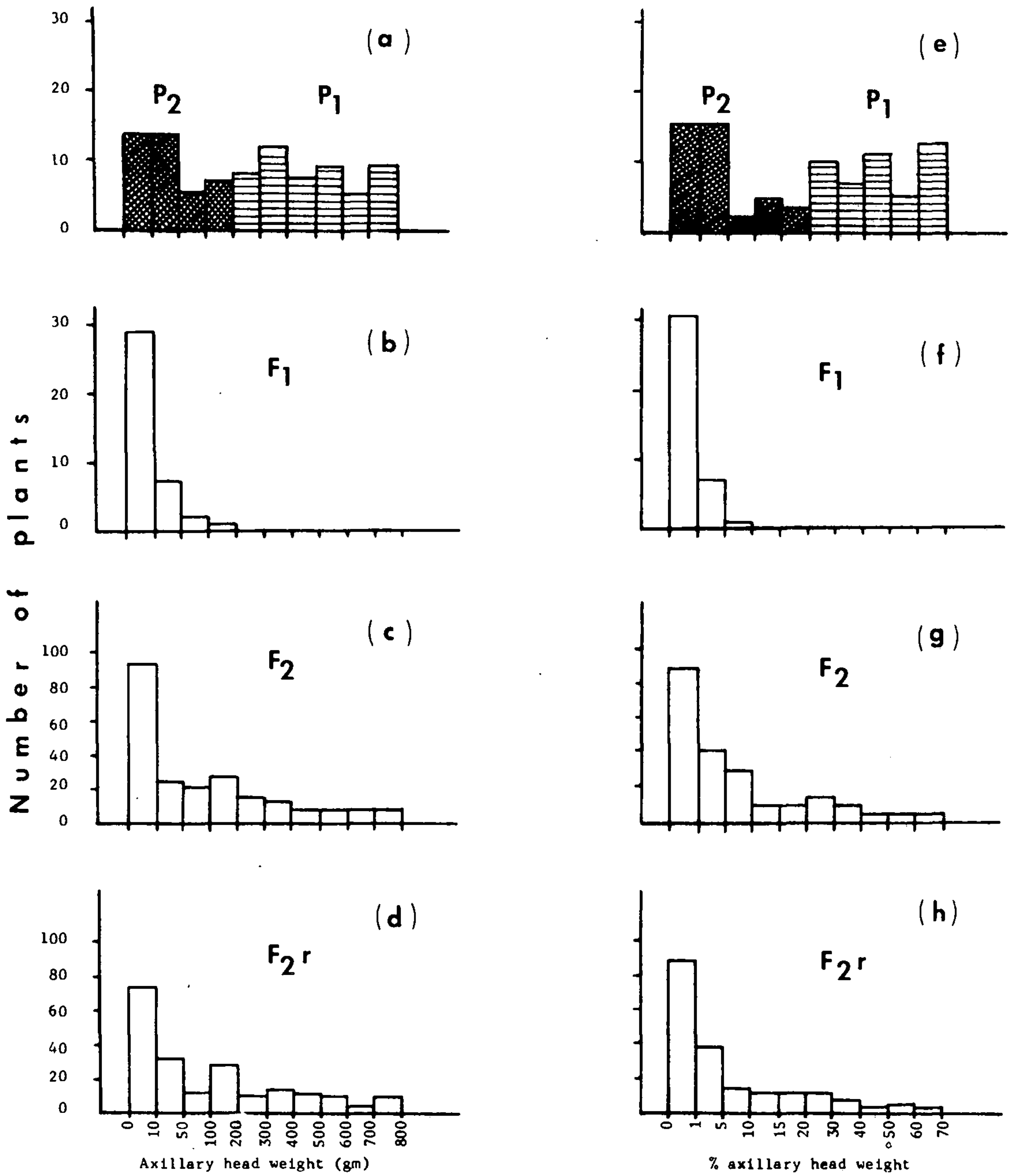

Figure 3. Frequency diatributiona of axillary head weight (left) and percent of axillary head weight (right) in croaa W11. Parenta (a and e), F_1 (b and f), F_2 (c and g), and reciprocal F_2 (d and h).

P1 (C78-4-10-2) P_2 (R52-4-1)

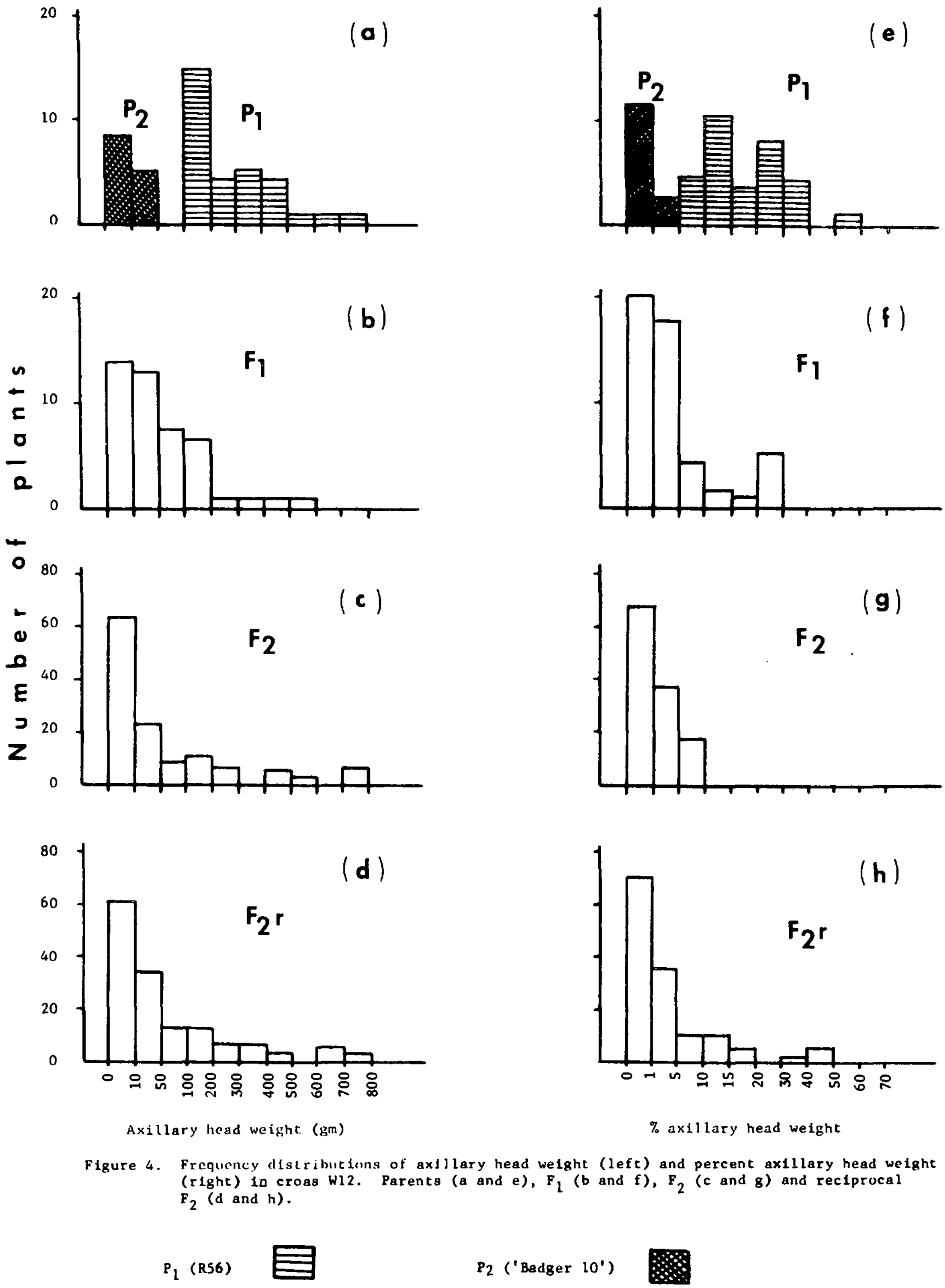

Figure 4. Frequency distributions of axillary head weight (left) and percent axillary head weight (right) in cross W12. Parents (a and e), F_1 (b and f), F_2 (c and g) and reciprocal F_2 (d and h).

P_1 (R56)

P_2 ('Badger 10')

Table 2. Inheritance of axillary head tendency in F_2 and backcross populations as determined by scoring.

Cross	Parentages[b]				No. of F_2 plant							X^2	No. of BC1[c] plt.		X^2	No. of BC2[d] plt.		C.I.[a]
					Score					Class			Class			Class		
	Female	Score	Male	Score	1	2	3	4	5	1&2	3&4&5	(3:1)	1&2	3&4&5	(1:1)	1&2	3&4&5	(1:0)
W1	R69	5.0	R51-2-2-2	1.0	127	60	22	17	11	187	50	1.925						
W2	R69	5.0	R51-3-2-4	1.0	153	62	13	5	4	215	22	31.225**						
W3	R69	5.0	R51-3-5-6	1.0	69	45	8	5	3	114	16	11.169**						
W4	C82	5.0	R51-3-2-5	1.0	77	53	12	14	16	130	42	0.031						
W5	C82	5.0	R51-2-1-2	1.0	65	60	45	16	11	125	72	14.012**						
W6	C88	5.0	R51-1-1-3	1.0	77	52	41	18	15	129	74	14.201**						
W7	C88	5.0	R51-2-1-2	1.0	148	113	40	11	11	260	62	5.669*						
W8	C88	5.0	R51-2-2-3	1.0	168	78	39	14	16	246	69	1.609						
W9	R56	5.0	R52	1.5	32	32	15	8	5	64	28	1.449	65	22	21.253**	96	10	0.871-0.979**
W9R	R52	1.5	R56	5.0	36	42	27	11	16	78	54	17.818**						
W10	C70	5.0	R52	1.5	34	20	11	5	4	54	20	0.162	25	12	4.193*	84	3	0.928-1.004
W10R	R52	1.5	C70	5.0	25	20	13	6	5	45	24	3.521						
W11	C78	5.0	R52	1.5	73	60	22	17	8	133	47	0.118	43	21	7.562*	88	3	0.930-1.004
W11R	R52	1.5	C78	5.0	84	53	38	14	13	137	65	5.551*						
W12	R56	5.0	B10	1.0	29	24	9	2	1	47	15	0.021	32	6	17.789**	18	1	0.847-1.047
W12R	B10	1.0	R56	5.0	30	17	9	4	2	53	12	1.481						
W13	C70	5.0	B10	1.0	62	18	9	2	1	80	13	6.025*	41	24	4.446*	45	15	0.600-0.892**
W13R	B10	1.0	C70	5.0	17	6	2	1	1	23	4	1.494						
W14	C78	5.0	B10	1.0	111	55	20	5	6	166	31	8.816**	35	33	0.059	12	3	0.598-1.002
W14R	B10	1.0	C78	5.0	91	36	4	3	3	127	10	22.893**						
W15	C70	5.0	Bonz.	2.0	97	41	22	7	2	138	31	3.994*	37	35	0.056	17	8	0.440-0.920**
W15R	Bonz.	2.0	C70	5.0	39	25	13	3	2	64	18	0.406						
W16	R56	5.0	C78	5.0	5	12	36	32	115	48	177	0.717 -0.857**[a]	4	23	0.718 -0.986*[a]	4	37	0.811-0.993*

* Significant difference at 0.05 level of probability

**Significant difference at 0.01 level of probability

[a] Confidence interval

[b] Some designations abbreviated, complete number given in Table 1

[c] Backcross F_1 to high scoring parent

[d] Backcross F_1 to low scoring parent

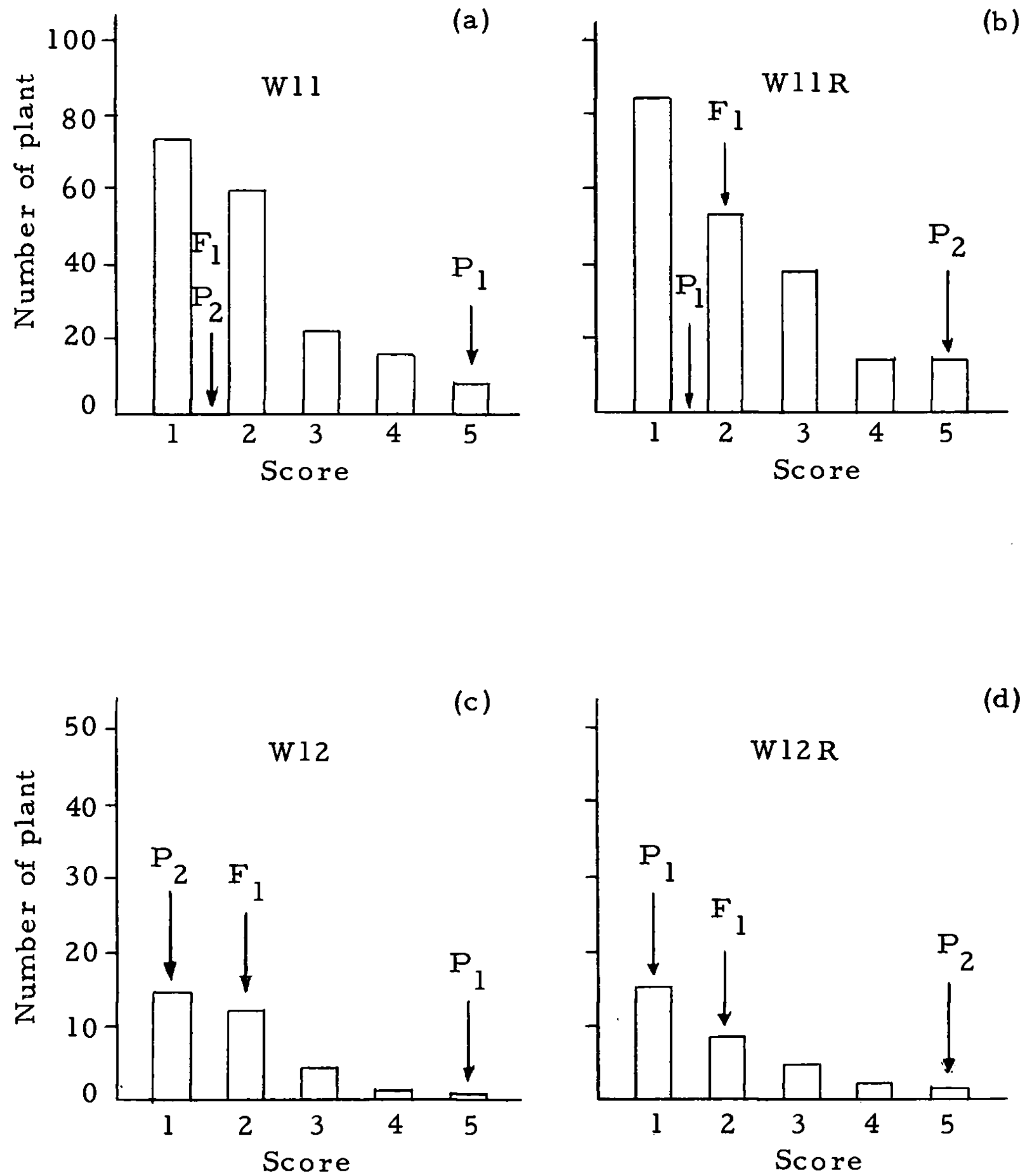

Figure 5. Frequency distribution of scores for axillary head development in F_2 and reciprocal of cross W11 (top: a and b) and W12 (bottom: c and d).

F_3 populations from single F_2 plants of W7 (C88-6-1-3 X R51-2-1-2) showed considerably less than the expected tendency to segregate plants with high axillary head scores (Table 3). Most of the F_3 plants had low scores for axillary head development, including those from F_2 plants scoring 5. However, the F_2 populations derived from the higher scoring F_2 plants had a greater number of high scoring plants than those derived from low scoring plants.

Mean weights of axillary and main heads were obtained from two crosses, W11 and W12, and are presented in Tables 4 and 5 along with average percent axillary head weight and average scores derived from the same populations. Frequency distributions of individual plant data (Figure 3 and 4) indicated that logical separations could be made to derive experimental F_2 and backcross ratios. There was no overlapping of parental data shown in these figures; in Figure 3a the terminating point for P_2 (R52-4-1) was 175 grams, and all P_1 (C78-4-10-2) plants were over 200 grams in axillary head weights. Genetic ratios for W11 shown and tested in Table 5 were derived by considering weights of less than 175 grams and percentage of axillary head weights of less than 20%, as low class and all weights and percentages above these levels as the high class. For cross W12 the low class consisted of plants with less than 50 grams and percent of axillary head weight of less than 3% (Table 7).

Table 3. Inheritance of axillary heading in F_3 populations[1] from the individual F_2 plants in W7 (C88-6-1-3 X R51-2-1-2).[2]

F_2 score	Number of plants in each score class				
	1	2	3	4	5
1	34	6	-	-	-
1	41	4	-	-	-
1	30	5	-	-	-
1	40	-	-	-	-
1	27	2	-	-	-
1	22	1	1	-	-
1	26	1	-	-	-
1	42	1	-	-	-
1	22	2	1	-	-
1	37	3	2	-	-
2	28	8	2	-	-
2	25	3	-	-	-
2	21	7	1	1	2
2	14	2	1	-	-
2	24	6	-	1	-
2	31	-	1	-	-
2	33	4	3	-	-
2	37	1	-	-	-
2	34	3	-	-	-
2	12	11	-	1	-
2	36	2	1	-	-
2	19	5	3	-	-
2	27	3	1	-	-
2	12	2	3	2	-
2	10	4	-	1	1
2	43	7	-	-	-
2	35	11	1	-	-
2	23	8	3	-	-
3	13	7	2	-	-
3	10	5	2	1	1
3	32	4	-	-	-
3	20	4	-	-	-
3	13	7	1	-	-
3	25	4	1	1	-
3	22	3	1	2	1
3	13	4	2	1	1
3	38	2	-	-	-
3	29	4	-	-	-
4	43	7	2	1	-
4	19	10	5	2	3
4	25	4	-	-	-
4	17	3	3	2	1
4	34	3	1	1	-
5	27	8	3	1	-
5	27	6	3	1	-
5	11	10	2	2	-
5	13	5	2	-	-
5	11	7	3	2	2

[1]Derived from previously scored F_2 plants, selected to provide a sample of each score class, but randomly in the field.

[2]C88-6-1-3 scored 5 and R51-2-1-2 scored 1.

Table 4. Average main and axillary head weights, percent axillary head weight and scores for parents and progenies of W11 (C78-4-10-2 X R52-4-1).

Generation	Pedigree	Ave. main head wt. (gm)	Ave. axil. head wt. (gm)	Ave. % axil. head wt.	Ave. score
P_1	C78-4-10-2	1119.56	503.02	44.93	5.00
P_2	R52-4-1	1025.68	43.12	4.20	1.50
F_1	C78 X R52	2537.77	15.46	0.61	1.50
F_2	C78 X R52	2054.27	131.65	6.41	2.10
F_2	R52 X C78	2014.85	141.45	7.02	2.12
BC	(C78 X R52) X R52	2299.32	171.80	7.47	2.08
BC	(R52 X C78) X R52	2097.48	198.08	9.44	2.52[b]
BC	(C78 X R52) X C78	2458.86	418.08	17.00	2.75
BC	C78 X (C78 X R52)	2518.42	763.12	30.30	3.21
BC	(R52 X C78) X C78	1926.55	255.60	13.27	2.76
BC	C78 X (R52 X C78)	2112.12	500.94[a]	23.72	3.42[a]

[a]Significant difference between reciprocal populations at 0.05 level

[b]Significant difference between reciprocal populations at 0.01 level

Table 5. Inheritance of axillary head weight and percent of axillary head weight in F_2 and backcross populations of cross W11 (C78-4-10-2 X R52-4-1).

Generation	Pedigree	Expected ratio (low:high)	Number of plants Axillary head wt. (gm)		X^2 or C.I.	Number of plants % axillary head wt.		X^2 or C.I.
			<175	>175		<20	>20	
F_2	C78 X R52	3:1	152	52	0.007	179	25	17.673**
F_2	R52 X C78	3:1	135	47	0.029	159	23	14.835**
BC	(C78 X R52) X C78	1:1	17	19	0.111	29	7	13.444**
BC	C78 X (C78 X R52)	1:1	10	14	0.667	15	9[a]	1.500
BC	(R52 X C78) X C78	1:1	27	15	3.428	31	11	9.524**
BC	C78 X (R52 X C78)	1:1	13	20[b]	1.485	18	15[a]	0.073
BC	(C78 X R52) X R52	1:0	34	20	0.510-0.850**	45	5	0.792-1.108*
BC	(R52 X C78) X R52	1:0	17	8	0.587-0.773**	20	5[a]	0.593-1.006*

* Significant difference between observed and expected ratios at 0.05 level of probability

** Significant difference between observed and expected ratios at 0.01 level of probability

[a] Significant difference between reciprocal populations at 0.05 level of probability

[b] Significant difference between reciprocal populations at 0.01 level of probability

Table 6. Average main and axillary head weights, percent axillary head weight and scores for parents and progenies of W12 (R56 X 'Badger10').

Generation	Pedigree	Ave. main head wt. (gm)	Ave. axil. head wt. (gm)	Ave % axil. head wt.	Ave. score
F_1	R56	1439.70	291.10	20.22	5.00
P_2	B10	2612.48	8.85	0.34	1.15
F_1	B10 X R56	3575.59	76.66	2.23	2.00
F_2	R56 X B10	2773.58	106.24	3.83	1.89
F_2	B10 X R56	2606.75	91.01	3.49	1.91
BC	(B10 X R56) X R56	2611.62	184.23 [b]	7.06 [b]	2.12 [b]
BC	R56 X (B10 X R56)	2279.38	398.50	17.48	2.85
BC	(B10 X R56) X B10	2931.98	26.89	0.92 [b]	1.26
BC	B10 X (B10 X R56)	3009.57	96.04	3.19	1.61

[b]Significant difference between reciprocal populations at 0.01 level

Table 7. Inheritance of axillary head weight and percent of axillary head weight in F_2 and backcross populations of cross W12 (R56 X 'Badger 10').

Generation	Pedigree	Expected ratio (low:high)	Number of plants Axillary head wt. (gm) <50	>50	X^2 or C.I.	Number of plants % axillary head wt. <3	>3	X^2 or C.I.
F_2	R56 X B10	3:1	44	19	0.895	46	17	0.132
F_2	B10 X R56	3:1	46	22	1.961	50	18	0.079
BC	(B10 X R56) X R56	1:1	17	22	0.641	18	21	0.231
BC	R56 X (B10 X R56)	1:1	9	17	2.461	11	15	0.615
BC	(B10 X R56) X B10	1:0	70	10	0.780-0.970**	73	7	0.826-0.998**
BC	B10 X (B10 X R56)	1:0	16	7	0.447-0.943**	17	6	0.504-0.975**

**Significant difference between observed and expected ratios at 0.01 level of probability

No significant difference between reciprocal populations

The segregation of axillary head weight in F_2 and reciprocal F_2 populations of W11 fit ratios of 3 low : 1 high (Table 5). Ratios for low to high percent axillary head weight did not fit the expected 3:1 with an excess number of plants in the low class. All backcross populations from crossing the F_1 generation and the high parent fit the expected 1:1 ratio for axillary head weights, but two of these backcrosses deviated significantly from 1:1 ratio for percent axillary head weight, again with an excess of plants with low axillary heading. Separations of low and high groups at a 10% axillary head weight rather than 20% gave good fits of 3:1 ratios for F_2 and 1:1 ratios for backcrosses. However, the parental data suggest that the 10% is not a valid point of separation and these tests are not included in the tables.

Backcross populations obtained from crossing F_1 to the low parent did not fit 1:0 rather for either axillary head weight or percent.

Frequency distributions shown in Figures 3 and 4 for quantitative measurement and in Figure 5 for scoring suggest an approximate single gene ratio with dominance for low axillary head development, even though several tested progenies did not fit 3:1 ratios.

In cross W12, segregation for both axillary head weight and percent axillary head weight fit 3 low : 1 high ratios in F_2 and reciprocal populations (Table 7). Backcross populations from the crosses of the F_1 to the high parent closely fit 1:1 ratios for low to high. As in cross W11, 1:0 ratios were not obtained from the backcross of F_1 to its low parent.

Maternal Effect

Maternal effects on the determination of axillary heading were usually not apparent. The average scores from the F_1 populations were equal or very close to their reciprocal scores (Table 1). Results of chi-square tests of the differences between F_2's or backcrosses with their reciprocal were indicated in Tables 4, 5, 6, and 7. There were no significant differences between the reciprocal and F_2 in both weights and percent axillary head weight of the cross W11. But there were differences between some of the backcrosses and their reciprocals. In the cross W12, there were no differences in weights or percent axillary head weight between F_2 or backcrosses with their reciprocals. Differences in the scores of F_2 and reciprocal F_2 of the crosses W9, W13, W14 and W15 (Table 1) were obtained.

Because maternal effects were not consistent, they were probably not important in the inheritance of axillary heading.

Heritability Estimates

Broad sense heritability estimates for axillary head weight and percent axillary head weight were high, 76.40 and 51.98% for cross

W11 and 93.54 and 87.06 for cross W12 (Table 8).

Narrow sense heritability estimates for axillary head weight were negative, -7.39 and -5.37%, for both W11 and W12. For percent axillary head weight, they were -45.13 and 8.90% for W11 and W12 respectively.

High broad sense heritability estimates and very low narrow sense estimates indicate that the genetic control of axillary heading involves dominance rather than additive gene action. Skewed frequency distribution for low axillary heading tendency in F_2 populations and behavior of most F_1 progenies also indicated dominance rather additive gene action.

Correlation Between Weights of Main and Axillary Heads

Correlation coefficients shown in Table 9, for the F_2 populations of W11, W11R, and W12 indicate that the yields of main heads and axillary heads were not significantly related. But in the F_2 population of W12R, the correlation coefficient of -0.2894 was significant at 5% probability level. This could mean that increasing development of axillary heads decreased the main head weights. Or, conversely it could mean that F_2 plants with the greatest inherent vigor, possibly because of heterosis, tended to produce fewer axillary heads. However, because all of the four correlation coefficient values were small

Table 8. Estimates of heritability for axillary head development.

Family	% Broad sense heritability		% Narrow sense heritability	
	Axillary head wt.	% axillary head wt.	Axillary head wt.	%axillary head wt.
W11*	76.40	51.98	-7.39	-45.13
W12*	93.54	87.06	-5.37	8.90

*Pooled variances of both F_2 and reciprocal F_2 used

Table 9. Degrees of association between the yield of main head and axillary heads.

F_2 population	Number of plants	Correlation coefficient
W11	203	-0.0068
W11R	182	-0.0877
W12	68	0.1784
W12R	62	0.2894*

*Significant correlation at 0.05 level of probability and mostly non-significant, and because those for the reciprocal of cross W12 were contradictory, it is likely that no real relationship existed.

Effects of Cultural Practices

Spacing and Fertilization

Yield of main and axillary heads and percent axillary head weights for the 'Bonanza' cultivar as influenced by plant spacings and levels of fertilizer are presented in Tables 10, 11, and 12 and Appendix Table 1. Wide spacing and fertilizer application increased the yield of both main and axillary heads, and increased the percent of axillary head weights. Plant spacing had a greater effect on all three factors than did fertilization (Figure 6). Although the weight of main head was increased about 50% by spacing, axillary head weight was increased by 400% and the percent axillary head weight at 80 cm was over four times as great as at 40 cm. Spacing may be an important factor in the occurrence of axillary heads in commercial cabbage production and may influence the expression of this factor in genetic studies. Both spacing and fertilizer application affected plant size, which in turn may have been the basic factor affecting axillary head development. There were no significant spacing- fertilizer interactions (Figure 7).

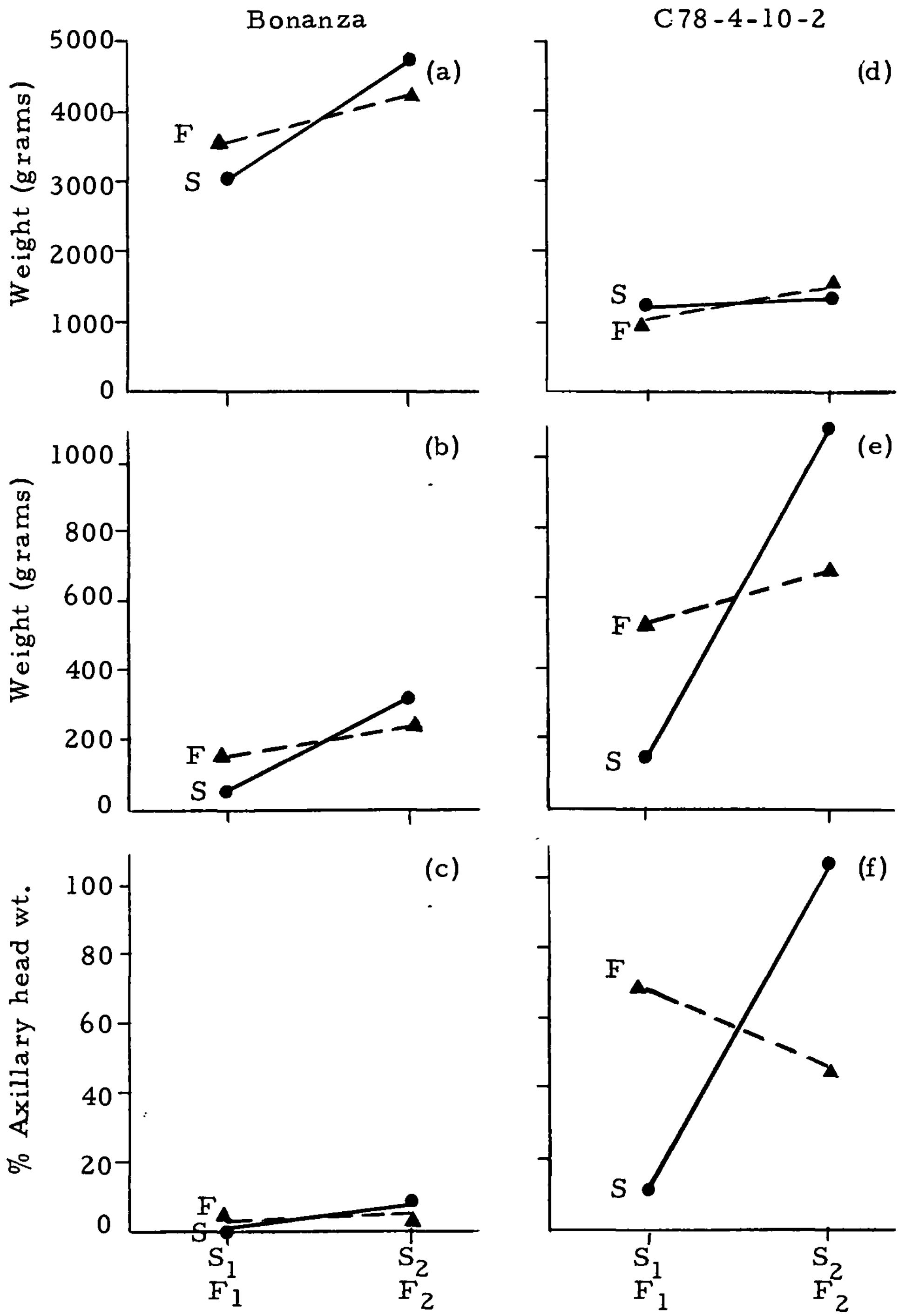

Figure 6. Mean yield in grams of main head, axillary heads and percent axillary head weight of 'Bonanza' cultivar (left; a, b, and c) and of 'C78-4-10-2' inbred line (right; d, e, and f) as influenced by two different spacings or two levels of fertilizer respectively.

S_1: narrow spacing S_2: wide spacing

F_1: no fertilizer F_2: fertilizer

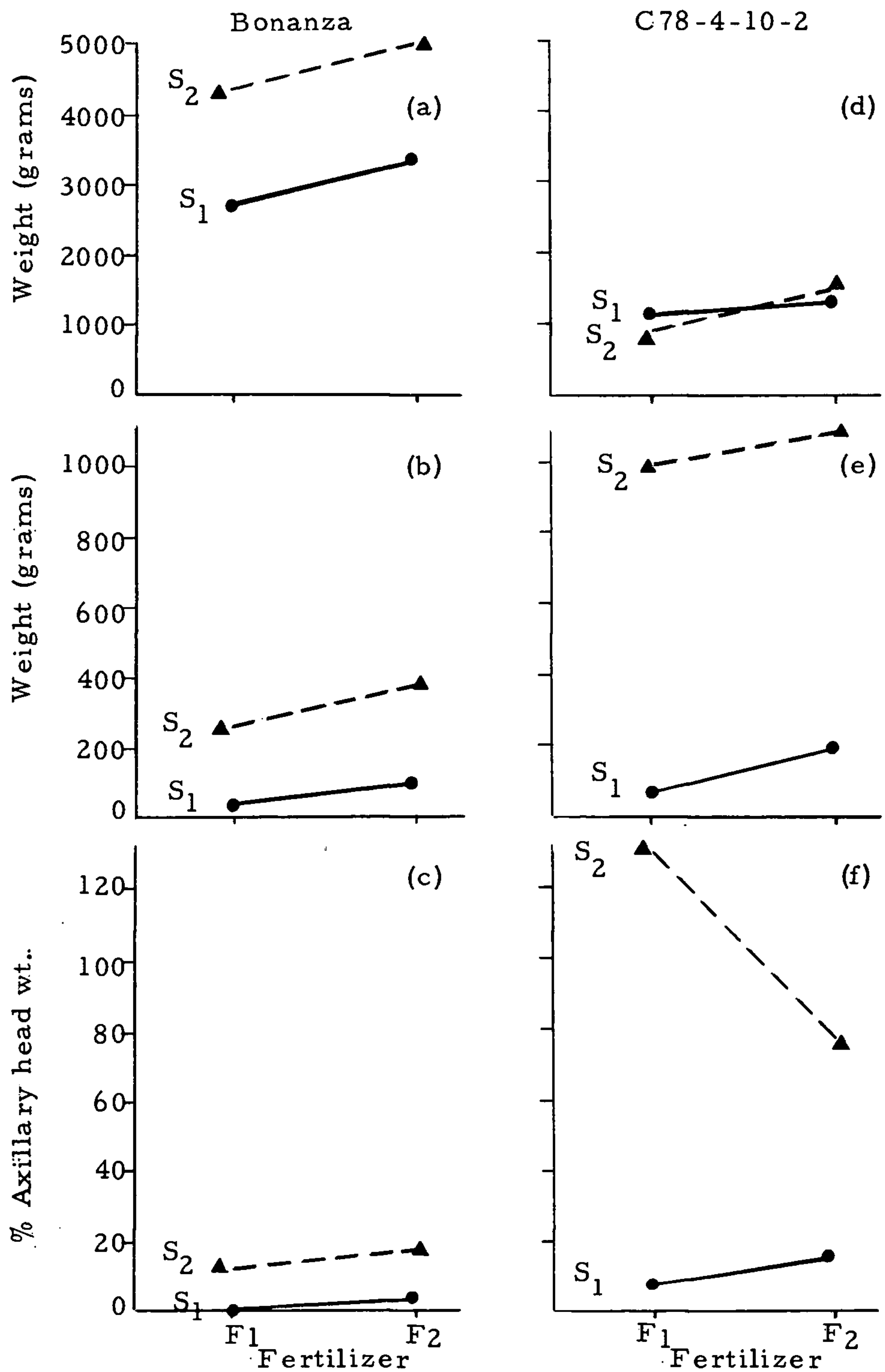

Figure 7. Mean yield in grams of main head, axillary heads and percent axillary head weight of 'Bonanza' cultivar (left; a, b, and c) and of 'C78-4-10-2' inbred line (right; d, e, and f) as influenced by both spacings and fertilizer application.

S_1: narrow spacing F_1: no fertilizer

S_2: wide spacing F_2: fertilizer

When inbred line 'C78-4-10-2' was used in 1973, the wider plant spacing increased the weight of axillary heads and the percent of axillary head weight (Tables 13, 14, and 15 and Appendix Tables 2). Plant spacing effects on main head weight were not significant. Spacing effects on axillary head weight and percent axillary head weight were ten times greater than the effect on main head weight and were both significant at 1% probability level.

Again, with this cultivar, spacing had a stronger influence on axillary head weights than fertilizer (Figure 6). Application of fertilizer increased the yields of axillary heads, and increases in yields of main heads due to fertilizer were highly significant. There were highly significant spacing-fertilizer interactions as expressed in yields of main head and percent axillary head weights. In the case of main heads, plants were more responsive to fertilizer at wider spacing; or, increase in yield due to spacing did not occur where fertilizer was limiting. In the case of percent axillary head weight, the interaction (a decrease in percent axillary head at wide spacing vs. an increase at narrow spacing) is related to different responses of main head and axillary head weight to spacing.

Table 10. Mean yield in grams of main heads of 'Bonanza' cabbage as influenced by two different spacings and two levels of fertilization.

Treatment	Not fertilized[1]	Fertilized[1]	Spacing mean[2]
40 cm spacing[1]	2689	3382	3036
80 cm spacing[1]	4370	5046	4708
Fertilizer mean[2]	3530	4214	

[1] L. S. D. for individual means: 498 at 0.05%, 676 at 0.01% level

[2] L. S. D. for main treatment effects: 470 at 0.05%, 639 at 0.01% level

Table 11. Mean yield in grams of axillary heads per plant of 'Bonanza' cabbage as influenced by two different spacings and two levels of fertilization.

Treatment	Not fertilized[1]	Fertilized[1]	Spacing mean[2]
40 cm spacing[1]	32	94	63
80 cm spacing[1]	263	378	320
Fertilizer mean[2]	148	236	

[1] L. S. D. for individual means: 123 at 0.05%, 166 at 0.01% level

[2] L. S. D. for main treatment effects: 87 at 0.05%, 118 at 0.01% level

Table 12. Mean percentages of axillary head weight based on main head weight of 'Bonanza' cabbage as influenced by two different spacings and two levels of fertilization.

Treatment	Not fertilized[1]	Fertilized[1]	Spacing mean[2]
40 cm spacing	0.637	2.642	1.640
80 cm spacing	6.092	8.698	7.395
Fertilizer mean[2]	3.364	5.670	

[1] L. S. D. for individual means: 0.213 at 0.05%, 0.289 at 0.01% level

[2] L. S. D. for main treatment effects: 0.151 at 0.05%, 0.204 at 0.01% level

Table 13. Mean yield in grams of main heads of inbred cabbage 'C78-4-10-2' as influenced by two different spacings and two levels of fertilization.

Treatment	Not fertilized[1]	Fertilized[1]	Spacing mean[2]
30 cm spacing[1]	1081	1312	1196
60 cm spacing[1]	906	1541	1224
Fertilizer mean[2]	994	1426	

F for both spacing and fertilizer significant at 0.01% level

[1] L.S.D. for individual means: 184 at 0.05%, 250 at 0.01% level

[2] L.S.D. for main treatment effects: 130 at 0.05%, 177 at 0.01% level

Table 14. Mean yield in grams of axillary head per plant of inbred cabbage'C78-4-10-2' as influenced by two different spacings and two levels of fertilization.

Treatment	Not fertilized[1]	Fertilized[1]	Spacing mean[2]
30 cm spacing[1]	74	190	132
60 cm spacing[1]	1027	1181	1104
Fertilizer mean[2]	550	686	

[1] L.S.D. for individual means: 131 at 0.05% level, 178 at 0.01% level

[2] L.S.D. for main treatment effects: 96 at 0.05%, 130 at 0.01% level

Table 15. Mean percentages of axillary head weight based on main head weight of inbred cabbage 'C78-4-10-2' as influenced by two different spacings and two levels of fertilization.

Treatment	Not fertilized[1]	Fertilized[1]	Spacing mean[2]
30 cm spacing	6.870	15.378	11.124
60 cm spacing	130.358	77.996	104.177
Fertilizer mean	68.614	46.687	

F for both spacing and fertilizer significant at 0.01% level

[1] L.S.D. for individual means: 0.228 at 0.05%, 0.309 at 0.01% level

[2] L.S.D. for main treatment effects: 0.160 at 0.05%, 0.217 at 0.01% level

Transplanting

The effect of transplanting on the development of axillary heads in segregating populations is presented in Table 16 and Figure 8. The distribution of scores in all of eight F_2 populations W1-W8, showed highly significant differences between direct-seeded and transplanted plants. Transplanting decreased the occurrence of axillary heads and thus increased the number of plants in the low scoring classes.

The effect of transplanting and direct-seeding on mean fresh weight of axillary heads and percent axillary head weights in three susceptible inbred lines is shown in Table 17. T-values indicated that transplanting caused a highly significant reduction in yield and percent of axillary head weights. The mean of axillary head weight for direct-seeding was 85 times as great as that for transplanting. Likewise the mean of percent axillary head weights was 122 times greater than in the case of non-transplanted plants.

These differences confirm observed results where transplanting was done in routine cabbage breeding. However, in these previous cases there was also reduced vigor due to a cultural situation and the effect may have been partially due to vigor. In the present tests the transplanting effect is well defined and was no different in other cultural practices or vigor of the plants. The effect may be associated with the check in growth caused by transplanting.

Table 16. Frequency distribution of scores for axillary heading in direct-seeded and transplanted plants in F_2 populations, W1-W8.

Population	Number of plants in scoring class								X^2	Average score	
	Direct-seeded				Transplanted						
	1	2	3	4&5	1	2	3	4&5		Direct-seed	Transplt.
W1	127	60	22	28	206	23	7	1	108.22**	1.79	1.17
W2	153	62	13	9	229	4	3	1	107.08**	1.48	1.05
W3	69	45	8	8	119	10	1	0	77.58**	1.65	1.03
W4	77	53	12	30	122	30	8	12	48.41**	1.97	1.48
W5	65	60	45	27	150	29	10	8	167.76**	2.11	1.37
W6	77	52	41	33	160	28	14	0	151.32**	2.15	1.28
W7	148	113	40	22	309	14	0	0	323.88**	1.80	1.03
W8	168	78	39	30	288	23	4	0	185.90**	1.78	1.10
Mean	110	65	28	23	198	20	6	3	769.83**	1.85	1.00

**Significant difference at 0.01 level of probability

Table 17. Mean axillary head weights and mean percent axillary head weight of direct-seeded and transplanted plants of three inbred cabbage lines susceptible to axillary heading.

Line	Mean axillary head wt. (gm)			Mean % axillary head wt.		
	Direct-seeded	Transplanted	T-value	Direct-seeded	Transplanted	T-value
C88-6-1-3	327.100	2.450	6.950**	16.355	0.141	5.685**
C78-4-10-2	503.020	5.350	9.406**	52.899	0.284	6.773**
R56	291.100	5.429	7.705**	20.164	0.318	8.581**
Mean	373.740	4.407	8.020**	29.806	0.248	7.013**

**Significant difference at 0.01 level of probability

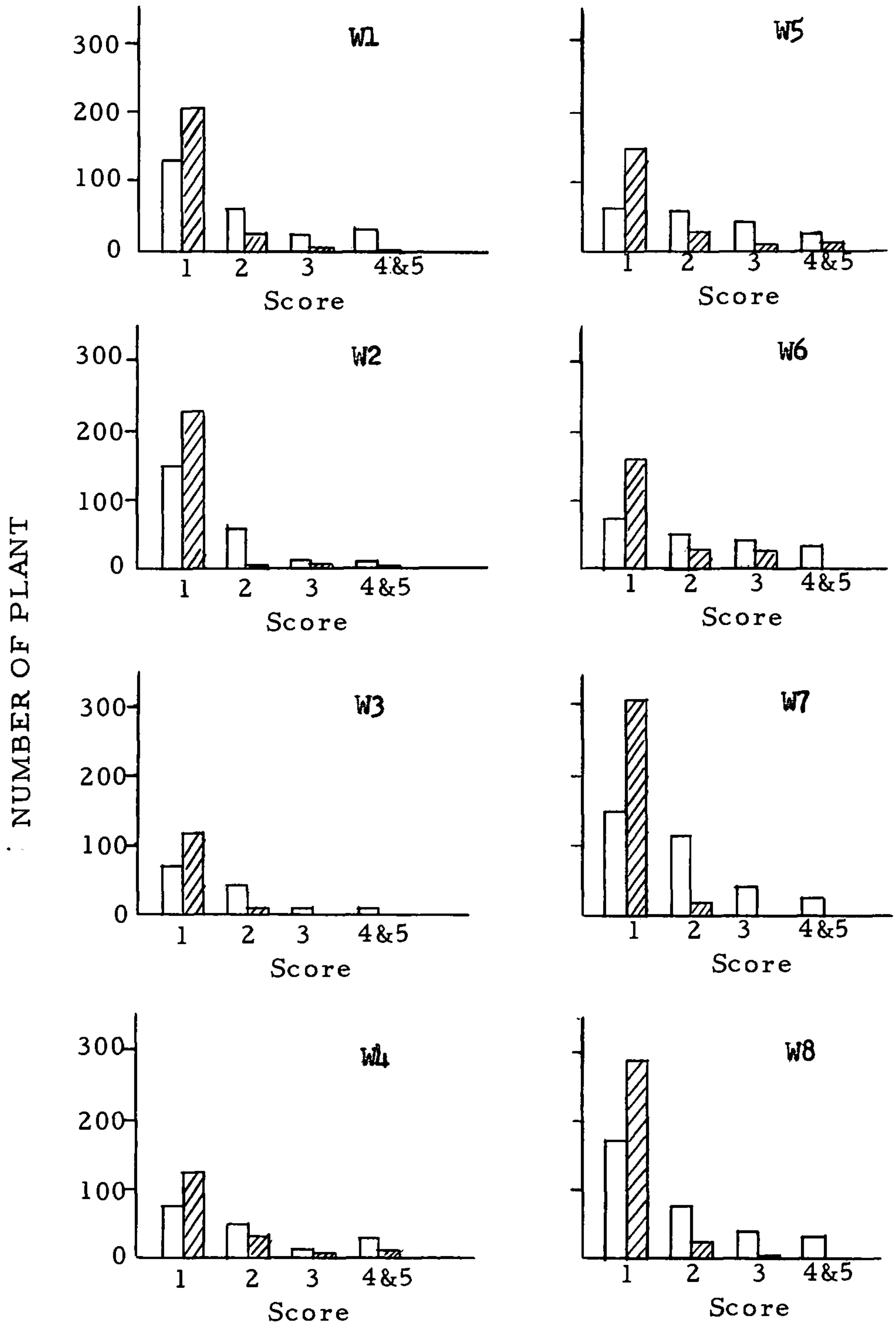

Figure 8. Frequency distribution of scores in direct-seeded and transplanted populations of eight F_2's, W1-W8.

Direct-seeded Transplanted

DISCUSSION

Genetics

Dominant and recessive gene effects are apparently important in the control of axillary head development. Segregation in some of the F_2 and backcross populations studied specifically support the hypothesis that one major dominant gene is responsible for low axillary head formation, or in other words one major recessive gene is responsible for axillary head development. Curves for all F_2 populations generally support this conclusion. However, many of the F_1's from low and high parents were not scored as low as the low parents, as they should have been for completely dominant gene action. Modifying genes present in some of the parents may interact to affect the behavior of F_1 and subsequent progeny plants. Environmental effects interacting with both major and minor gene effects could account for variation between plants and seasonal variation as observed in one parent line, C70-2-1-6. These effects of environment and modifying factors are probably also responsible for the continuous nature of F_2 variation and possibly the failure of some F_2 populations to fit discrete 3:1 ratios, even though their general patterns fit this hypothesis. Another possible reason why F_2 progenies failed to fit 3 low : 1 high ratio and backcross progenies to fit 1:1 or 1:0 of low to high ratios, is the arbitrary nature of the scoring system used.

Not only was the scoring system necessarily arbitrary and discontinuous but the same was true of the division of scores into low (scores 1 and 2) and high (scores 3, 4, and 5) classes for genetic analysis.

In the F_3 populations studied, the small number of plants in high axillary heading categories was unexpected. This suggests that some of the F_2 plants scoring 5 for axillary head development carried the main recessive gene, but possibly new combinations of modifier genes tended to reduce its expression in the F_3 generation.

Quantitative measurement of axillary heading by obtaining weights of main and axillary heads appears to offer more precision and flexibility than scoring systems. However, some of the observed F_2 ratios for cross W11 (C78-4-10-2 X R52-4-1) and W12 (R56 X 'Badger10') for percent axillary head weights did not fit 3 low : 1 high ratio as did the actual axillary head weights on both crosses. Although percent axillary head weight would appear to be more important from a practical and biological viewpoint, this parameter was sometimes difficult to interpret because it is affected by various interactions between actual main and axillary head weights and the environmental factors affecting them. Swarup et al. (1963) and Chiang (1969) reported that dominant genes are important in determining main head weight. Thus the segregation of main head weight as a separate factor may alter the F_2 data in such a way to change the percent of axillary head weight. A more specific example may be seen in Tables 13-15 where fertilizer and spacing interacted differentially on main and axillary head weights with the result that percent axillary head weight showed a drastic and seemingly contradictory effect.

Some of the F_2 populations tended to have larger numbers of low axillary heading plants than was expected with either scoring or quantitative measurement. In fact, most deviations from expected single gene ratios involved an excess of plants in the low axillary heading class. The high scoring parents chosen because of conspicuous axillary heading for several seasons, were consistent and uniform for the most part. Since these parents were highly inbred it is possible that heterosis was somehow involved in modifying the apical dominance in the various progenies. This possible effect of heterosis on apical dominance may have caused the departure from expected backcross ratios. No 1:0, low:high ratio was obtained from the backcross of F_1's to their low parents. When 1 low : 0 high was expected, there were always some high scoring plants. This may have been caused by a reduction in heterosis or increase of inbreeding depression. However, the behavior of the F_1 progenies as determined by scoring contradicts a heterosis theory since the F_1 plants tended to have more axillary head development than the low parents. In the populations studied by quantitative measurement, increased apical dominance was apparent in the F_1 of W11, where there was less axillary heading than in the low parent, but not in W12. It appears more logical to explain the behavior of the W11 F_1 generation on the basis of modifying genes. Likewise the occurrence of a large excess of low scoring plants in F_3 families does not support a heterosis theory, since heterosis would be lower in the F_3 than in the F_2 generation.

Therefore the idea that heterosis has a significant modifying influence on axillary heading is inconclusive. Minor genes are likely to be involved in the modification of the effect of a major gene pair controlling the development of axillary heads.

Low narrow sense heritability and high broad sense heritability estimates for axillary head development also support the conclusion that a dominant gene is the main factor responsible for the reduction of axillary heading with little or no additive gene action involved.

Few maternal effects were observed, suggesting that cytoplasmic inheritance was not important.

Cultural Practices

An increase of space for plants or the addition of complete fertilizer increased the yield of main heads. Since the objective of these experiments was to obtain different levels of plant size and vigor, the major elements N, P, and K were not studied separately.

Spacing differentials were chosen to give large differences when used with and without fertilizer. The greater effect of plant spacing over that of fertilization on the yield of 'Bonanza' suggests that (1) the unfertilized plots were not greatly deficient in fertilizer elements because of fertilizers used on previous crops and (2) other general growth factors such as water and light were also somewhat limiting at the closer spacings.

In the case of inbred 'C78-4-10-2' there was no effect of plant spacings on the yield of main heads probably because of the limited vigor or limited capacity to respond to growth factors. However, this does not explain why fertilization increased the main head weights.

Axillary heading in 'C78-4-10-2' was very responsive to both factors, but especially to spacing and thus resembled the more vigorous 'Bonanza.' Although the differences in response to growth factors between the inbred line and open-pollinated cultivar may be related to vigor associated with heterosis, there are also general differences in genetic background.

There was a great reduction in the development of axillary heads in transplanted plants. Perhaps this effect was associated with the check in growth caused by transplanting but this study was not designed to provide information on the physiological mechanisms of control of axillary head development. It could be speculated that the transplanting effect and other effects including genetic control involve the growth hormone, cytokinin. In plants, the naturally occurring cytokinins appear to be synthesized in the root apex and are translocated to the shoot (Galston and Davies, 1970). High molecular ratios of kinetin to auxin were found to lead to the formation of buds. Kinetin tends to inhibit auxin-stimulated longitudinal growth and to promote transverse growth. The higher the ratio of auxin to kinetin, the more inhibited was the bud growth (Skoog and Miller, 1957). Kinetin applied to lateral buds increased lateral shoot growth in sprouting broccoli (Fontes and Ozbun, 1966).

Thus transplanting may destroy the root apex sites of cytokinin formation and resulting lower ratios of cytokinins to auxin could increase apical dominance and reduce axillary head development.

To fully elaborate the control of axillary heading by genetic factors, by factors affecting plant vigor, by transplanting, and perhaps by other factors not yet recognized, will require considerable more research with greater depth in the area of plant physiology, beyond the present study.

SUMMARY AND CONCLUSIONS

1. The development of axillary heads is a heritable characteristic, mainly controlled by a single recessive gene.
2. Minor genes and environmental factors modified the expression of the major gene pair.
3. Broad sense heritability estimates were high but narrow sense heritability estimates were very low, supporting the conclusion that gene action was largely dominance rather than additive.
4. Maternal inheritance was not important.
5. There was no association between the yield of main and axillary heads.
6. Wider spacing and fertilizer addition increased the development of main and axillary heads. Axillary heads increased much more than main heads, and the effect of spacing was greater than that of increased soil nutrients.
7. Transplanting greatly decreased the development of axillary heads.

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APPENDIX

Appendix Table 1. Analysis of variance for the yield of main, axillary heads and percent of axillary head weight of 'Bonanza' cabbage as influenced by two different spacings and two levels of fertilization.

Source of Variation	F-value		
	Main head wt.	Axillary head wt.	% axillary head wt.
Replication	6.329*	0.969	0.627
Spacing	96.417**	37.767**	33.171**
Fertilization	16.174**	4.500*	5.117*
Spacing X Fertilization	0.002	0.412	0.910

* Significant difference at 0.05 level of probability

** Significant difference at 0.01 level of probability

Appendix Table 2. Analysis of variance for the yield of main, axillary heads and percent of axillary head weight of inbred cabbage 'C78-4-10-2' as influenced by two different spacings and two levels of fertilization.

Source of Variation	F-value		
	Main head wt.	Axillary head wt.	% axillary head wt.
Replication	2.218	2.712	1.470
Spacing	0.182	414.798**	145.920**
Fertilization	47.274**	4.873*	1.237
Spacing X Fertilization	10.228**	0.068	12.177**

* Significant difference at 0.05 level of probability

** Significant difference at 0.01 level of probability