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The Inheritance of Axillary Heading Tendency in Cabbage, *Brassica oleracea* L. (Capitata Group)[1]

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Abstract. **The tendency for axillary head (AH) development in** *Brassica oleracea* **(Capitata group) was shown to be a heritable characteristic. In 11 crosses between high and low AH lines carried at least through the F_2 generation, AH was recessive and largely controlled by one or a few genes. In other crosses, in which only the F_1 generation was studied, AH tendency usually resembled that of the parent having a low level of AH, but in certain crosses was intermediate or closer to the high scoring parent. Expression of AH was continuous and apparently influenced by modifying genes and the environment. Broadsense heritability estimates were high, but narrowsense heritability estimates were very low indicating dominance effects. No consistent or apparently important differences were found between reciprocals. The weight of AH was not related to yield of main heads in F_2 plants.**

The tendency to develop axillary heads (AH) below the main head is a serious defect in commercial cabbage cultivars. In addition to hindering efficient mechanical harvest, AH may alter the shape of the head and result in an untidy appearance. Plants with this tendency also may develop AH within the main head, causing variation in color and texture. Nieuwhof (2) observed that removal or abortion of growing points in cabbage caused axillary buds to develop. Walkof (3) reported on the development of strains of cabbage which produced, after the primary heads were harvested, a crop of secondary heads resembling the buds of Brussels sprouts in size, appearance and flavor. Most commercial cultivars are relatively free from the problem, though certain cultivars with this tendency have been promoted for home garden use.

Our study involved inbred cabbage lines, derived from a club root resistance program, which develop AH to an extreme degree without removal of the main head or terminal growing point.

Materials and Methods

Eleven crosses, listed in Table 1, between inbred lines differing widely in tendency for AH were studied through the F_2 generation. An F_3 population was studied for one cross, W3. For 30 additional crosses, parents and F_1 only were observed. All Oregon State Univ. lines (C and R lines) were derived by 6–8 generations of inbreeding. The lines designated 'Badger 10' (B10) and 'Bonanza' were obtained from a seed firm as uniform inbred lines derived from the respective commercial cultivars.

Crosses W4-W10 were made and studied in reciprocal. Backcrosses between F_1 and each parent in crosses W4-W10 were also made in reciprocal. Backcross seeds harvested from the F_1 and parent were combined in each case. Because no consistent or apparently important differences were found between reciprocals, the data have been combined.

All seeds used in this study were from hand pollinations made in the bud stage in the greenhouse. Because pollinating insects were not observed in the greenhouse during the winter and early spring when pollination was done, the flowers were not bagged.

Scores were assigned for degree of AH for all parents and progeny. Fig 1 shows examples of the extreme classes: score 1.0 for none and 5.0 for strong AH. Most crosses involved parents with scores of 5.0 and 1.0, but in few cases intermediate combinations were used. For 2 crosses, W6 and W7, AH and main head wt were obtained; % wt of AH based on main head wt was then calculated. Broadsense and narrowsense heritability estimates were determined for those weight data by the methods described by Empig, Lantican and Escuro (1), and Warner (4), respectively. Correlation between main head and AH wt was determined for crosses W6 and W7.

Test plots were planted at Corvallis, Oregon from 1971 to 1973. Prior to planting experimental materials in each year, a band of 600 kg/ha of 8N–10.3P–6.6K fertilizer was applied. Seeds were planted in rows 90 cm apart with 45 cm between plants. Water was applied by sprinkler to maintain normally vigorous growth.

Results and Discussion

Genetic populations. High AH tendency was generally recessive in F_1 plants. In crosses W1-W3 (Table 1) where parental scores were the extremes (5.0 and 1.0), dominance of low AH was complete. Where the low scoring parent had slight AH (score 1.5 or 2), there was usually less dominance for low scoring tendency (i.e W4 and W5). In crosses W8 and W9, involving a low parent scoring 1.0, the F_1 scored 2.0, and in W10 the low parent and the F_1 both scored 2.0. Crosses not studied beyond the F_1 generation generally followed this pattern, but included examples of F_1 scores intermediate between parents, close to the high scoring parent, and lower than either parent. The %

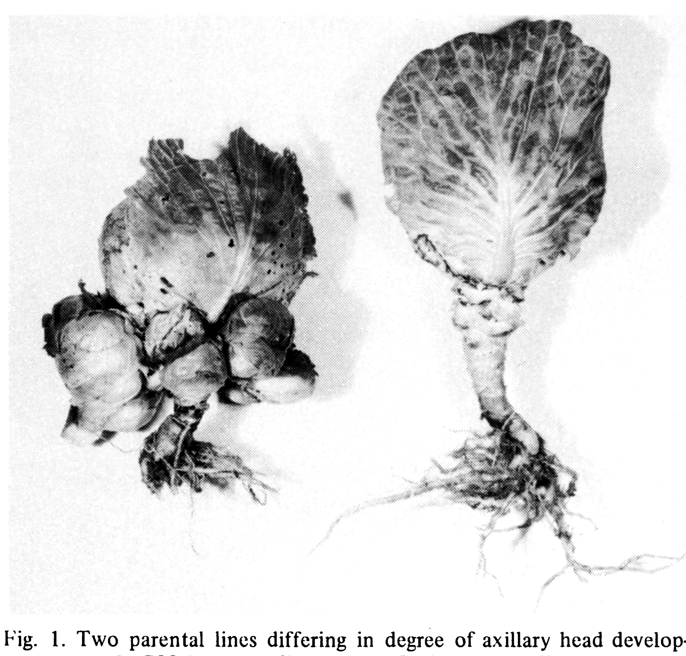

Fig. 1. Two parental lines differing in degree of axillary head development: left, C88 (scored 5.0) and right, R51 (scored 1.0).

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Table 1. Inheritance of axillary heading tendency as determined by scoring.[z]

Cross	Parents: Female Line	Female Score	Male Line	Male Score	F_1[y] Score	F_2 plants: No. scoring 1	2	3	4	5	% 1+2	BC 1[x]: No. in class 1+2	3+4+5	% 1+2	BC 2[x]: No. in class 1+2	3+4+5	% 1+2
W1	R69	5.0	R51	1.0	1.0	349	167	43	27	18	85*						
W2	C82	5.0	R51	1.0	1.0	142	113	57	30	27	69*						
W3	C88	5.0	R51	1.0	1.0	393	243	120	43	42	76						
W4	R56	5.0	R52	1.5	2.5	68	74	42	19	21	63*	65	22	75*	96	10	91*
W5	C70	5.0	R52	1.5	2.0	59	40	24	11	9	69	25	12	68*	84	3	97*
W6	C78	5.0	R52	1.5	1.8	157	113	60	31	21	71	43	21	67*	88	3	97*
W7	R56	5.0	B10	1.0	2.0	59	41	18	6	3	79	32	6	84*	18	1	95*
W8	C70	5.0	B10	1.0	2.0	79	24	11	3	2	87*	41	24	63	45	15	75*
W9	C78	5.0	B10	1.0	2.0	202	91	24	8	9	88*	35	33	51	12	3	80*
W10	C70	5.0	Bon[w]	2.0	2.0	136	66	35	10	4	80	37	35	51	17	8	68*
W11	R56	5.0	C78	5.0	5.0	5	12	36	32	115	9*	4	23	15*	4	37	10*

[z]Score 1.0=no AH; 5.0=severe AH.

[y]Reciprocal F_1 scores were identical except in W6: 1.8 represents average of reciprocal scores 1.5 and 2.0.

[x]Backcross scores not available for individual score categories 1-5. BC 1 = F_1 x high scoring parent; BC 2 = F_1 x low scoring parent.

[w]Bonanza

*Unacceptable fit when 95% exact confidence limits used to test the hypothesis that 75% of the F_2 population, 50% of the BC 1, and 100% of BC 2 were in the low scoring (1+2) class. In cross W16 the proportion tested was 0% in each case.

Table 2. Inheritance of axillary head wt and % axillary head wt in cross W6 and W7.

Generation	Pedigree	Main head wt (g)	Axill. head wt (g)	% axill. head wt	Axillary head wt[z]: No. of plants low	high	% low	% axillary head wt[y]: No. of plants low	high	% low
Cross W6										
P1	C78	1120	503	44.9						
P2	R52	1026	43	4.2						
F1	R52 × C78	2054	15	0.6						
F2	R52 × C78	4069	273	6.7	290	99	75	338	48	88*
BC 1	F1 × C78	4508	969	21.5	67	68	50	93	42	69*
BC 2	F1 × R52	2198	185	8.4	51	28	65*	65	10	87*
Cross W7										
P1	R56	1440	291	20.2						
P2	B 10	2612	9	0.3						
F1	R56 × B10	3576	77	2.2						
F2	R56 × B10	5381	197	3.7	90	41	69	96	35	73
BC 1	F1 × R56	4891	583	11.9	26	39	40	29	36	45
BC 2	F1 × B10	5963	123	2.1	86	17	83*	90	13	87*

[z]For W6, low and high classes = below and above 175 g; for W7, low and high = below and above 50 g.

[y]For W6, low and high classes = below and above 20%; for W7, low and high = below and above 3%.

*Unacceptable fit when 95% exact confidence limits used to test the hypothesis that 75% of the F_2, 50% of the BC 1, and 100% of the BC 2 were in the low scoring class.

wt of AH in the F_1 (Table 2) was below that of the low parent in W6 and slightly higher than the low parent in W7.

Although the expression of AH tendency was continuous, F_2 data obtained by both scoring and weight were arbitrarily tested against monogenic ratios. High and low classes were based on the ranges of variation of the parents and were considered to approximate commercially tolerable and unacceptable degrees of AH. The separation of F_2 scores into low (scores 1 and 2) and high (scores 3, 4, and 5) groups resulted in acceptable 3:1 low to high ratios in 5 crosses (Table 1) based on a confidence interval test. For 5 other crosses, ratios differed significantly from 3:1 with either high scoring or low scoring plants in excess. Because the scoring system and the separation of scores into high and low groups was arbitrary, separation of crosses into those which do or do not fit 3:1 ratios should not be stressed. Rather, it appears that the F_2 generations only generally support dominance of low AH tendency and the action of one or a few major genes with modifiers. In W11, between 2 parents scoring 5.0, there were 17 of 200 F_2 plants in the low class, even though the F_1 scored uniformly 5.0. This behavior suggests that new combinations of modifiers affected expression of AH in the F_2.

High and low classes (Table 2) used to determine F_2 ratios for AH wt and % AH wt (crosses W6 and W7) were based on the distribution of parent plants as shown in Fig. 2. There was no overlapping in these ranges in any case. F_2 populations of both crosses easily fit 3:1 low to high ratios for AH wt. Only W7 F_2 fit the 3:1 ratio for % AH wt, with W6 F_2 having too many plants with over 20% wt of AH. Fig. 2 shows that dominance of low % AH wt was well defined, with most F_2 plants resembling the low parent.

There was no strong relationship between weight of main and AH. Correlation coefficients were small and nonsignificant except in the case of the reciprocal of W7 (B10 × R56). For that cross the correlation coefficient of 0.29 was significant at the 5% probability level.

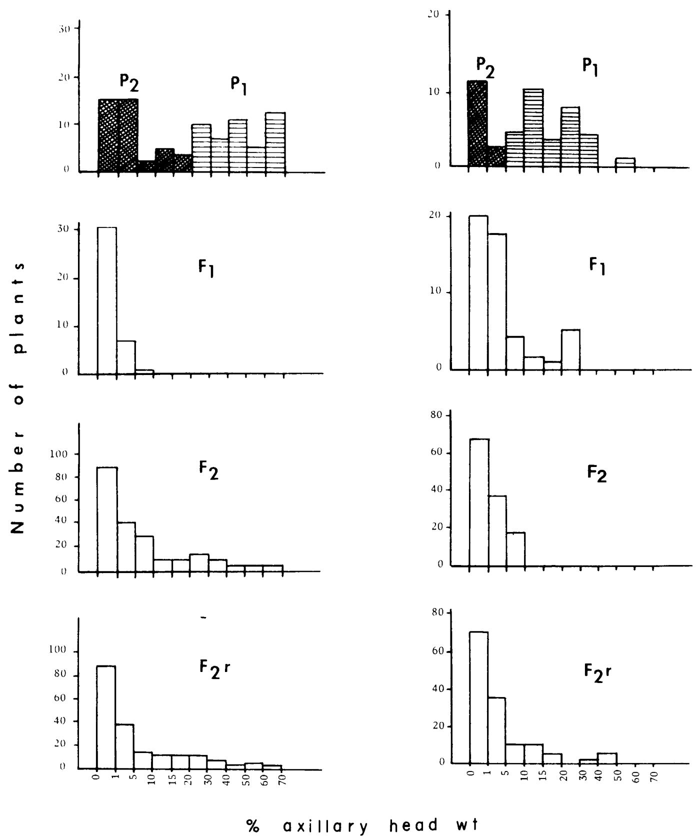

Fig. 2. Frequency distributions for per cent axillary head wt in parents, F_1, and F_2, and reciprocal F_2 of cross W6 (left) and W7 (right).

Backcross data did not generally support a single gene hypothesis (Tables 1 and 2). Deviations from 1:1 ratios in the backcross $F_1 \times$ high parent (BC_1) were usually from an excess number of plants with low AH. All backcrosses of $F_1 \times$ low scoring parent (BC_2) had at least one plant in the high AH class and all deviated significantly from the expected 100% low AH.

An F_3 population of 48 families from cross W3, selected nonrandomly to represent F_2 plants in each scoring class, did not confirm F_1 and F_2 results. While families from low scoring F_2 plants scored mostly low, families from high scoring F_2 plants scored low to medium with few scoring 4 or 5.

The behavior of F_1, F_2, and some backcrosses generally suggests strong dominance of low AH tendency, largely involving a single gene. The continuous distribution of % wt of AH (Fig. 2), suggest modifying genetic factors with relatively strong effects in some crosses. Environmental effects are also likely to be important. The range of % axillary head wt for the highly inbred parents (Fig. 2) indicates that expression is somewhat variable even in a single genotype. Related research (unpublished) involving some of these same materials has shown that AH development can be affected by cultural factors such as spacing, fertilizer application, and by transplanting.

Heritability estimates. Broadsense heritability estimates for AH wt and per cent axillary head wt were high, 76.4 and 52.0% for cross W6 and 93.5 and 87.1% for cross W7. Narrowsense heritability estimates for AH wt were −7.4 and −5.4% for crosses W6 and W7 respectively. For % AH wt, they were −45.1 and 8.9% for crosses W6 and W7 respectively.

High broadsense heritability estimates and very low narrowsense estimates indicate that the genetic control of AH involves dominance rather than additive gene action. Skewed frequency distributions for low AH tendency in F_2 populations and behavior of most F_1 progenies also supported dominant gene action.

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