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Flowers with Abnormal Numbers of Involucral Bracts in Cotton[1]

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ABSTRACT

A primitive race stock of cotton (*Gossypium hirsutum* L.) Texas 703, had 26 to 59% flowers with more than the usual number of three involucral bracts in four seasons in the field at Phoenix, Ariz. The most common variant was a flower with a fourth, almost full-sized bract, but other flowers had up to seven bract segments. Two cultivars, 'Deltapine 16' and 'Stoneville 7A', had lower frequencies of flowers with abnormal numbers of bracts. Plants of the race stock and cultivars had only three-bract flowers in the winter greenhouse. We selected race stock $\times$ cultivar F_5 progenies that were almost true-breeding for abnormal (98.9%) and normal (99.5%) numbers of bracts. About one-third of the F_4 plants selected for all abnormals in the field had low frequencies of abnormals when cut back and moved into the greenhouse in the fall. The most common variant in the advanced-generation selections, as in the race stock, was a flower with four bracts; one progeny had 95% four-bract flowers. Others, however, had lower proportions of four-bract flowers in relation to other abnormal numbers. Thus, it may be possible to select plants having flowers with more than four bracts. An inheritance study of selected F_3 parents and four hybrid generations suggested that abnormal bract number is conditioned by three or four pairs of genes that show additive, intra-allelic, and interallelic effects.

Additional index words: Gossypium hirsutum L., Quantitative inheritance, Penetrance, Expressivity, Canalization.

DEVIANTS from constant numbers of floral parts in higher plants are not common, presumably because constant numbers represent the end product of adaptive developmental processes (canalization). Nevertheless, deviants have been observed in numerous species representing several plant families (5).

Huether (2, 3) studied corolla lobes deviating from the usual number of five in *Linanthus* spp. (Polemoniaceae) growing in natural stands in California. He concluded that these deviants represented genetic variants and were not merely the result of developmental accidents. Apparently the normal pentamerous corolla usually found in *Linanthus* spp. is adaptive and is maintained at a high frequency by natural selection.

Cotton (*Gossypium hirsutum* L.) normally has three involucral bracts that subtend the flower. In 1974, plants of a primitive race stock, Texas 703 (T-703), had over 50% flowers with more than three bracts when grown in the field at Phoenix, Ariz. T-703 was crossed to two cultivars, 'Deltapine 16' (DPL-16) and 'Stoneville 7A' (St 7A). When parents and hybrids were scored in 1975, it was discovered that the parental cultivars also had some (11 to 17%) flowers with more than three bracts. The most common variant was the appearance of a fourth, almost full-sized bract (Fig. 1). Other abnormal numbers were one, two, or three extra, small appendages associated with three or four full-sized bracts. Rarely, flowers had two or five full-sized bracts. Only three-bract flowers were observed in the race stock and cultivars after they had been cut back and moved into the greenhouse in the fall.

The objectives of this paper are: 1) to present the results of scoring bract number in T-703 and St 7A and in hybrid generations between these parents; 2) to show the results of selecting for both higher and lower frequencies of abnormal bract number in advanced-generation progenies; 3) to discuss the possibility of devtloping strains true-breeding for abnormal bract numbers.

MATERIALS AND METHODS

On 31 Mar. 1975, seeds of T-703, St 7A, DPL-16, F_1, F_2, and backcross populations between the race stock and cultivars were planted in expanded peat pellets in the greenhouse of the Cotton Research Center, Arizona Agricultural Experiment Station, Phoenix. On 16 April, seedlings were transplanted 46 cm apart in unreplicated, single-row plots 1 m wide $\times$ 9.1 m long in the field. When all plants were flowering, bract numbers were recorded for 10 randomly chosen flowers per plant. Number of full-sized bracts was recorded (e.g., 3, 4) as well as smaller appendages (e.g. 3^{+1}).

In 1976, we recorded bract numbers for another set of the T-703 and St 7A parents, F_1 and F_2 populations, and F_3 progenies from F_2 plants selected the previous season for high frequencies of three- or four-bract flowers. Seeds were planted in the greenhouse 24 March and seedlings were transplanted to the field 8 April; plant and row spacings were the same as those in 1975. Crosses were made in the field between an F_3 plant, 1024-7, selected for 80% four-bract flowers (no plants with a higher frequency were available), and two F_3 plants, 1025-9 and 1025-12, which had only three-bract flowers. In 1976-77, 1024-7, 1025-9, and 1025-12, and F_1 hybrids (10259 $\times$ 1024-7 and 1025-12 $\times$ 1024-7) were grown and crossed in a winter nursery at Iguala, Mexico to produce F_2 and backcross progenies.

In 1977, plants of the original parents, F_1, and F_2 generations were scored in the field at Phoenix, as were F_4 progenies from the selected F_3 plants. Parents, F_1, F_2, and backcross populations from the seeds sent to Iguala were also scored. Seeds from Arizona were planted in the greenhouse 24 March and seedlings were transplanted to the field 7 April. Seeds returned from Iguala were planted in the greenhouse 8 April and transplanted to the field 25 April. In 1978, parents and F_5 progenies from selected F_4 plants were grown at Phoenix, along with several other hybrid progenies. Each fall, selected plants were cut back, moved into a greenhouse at Phoenix and scored for number of bracts.

We estimated the number of genes controlling differences in bract number by weighting the observed number of F_2 and backcross plants in each bract-number class with the frequency of the selected parental populations in that class. For example, the "observed" number of plants carrying the 1024-7 parental genotype in the 4/10 class in (1025-9 $\times$ 1024-7) F_2 is (2/40) (7) = 0.35 (see Table 2). Extending this method to all classes in F_2 that are also represented in the 1024-7 parental population results in an "observed" number of two plants with the 1024-7 genotype among the 181 plants in the F_2 population.

F_2 and backcross data were uninformative when we calculated "observed" number of plants that presumably represented the 1025-9 and 1025-12 parental genotypes. We did not attempt a gene-number analysis for T-703, St 7A, and their hybrid generations because of the bimodal distribution in T-703 and because parental values overlapped.

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Fig. 1. Bases of two cotton flowers showing the normal three-bract and the abnormal four-bract condition.

For a quantitative genetic analysis, counts of abnormal-bract flowers per 10 flowers per plant were transformed [$(X+1)^{1/2}$ was used because the original counts included many zeroes], and means and variances were calculated for each parental and hybrid population. Differences between generation means were tested for significance with the t-test. For 1025-9 and 1024-7 and their four hybrid generations, the generation-mean analysis of Mather and Jinks (4, p. 90 et seq.) was used to estimate genetic effects.

RESULTS

The mean frequency of flowers with abnormal numbers of bracts in T-703 was over 50% in 1975, 1976, and 1978, but only 26% in 1977 (Table 1). Penetrance was complete 3 of the 4 years because at least some flowers on all 84 plants had more than three bracts. In 1977, however, one plant apparently had only three bract flowers (Table 1). All plants of T-703 had only three-bract flowers in the greenhouse in 1974-75, 1975-76, and 1977-78.

Both cultivars, St 7A and DPL-16, also had some flowers with abnormal bract numbers in the field all four seasons (an unexpected occurrence in 1975, when we first observed it). Frequency of abnormal bract number varied in St 7A from 1.0% in 1977 to 47.5% in 1978 (Table 1; DPL-16 data not shown). Both cultivars had only three-bract flowers in the winter greenhouse.

(T-703 × St 7A) F_1 and F_2 means were usually intermediate between and significantly different from those of the parents. F_1 populations showed considerable variability in bract number in 1975 and 1976. In 1977, however, 90% of the F_1 plants had only three-bract flowers. Backcross means (B_1 and B_2) were intermediate between F_1 and the respective recurrent parent, and significantly different from both parents (Table 1). Considerable interseasonal variation was also observed in the hybrid populations. F_1 and F_2 means were not dissimilar in 1975 and 1976, but were markedly lower in 1977.

We selected higher frequencies of both normal and abnormal bract numbers in (T-703 × St 7A) F_3 than in the original parents. In 1976, an F_3 plant, 1024-7, had 80% abnormal flowers. An F_4 progeny from this plant averaged 78% abnormals in 1977. Eight of 40 plants in this progeny had 100% abnormal flowers when scored in midseason (Table 2), as compared to T-703, scored at the time time, which had no plants with more than 50% abnormals (Table 1). These eight plants had lower frequencies of abnormal flowers in the field in late September. In the greenhouse, one of the eight that had been moved in from the field showed 20% abnormal flowers; the other seven had only three-bract flowers. In the field in 1978, the mean percentage of abnormal-bract flowers 98.9% in F_5 progeny rows from these eight plants (Table 2).

Two other F_3 plants, 1025-9 and 1025-12, had only three-bract flowers in the field in 1976. F_4 progenies in 1977, and the F_5 progenies in 1978 stemming from 1025-9, had low frequencies of abnormal-bract flowers in the field (Table 2). One of the 21 plants of the 1025-9 F_4 progeny moved into the greenhouse in 1977 had 10% abnormal flowers, but the other 20, and the five of 1025-12 F_4, had only three-bract flowers.

Table 1. Frequency distributions and mean frequencies of flowers with abnormal bract numbers per 10 flowers per plant in parental, F_1, and segregating generations of cotton.

Parent or generation	Year	Plants	Abnormal bract-no. flowers/10 flowers/plant											$\bar{X}\pm$S.E.*	Significantly different from*
			0	1	2	3	4	5	6	7	8	9	10		
		No. plants													
T-703 (P_1)	1975	35			1	4	9	4	2	11	3	1		5.49±0.13	P_2, F_1, F_2, B_1, B_2
St 7 A (P_2)		41	10	21	7	3								1.07±0.04	P_1, F_1, F_2, B_1, B_2
F_1		28	1	7	11	3	4	2						2.29±0.09	P_1, P_2
F_2		137	16	30	23	28	15	8	7	6	3		1	2.76±0.06	P_1, P_2, B_2
$F_1 \times P_1$ (B_1)		24	3	4	5	7	3	2	1					2.38±0.12	P_1, P_2
$F_1 \times P_2$ (B_2)		190	29	67	47	19	19	3	5		1			1.78±0.03	P_1, P_2, F_2
P_1	1976	16			1	5	3		1	2	4			5.06±0.25	P_2, F_1, F_2
P_2		20	2	4	8	2	3	1						2.15±0.11	P_1, F_1
F_1		20		2	5	4	2	4	2	1				3.55±0.15	P_1, P_2, F_2
F_2		199	43	52	51	30	13	8	1		1			1.76±0.03	P_1, F_1
P_1	1977	7	1	1	1	2	1	1						2.57±0.81	P_2, F_2
P_2		20	18	2										0.10±0.01	P_1, F_1, F_2
F_1		20	11	5	2	2								0.75±0.05	P_2
F_2		99	43	36	13	6	1							0.85±0.02	P_1, P_2
P_1	1978	33				2	4	9	8	4	4	2		5.85±0.12	P_2
P_2		20			3	3	2	6	2	3		1		4.75±0.18	P_1

* Transformed means $[(X + 1)^{1/2}]$ significantly different, within years, at the 0.05 level of probability, according to the t-test; means and standard errors presented in this table were converted back to the original units.

Table 2. Frequency distributions and mean frequencies of flowers with abnormal bract numbers per 10 flowers per plant in F_3, F_4, and F_5 progenies of cotton and in hybrid generations from crosses between selected F_3 plants.

Parent or generation	Year	Plants	Abnormal bract-no. flowers/10 flowers/plant											$\bar{X}\pm$S.E.*	Significantly different from*
			0	1	2	3	4	5	6	7	8	9	10		
		No. plants													
(T-703 × St 7A)F_3 (1024)	1976	13					2	2	4	3	2			6.08±0.16	1025
1024-7 F_3 selection		1									1			8.00	
(T-703 × St 7A)F_3 (1025)		20	16	4										0.20±0.01	1024
1025-9 F_3 selection		1	1											0.00	
1025-12 F_3 selection		1	1											0.00	
1024-7 F_4 progeny (P_1)	1977	40					2	6	4	4	4	12	8	7.75±0.13	P_2, F_1a, F_2a, B_1, B_2, P_3, F_2b, B_3, B_4
1025-9 F_4 progeny (P_2)		28	27	1										0.04±0.00†	P_1, F_1a, F_2a, B_1
F_1a (=1025-9 F_3 × 1024-7F_3)		7	4	3										0.43±0.03	P_1, P_2, B_1
F_2a		181	92	42	14	13	7	3	5	2	2	1		1.22±0.03	P_1, P_2, B_1, B_2
B_1 (=F_1a × 1024-7F_3)		98	5	10	8	10	17	15	13	10	6	3	1	4.41±0.12	P_1, P_2, F_1a, F_2a, B_2
B_2 (=F_1a × 1025-9F_3)		96	81	9	3	2		1						0.28±0.01	P_1, F_2a, B_1
1025-12 F_4 progeny (P_3)		38	35	3										0.08±0.00†	P_1, F_2b, B_3
F_1b (=1025-12F_3 × 1024-7F_3)		0													
F_2b		197	104	45	22	14	8	4						0.93±0.02	P_1, P_3, B_3, B_4
B_3 (=F_1b × 1024-7F_3)		98	5	7	6	7	11	16	16	9	10	4	7	5.20±0.13	P_1, P_3, F_2b, B_4
B_4 (=F_1b × 1025-12F_3)		97	90	3	2	2								0.13±0.00†	P_1, F_2, B_3
1024-7F_5‡	1978	155									2	13	141	9.89±0.01	1025-9F_5
1025-9F_5§		194	184	10										0.05±0.00†	1024-7F_5
(1025-9F_4 × 1024-7F_4)F_1		57	2	3	3	10	3	13	10	10	2	1		4.75±0.13	1025-9F_5, 1024-7F_5

* Transformed means $[(X+1)^{1/2}]$ within year and cross, significantly different at the 0.05 level of probability, according to the t-test; means and standard errors presented in this table were converted back to the original units. † Rounded to nearest 0.01; calculated values: P_2 = 0.0004; P_3 = 0.00016; B_4 = 0.0025; 1025-9F_5 = 0.0003. ‡ Progenies from eight plants selected in 1977 for 100% abnormals. § Progenies from 10 plants selected in 1977 for all three-bract flowers.

Seven of 15 other plants from various (T-703 × St 7A) F_4 and BC_1 progenies, that had all abnormal flowers in the field in 1977, had 10 to 30% abnormals when moved into the greenhouse. In the field in 1978, the percentage of abnormals in 12 progeny rows from various plants selected with all abnormal flowers in 1977, varied from 83.0 to 100.0%. Among these were four F_5 progenies (79 plants), descended from one F_3 plant, 1024-6, that had 100% abnormal flowers.

In the field in 1977, mean numbers of abnormal-bract flowers in (1025-9 × 1024-7) F_1 and F_2 were significantly different from those in both parents, but closer to that of the normal-bract parent, 1025-9. Backcross means were intermediate between F_1 and the respective recurrent parent, and significantly different from both parents and the other three hybrid generations (except B_2, the backcross between F_1 and 1025-9). Distribution of the backcross generations of 1025-12 × 1024-7 were similar to those of 1925-9 × 1024-7, but distribution of F_2 was skewed more towards the three-bract phenotype (Table 2).

In 1978, (1025-9 × 1024-7) F_1, the only hybrid generation represented, had a mean intermediate between and significantly different from both parents. This population showed considerable instability, with a range of 0 to 9 abnormal-bract flowers and a distribution completely different from the small (1025-9 × 1924-7) F_1 in 1977 (Table 2).

The most common abnormal phenotype, in progenies selected for all abnormals, was four full-sized

Table 3. Frequency distributions of number of bract segments in F_5 and BC_1S_1 progenies of cotton plants selected in 1978 for all abnormal bract flowers.

Progeny	Total plants	Plants selected with all abnormals	No. bracts/flower						
			3^{+1}	4	3^{+2}	4^{+1}	3^{+3}	4^{+2}	4^{+3}
	No.		%						
(1020-9)F_5†	17	16	10.0	63.1	10.6	11.9		4.4	
(1024-2)F_5	14	10	4.0	80.0		14.0		2.0	
(1024-6)F_5	79	79	0.4	88.5	1.3	8.2		1.5	0.1
(1024-7)F_5	156	141	1.2	94.9	1.8	1.5		0.6	
[(1025-12 × 1024-7) × 1024-7]BC_1S_1	126	90	4.3	84.3	4.3	5.9	0.3	0.9	
Total no.	375	320							
Mean %			2.0	89.9	2.3	4.8	0.1	1.0	<0.1

† (DPL-16 × T-703)F_5, all others = (T-703 × St 7A)F_5 and BC_1S_1; totals and means include only the latter.

Table 4. Frequency distributions of number of bract segments in F_1 progenies from crosses of plants selected for all abnormal-bract numbers with those selected for all three-bract flowers.

Progeny	Plants	No. bract segments/flower						
		3	3^{+1}	4	3^{+2}	4^{+1}	3^{+3}	4^{+2}
	No.	%						
(1025-9F_4 × 1024-7F_4)F_1	57	52.4	14.3	15.3	7.2	7.6	0.9	2.3
1025-9 × [(1025-9 × 1024-7) × 1024-7]F_1	55	52.4	16.2	14.5	2.8	8.7	3.5	1.9
1025-9 × [(1025-12 × 1024-7) × 1024-7]F_1	75	53.3	15.2	12.1	4.9	9.3	2.4	2.8
Total no.	187							
Mean, 1,870 flowers, %		52.7	15.3	13.8	4.9	8.7	2.2	2.4
Mean, 881 flowers with abnormal nos., %			32.3	29.2	10.4	18.4	4.7	5.0

Table 5. Generation-mean analysis for 1024-7, 1025-9, and four hybrid generations.

Genetic effect	$\bar{X}$ ± S.E.
Additive [d]	0.96 ± 0.03*
Dominance [h]	1.85 ± 0.49*
Epistasis:	
Homozygous × homozygous [i]	1.12 ± 0.19*
Homozygous × heteroxygous [j]	0.40 ± 0.14*
Heterozygous × heteroxygous [l]	−1.53 ± 0.11*

* Significantly different from zero at the 0.05 probability level, according to t-tests.

bracts. In the field in 1978, 89.9% plants in three (T-703 × St 7A) F_5 progenies and one BC_1S_1 progeny (from F_4 and BC_1 plants selected for all abnormal-bract flowers) had only flowers with abnormal numbers of bracts. A (DPL-16 × T-703) F_5 progeny, 1020-9 F_5, had a lower frequency, but nevertheless a majority (63.1%) of flowers with four full-sized bracts (Table 3). In contrast, F_1 progenies from crosses of F_4 plants selected for all abnormals with those selected for all three-bract flowers had much lower frequencies of flowers with four full-sized bracts (Table 4).

Data from the two F_2 populations (F_2a and F_2b in Table 2) fit both three- and four-gene models (three of 378 plants were estimated to have the same genotype as the 1024-7 parent). Data from the F_1 × 1024-7 testcross populations (B_1 and B_3 in Table 2) fit a four-gene model (16 of 196 plants were estimated to have the 1024-7 genotype).

The generation-mean analysis of 1025-9, 1024-7, and four hybrid generations showed that additive [d], dominance [h], and all three epistatic [i], [j], and [l] sources of genetic variation were significant (Table 5).

DISCUSSION

Three-bract flowers in *G. hirsutum* and in other *Gossypium* spp. (1) represent the visible end product of a series of developmental events that lead to a phenotype well adapted to normal environments (canalization). The irrigated desert environment, characterized by very high temperatures and intense sunlight, induces stresses probably rarely encountered by the ancestral stocks of the cottons studied. These stresses, coupled with the proper plant genotype, probably trigger a switch at a critical stage in the development of floral primordia, leading to abnormal bract-number phenotypes. A diminution of these stresses, or a genotype capable of producing only three-bract flowers, will result in the normal phenotype. Floral primordia are developing continuously because of the indeterminate growth habit of the cotton plant and will thus be subjected to a range of environmental conditions at the critical stage of determining bract number. Thus, some floral primordia borne on plants genetically capable of producing abnormal numbers of bracts will produce three bract flowers because environmental variables do not exceed the threshold required for expression.

Selection for abnormal numbers of bracts presumably lowers the threshold for expression and consequently decreases the flower-to-flower variability in number of bracts. Selection for three-bract flowers raises that threshold but also reduces variability. A genotype conditioning an intermediate expression, such as an F_1 heterozygous at all relevant loci, would then be expected to show more flower-to-flower variability; our data indicate that this is indeed the case.

Penetrance (considered complete if at least one flower on all plants of a population has an abnormal number of bracts) varied both within and between seasons. Penetrance was at its maximum during the long, hot days of June and July, declined in the field later in the season, and was practically nil in the greenhouse during the winter. Huether (2, 3) reported similar results in *Linanthus* spp., in which proportions of corollas having abnormal numbers of lobs increased both in nature and with greenhouse culture under long daylengths and high temperatures. Interseasonal differences in penetrance may be illustrated by reference to the original parents, T-703 and St 7A. In the former, penetrance was incomplete in 1977, but complete the other 3 years; in the latter, penetrance was complete only in 1978.

It should be possible to stabilize strains in advanced generations that will breed true for three-bract flowers because this phenotype represents the normal, adaptive condition. In F_5, however, progenies from plants selected for three-bract flowers in F_3 segregated a low frequency of plants with one flower of 10 showing three full-sized bracts plus a smaller segment.

Whether we can stabilize strains true breeding for an abnormal number of bracts remains to be seen, but results are encouraging. The mean percentage of abnormals increased from 58.5% in the original parent, T-703 (Table 1, 1978) to 98.9% in selected (T-703 × St 7A)F_5 progenies (Table 2, 1978), and variance decreased concomitantly. Perhaps most encouraging are the four F_5 progenies descending from (1024-6)F_3 that had all abnormal flowers when examined in the field in 1978. We must temper our optimism, however, because the mutant character was expressed more strongly in 1978 than in any previous season in which we had observed it. In fact, a number of breeding stocks unrelated to T-703, St 7A, or DPL-16, showed at least some abnormal bract numbers in the field in 1978.

Beforehand, we might expect that rigorous selection for a high frequency of four-bract flowers (the most common variant) would lead to instability, because this is presumably an unadapted phenotype. For example, Huether (2, 3) observed low frequencies of variant corollas, primarily with four to six (rarely three to 10) lobes, in natural populations of *Linanthus androsaceus* (Benth.) Greene ssp. *androsaceus*. These plants normally have pentamerous corollas. After plants had been inbred and subjected to environmental stress in the greenhouse, however, he observed corollas with one to 16 lobes.

Variation in expressivity for bract number in cotton, however, was much lower than that for corolla number in *Linanthus*. The number of bract segments varied from two to seven, but the former and the latter, and five full-sized bracts, occurred rarely. Three and four full-sized bracts represented the most common phenotypes; three or four full-sized bracts plus one or two small appendages occurred less frequently.

In 1978, the mean percentage of flowers with four full-sized bracts varied from 56.7% in 33 plants of the original parent, T-703 ($\overline{X}$=3.70 bracts per flower), to 94.9% in 141 plants of 1024-7 F_5 ($\overline{X}$=4.05 bracts per flower) from eight F_4 plants selected in 1977 for all abnormal-bract flowers. Thus, it appears possible to develop strains that consistently produce flowers with four full-sized bracts in the field in Arizona. It may also be possible, but probably more difficult, to select for diversity, or for a higher bract number. For example, the mean percentage of flowers with four full-sized bracts was 63.1% in 1020-9 F_5 ($\overline{X}$=4.31 bracts per flower), a derivative of DPL-16 × T-703.

The recent breaching of the environmental threshold for winter greenhouse expression of the trait encourages us to believe that we may be able to select for increased bract number under those conditions.

Genetic analyses suggest that the inheritance of abnormal numbers of floral bracts in cotton is conditioned by three or four gene pairs that show additive effects and both intra- and interallelic interactions. We interpret these data with caution, however, because of the small hybrid populations, the possibility of residual heterozygosity in the parents, and large amounts of non-additivity and the presence of a significant environmental component. A more precise analysis will not be possible unless we can in fact stabilize true-breeding lines in a uniform genetic background.

Three- and four-bract marker stocks, once developed, could have several uses; e.g., to study 1) the relationships between qualitative and quantitative inheritance patterns; 2) the possibility of partitioning individual gene effects, i.e., genes that condition the presence of abnormal bract numbers vs. those that determine thresholds for expression; 3) genotypic-environmental interactions in specified environments; 4) response of cotton insects and disease organisms to previously unencountered flower-bud phenotypes; 5) relationships between number and size of floral and fruiting parts.

Other possible approaches, using the abnormal-bract number germplasm, would be to 1) attempt to increase the number of bract segments per flower above four; 2) increase the range of environments in which abnormal bract phenotypes would be expressed.

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