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Genotype × Environment Interactions in Sweet Potato Yield and Quality Factors

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Abstract. **Genotype (G) × environment (E) interactions were measured in sweet potatoes (*Ipomoea batatas* L.) for yield (seven genotypes, six locations, 3 years) and selected quality factors (nine genotypes, six locations, 2 years). Yield of all grades of roots and all quality factors tested were affected significantly by genotype, environment, and G × E interactions. Quality factors were less affected by G × E interactions than yield factors. Broad-sense heritability estimates ranged from 75% to 92% for yield factors and 94% to 99% for quality factors. Estimates of variances of clonal means with varying years, locations, and replications suggest that 2 years, four locations, and four replications would provide reliable test data for yield and quality factors.**

Genotype × environment (G × E) interactions are of primary concern to plant breeders. The subject has been extensively reviewed in several publications (1, 11, 12). The effect of G × E interactions in breeding populations is to reduce correlations between phenotype and genotype resulting in invalid or biased conclusions about genetic variance. Knowledge of the type and extent of G × E effects for a particular crop results in more efficient use of available resources, more accurate use of breeding methods, and more gain over time through selection (5).

Sweet potatoes are grown over a wide array of environments. Many traits of interest to sweet potato breeders have been shown to be sensitive to environmental changes; however, few studies have assessed the extent of G × E interactions. Root weight (yield) is one of the most important traits to breeders and has been shown to be variable from one environment to another (3, 10). Crude protein and percent dry matter also differed with environments, and G × E interactions for those two traits and root yield were significant in a study conducted by Li (9) using Taiwanese cultivars. Total yield was also shown to be significantly affected by G × E interactions in a Philippine population of cultivars (3).

The objectives of this study were to estimate effects of G × E interactions on sweet potato yield and quality in germplasm currently being used in breeding programs and in the commercial industry in the United States.

Materials and Methods

Ten sweet potato clones, including cultivars and experimental selections, were grown at eight selected locations in each of 3 years. Transplants were produced from bedded roots at the Horticultural Crops Research Station, Clinton, N.C., and transplanted between 23 May and 4 June of each year. Stand counts were taken 2 weeks after transplanting and missing plants were replaced. Decisions concerning cultural practices during the growing season were left to individual growers and were considered to be a part of the particular environment represented. However, cultural practices were monitored each year through a questionnaire and were found to vary minimally among growers.

A randomized complete block design with four replications was used. Individual plots were 7.6 m long with plants spaced 0.3 m in the row with 1.1 m between rows. Replications were separated by 1-m unplanted buffer areas, and the entire test at each location was surrounded by 'Jewel' plants in adjacent rows.

Table 1. Effect of genotype on mean yield of sweet potatoes.[z]

Genotype	Yield (t·ha^{-1})[y]				
	Total marketable	No. 1	Canners	Oversize	Culls
Pope	27.3 a	18.1 a	5.6 c	2.0 a	2.2 d
Copper Skin Jewel	22.1 b	12.9 cd	7.3 b	0.7 bc	2.4 bcd
Jewel	21.9 b	14.1 b	5.5 c	1.1 b	2.6 cd
Centennial	21.6 b	13.6 bc	5.7 c	1.7 a	2.8 abc
NC PR198	20.7 bc	11.4 ef	7.9 a	0.4 c	2.9 abc
NC 317	19.6 cd	10.3 f	8.1 a	0.3 c	3.1 ab
NC 311	18.2 d	11.9 de	3.2 d	2.1 a	3.3 a

[z]Data averaged over six locations, 3 years.
[y]Mean separation by Duncan's multiple range test, 5% level.

Table 2. Effect of location and year on mean yield of sweet potatoes.

Treatment	Yield (t·ha^{-1})[z]				
	Total marketable	No. 1	Canners	Oversize	Culls
Location[y]					
Tyrrell	29.4 a	19.2 a	8.7 a	1.6 ab	1.6 b
Rowan	22.2 b	15.3 b	6.6 b	0.3 d	3.4 a
Columbus	20.5 c	13.4 c	5.2 d	1.9 a	2.5 b
New Hanover	20.4 c	12.1 d	5.8 c	1.0 bc	3.5 a
Wayne	19.3 cd	12.8 cd	5.1 c	1.4 bc	1.2 a
Nash	17.9 d	11.7 d	5.3 d	0.9 c	3.3 a
Year:[x]					
1	22.1 a	14.5 a	6.1 b	1.6 a	3.9 a
2	23.0 a	14.1 a	7.1 a	1.1 b	2.5 b
3	19.8 b	13.7 a	5.1 c	1.0 b	1.8 c

[z]Separation within locations and within years by Duncan's multiple range test, 5% level.
[y]Data averaged over 3 years, seven genotypes.
[x]Data averaged over six locations, seven genotypes.

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Table 3. Analysis of variance for yield and selected quality factors of sweet potatoes.

Source	Mean squares for yield (t·ha^{-1})[z]					Mean squares for quality factors				
	df	Total	No. 1	Canner	Oversize	Culls	df	Dry matter (%)	Intercellular space (%)	Protein (%)	Baking[y]
Environment (E)	71						47				
Years (Y)	2	469.4*	25.1	173.6*	18.2*	191.0*	1	1049.7**	0.0087**	97.6**	1.496**
Locations (L)	5	1382.9*	649.8*	155.6*	26.0*	62.7*	5	100.3**	0.0021**	85.4**	1.107**
Y × L	10	729.4*	452.8*	64.7*	18.8*	71.3*	5	65.0**	0.0006**	28.6**	0.0380*
Rep (Y × L)	54	48.5*	36.0*	6.2*	3.7*	4.2*	36	3.0*	0.00008**	0.9	0.366**
Genotypes (G)	6	582.2*	525.0*	221.5*	42.9*	10.4*	8	80.88*	0.00531**	23.10**	3.324**
G × E	102						88				
Y × G	12	79.8*	57.8*	13.4*	5.2	8.8*	8	3.73	0.000078*	1.297	0.2429
L × G	30	115.4*	94.4*	11.4*	6.6*	11.4*	40	3.64**	0.000058**	1.292**	0.1487
Y × L × G	60	46.3*	31.6*	6.7*	4.6*	5.4*	40	3.76**	0.000066*	1.239**	0.1945*
Error	321	30.3	18.7	3.5	3.2	2.8	277	1.95	0.000033	0.668	0.1311

[z]*,**Significance of F at the 5% and 1% levels, respectively.
[y]Rated on a 0 (poor) to 10 (best) scale.

Table 4. Effect of genotype on selected quality factors of sweet potatoes.[z]

Genotype	Percent dry matter	Intercellular space (ml/100 ml)	Percent protein[y]	Baking score[x]
NC PR198	26.16 a	10.56 a	7.20 bc	8.02 c
Centennial	25.89 a	9.83 b	7.53 b	8.11 c
NC 317	25.28 b	7.80 de	7.13 d	8.04 c
Pope	25.04 b	9.06 c	5.89 c	8.14 b
Jewel	23.78 c	7.51 ef	7.04 c	8.32 b
NC 311	23.47 cd	8.05 d	6.92 c	7.98 c
Goldrush	23.07 d	7.83 de	8.57 a	8.00 c
Scarlet	22.88 de	7.77 de	7.28 bc	8.72 a
Copper Skin Jewel	22.44 e	7.65 ef	7.49 b	8.57 a

[z]Data averaged over six locations, 2 years; separation by Duncan's multiple range test, 5% level.
[y]Calculated on a dry-weight basis.
[x]Rated on a 0 (poor) to 10 (best) scale.

Table 5. Effect of location and year on selected quality factors of sweet potatoes.

Treatment	Percent dry matter	Intercellular space (ml/100 ml)	Percent protein[y]	Baking score[x]
Location[z]				
New Hanover	26.22 a	9.24 a	6.04 d	8.07 c
Rowan	25.21 b	8.02 c	6.40 c	8.23 b
Nash	23.99 c	8.81 b	8.10 b	8.07 c
Sampson	23.49 d	8.19 c	6.30 c	8.38 a
Wayne	23.19 de	7.78 d	8.51 a	8.30 ab
Columbus	22.86 e	8.73 b	8.07 b	8.07 c
Year[w]				
1	26.07 a	7.98 a	7.70 a	8.15 b
2	22.54 b	8.88 b	6.76 b	8.27 a

[z]Data averaged over nine genotypes, 2 years; separation by Duncan's multiple range test, 5% level.
[y]Calculated on dry-weight basis.
[x]Rated on 0 (poor) to 10 (best) scale.
[w]Data averaged over nine genotypes, six locations.

Roots were harvested each year after a growing season of 135–140 days. Although 135 days was the preferred number of growing days, inclement weather occasionally caused a 1- to 5-day delay in harvest. Roots were collected and graded into U.S. No. 1, canner, oversize, and cull grades according to the National Sweet Potato Collaborator Group guidelines (13). Each grade then was weighed. A two-root sample of U.S. No. 1 roots was taken from each plot to determine dry matter and intercellular space; another two-root sample was taken to evaluate baking quality; and a six-root sample was taken for protein determination.

Dry matter was determined at harvest by drying 100-g samples in a forced air oven for 48 hr and reweighing. Intercellular space was calculated immediately after harvest according to the method of Kushman and Pope (8); percent protein was determined immediately after harvest using a semi-micro-Kjeldahl method (2) with a 6.25 conversion factor; baking scores were determined according to National Sweet Potato Collaborator Group guidelines, except that only two roots per treatment were baked. Samples for baking were cured (95% RH, 27° to 30°C) for 6 days and stored (12°) until evaluated by an untrained taste panel of four individuals (3 to 4 months after harvest).

Data were subjected to a standard analysis of variance (ANOVA). Locations and years were considered random, and treatments fixed. Variance components were estimated from expected mean squares. Standard errors of variance components were computed according to Kempthorne's method for determining variance of variance components (7). Variances of clonal means were computed according to Jones et al. (6).

Results and Discussion

Data were not available for all genotypes in each environment due to lack of plants or poor stand. Therefore, a balanced data set of seven genotypes, six locations, and 3 years was used for ANOVA of yield. For quality factors, the data set consisted of nine genotypes, six locations, and 2 years.

Summaries of root yield by grade averaged over genotypes, locations, and years are presented in Tables 1 and 2. Yields of all grades were significantly different for genotypes, locations, and years with one exception: yield of U.S. No. 1 grade roots did not change significantly over years. The ANOVA for the entire model (Table 3) reflects these significant differences as well as a strong interaction between years and locations. Location mean squares for the two most important yield factors

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Table 6. Estimated variance components and broad-sense heritability estimates for yield and selected quality factors of sweet potatoes.

Yield or quality factor	Estimate of variance component[z]						
	σ^2_g	σ^2_{gy}	σ^2_{gl}	σ^2_{gyl}	σ^2_e	σ^2_m	H
Total	6.02	1.40	5.76[y]	4.00[y]	30.3[y]	2.070	74.4
No. 1	5.62	1.09	5.23[y]	3.20[y]	18.7[y]	1.673	77.0
Canners	2.83	0.28	0.39	0.80[y]	3.50[y]	0.251	91.8
Oversize	0.50	0.03	0.17	0.35	3.20[y]	0.101	83.3
Culls	−0.06	0.14	0.50[y]	0.65[y]	2.80[y]	0.205	0.0
Percent dry matter	1.61[y]	0.0	0.0	0.45	1.95[y]	0.052	96.9
Percent intercellular space $\times 10^{-4}$	1.09[y]	0.01[y]	0.0	0.08	0.33[y]	0.01	99.1
Percent protein	0.45[y]	0.0024	0.0066	0.1430[y]	0.667[y]	0.191	95.9
Baking	0.65[y]	0.0039	0.0	0.0159[y]	0.131[y]	0.040	94.2

[z]σ^2_m = variance of a clonal mean = $\sigma^2_{gy}/y + \sigma^2_{gl}/l + \sigma^2_{gly}/ly + \sigma^2_e/rly$.
[y]Variance component estimate equal to or greater than twice the standard error of the estimate.

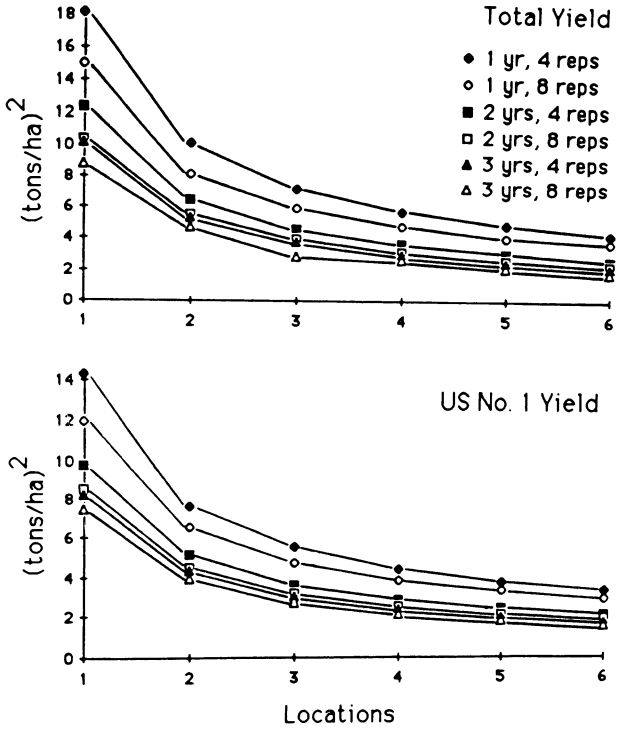

Fig. 1. Expected variance of total and U.S. No. 1 yield means with varying numbers of years, locations, and replications.

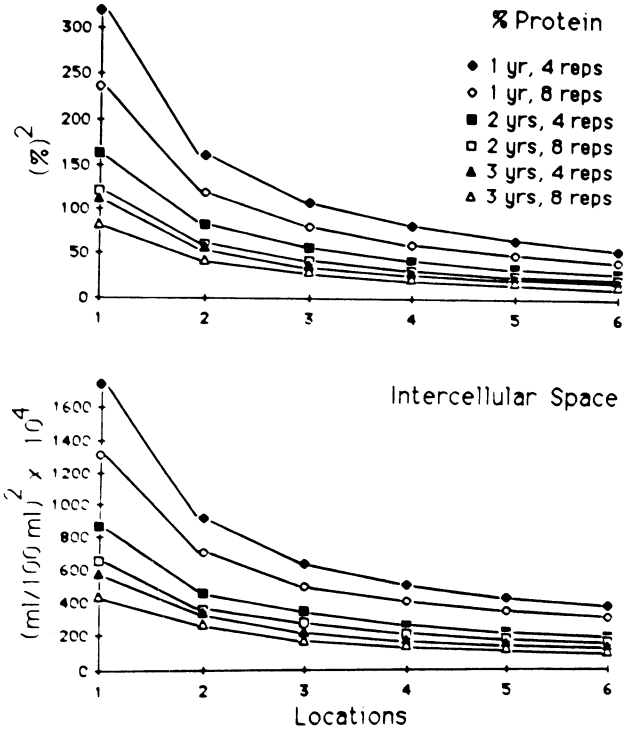

Fig. 2. Expected variance of percent protein and intercellular space with varying numbers of years, locations, and replications.

(total and U.S. No. 1) are greater than all other mean squares including those of genotype, although not always significantly greater. In addition, the ANOVA revealed significant G × E interactions in yield grades. First-order interactions [year × genotype and location × genotype (Y × G and L × G, respectively)] are significant for yields of all grades except that the oversize grade is not affected by year × genotype (Y × G) interaction. Second-order interaction year × location × genotype (Y × L × G) is also significant for yield in all grades. Even though Y × G, L × G, and Y × L × G effects are statistically significant in most cases, they are always smaller than genotype or environment effects, except in the case of the year mean square for No. 1 root yield.

All measured quality factors differed significantly over genotypes (Table 4) and locations and years (Table 5). Intercellular space (IS) has been reported to remain constant over years and locations (14); however, in this study, IS was significantly different between years and between locations. These data were based on measurements obtained in 12 environments (six locations, 2 years). A smaller, balanced data set for IS from this study, which included 3 years' data, was analyzed (data not shown) and also revealed a significant effect of years and locations on IS.

The ANOVA (Table 3) shows that, as with yield, environmental effects (Y, L, Y × L) account for much of the observed variability. These effects were especially evident in percent dry matter and percent protein. There are fewer significant G × E interactions for quality factors than for yield components, and

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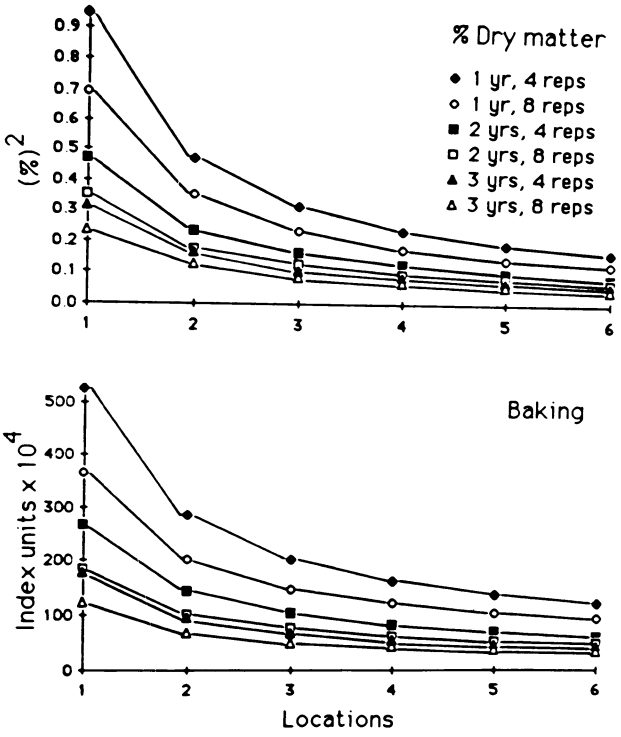

Fig. 3. Expected variance of percent dry matter and baking quality with varying numbers of years, locations, and replications.

interaction mean squares are small compared to genotype and environment mean squares. Only IS reveals a significant effect of both first-order (L × G, Y × G) and second-order (Y × L × G) interactions. Y × G was not a significant source of variation for dry matter, protein, or baking. Baking quality is affected significantly only by the second-order G × E interaction (Y × L × G).

Variance components were calculated for genotype and G × E interaction effects for yield and quality factors (Table 6). In every instance except IS and baking, the variance associated with error was larger than other variance components. In yield grades other than culls, the genotypic variance (σ_g^2) was always greater than any variance associated with interaction effects. In most instances with yield components, variance associated with Y × G (σ_{gy}^2) was the least important component of variance.

The two most important yield traits are total yield and U.S. No. 1 yield. Variance associated with G × L interaction (σ_{gl}^2) contributed almost as much to total variance of these two factors as did σ_g^2. Second-order interaction variance (σ_{gly}^2) also contributed largely to the total variance, probably because of inconsistency of L × G effects over years, since the Y × G effect was small and thus presumably consistent over locations.

With regard to quality factors, genotypic variance was the largest component of variance other than error variance. The most important interaction component was consistently σ_{gly}^2.

Broad-sense heritability estimates ($H = \sigma_g^2/\sigma_g^2 + \sigma_m^2 \times 100$) reflect effects of G × E interactions (Table 6). Because of the contribution of G × E interactions to σ_m^2, H estimates for total yield and U.S. No. 1 yield were lower than for other yield grades except culls and much lower than those for quality factors. Estimates of H for all quality factors were extremely high, with percent protein and percent dry matter showing the greatest effect of interactions due to the large second-order interaction effects.

Estimated variances of clonal means (σ_m^2 from Table 6) for total and U.S. No. 1 yield and for all quality factors were used to calculate theoretical variances of clonal means when numbers of replications, locations, or years were varied (Figs. 1–3). In all instances, variances based on a single year's data were extremely high but decreased dramatically with an increase in number of locations. The pattern of changes in variances of clonal means for total yield and U.S. No. 1 yield with changes in growing environments (Fig. 1) suggests that reducing σ_{gl}^2 and σ_{gyl}^2 by increasing locations would result in the most dramatic decrease in σ_m^2 in both grades. Increasing locations to three would reduce variance by ≈60%, and use of four would reduce variance by ≈70%. Smaller reductions would be associated with each further addition of locations. However, the magnitude of σ_{gyl}^2 enables σ_m^2 to be reduced significantly by also increasing years. Increasing from 1 to 2 years would result in a reduction of 30–35%, depending on number of locations. Increasing from 2 to 3 years would further reduce variances 15–20%. Although increasing replications would decrease σ_m^2 by decreasing σ_e^2, it appears to result in only small variance reductions (5% to 10%). Therefore, the breeder has a choice depending on available resources. Conceivably more genetic material could be screened if locations instead of years were increased so that undesirable material would not have to be stored over winter. Trends illustrated in Fig. 1 suggest that four locations, 2 years, and four replications would give acceptable and reliable test data. However, the decrease in variance associated with use of three locations would be a significant decrease if use of more locations were not possible.

Theoretical variances of clonal means for quality factors with varying years, locations, and replications are shown in Figs. 2 and 3. Trends in decreases of variances were similar for all four factors measured and were similar also to those for yield. Decrease in variance estimates between two and three locations would be small if testing for 2 or 3 years. This decrease can be related directly to the minimal or nonexistent contribution of σ_{gl}^2 to the clonal means (Table 6) for all quality factors measured. In addition, the effect of adding replications appears to be more important in reducing variances of clonal means in quality factors than in yield. A breeder may choose to sample over 2 years, eight replications, and only two locations with acceptable results. However, sampling over 2 years, three or four locations, and four replications probably would be more realistic, as it coincides with the environments suggested for yield testing. This combination of environments would result in almost the same reduction in variances with no extra time or plant material required.

These results suggest that sweet potato breeders should be concerned about magnitude of G × E interaction variances in different populations of breeding material. Contribution of these effects to variance of clonal means may be important. For example, Casler (4) has reviewed the bias in narrow-sense heritability estimates caused by G × E interactions in parent–offspring regressions studies. This type of study often is used to predict narrow-sense heritabilities in sweet potato. Results of our study show the importance of estimating narrow-sense heritability using parent–offspring regression by growing parents and progenies in different locations and different years to minimize the G × E interaction bias. Knowledge of the magnitude of these

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interactions also provides the first step in determining stability of sweet potato clones with much emphasis presently on high-yielding clones with wide adaptability.

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Histogenic Instability in Tissue Culture-proliferated Strawberry Plants

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Abstract. **A phenotypic and sexual analysis of *Fragaria vesca* 'Albo-Marginata' determined that the leaf variegation was of chimeral origin. Stable periclinal chimeras were established in vitro from runner tips. Plants were transferred to proliferation media containing 0.5 μM IBA, 0.3 μM GA_3, and BA at either 0, 1.3, 4.4, or 13.2 μM. Whereas the histogens of field-grown runner plants remained stable, more than 90% of the plantlets propagated in vitro varied from the original explants. Most variants were albino or were green, but some were mericlinal chimeras. Histological evidence indicated that many shoots were adventitious, arising from basal callus tissue or petioles. Chemical names used: 1*H*-indole-3-butanoic acid (IBA); gibberellic acid (GA_3); *N*-(phenylmethyl)-1*H*-purin-6-amine (BA).**

In dicots, the outer two cell layers or histogens (the LI and LII or "tunica") of the shoot apical meristem usually remain independent from each other and from the inner body (LIII or "corpus") (21). This development occurs because the planes of cell division in the tunica are anticlinal, with periclinal divisions being rare, and, if occurring, causing the occasional replacement of cell layers in the shoot apical meristem (23). A periclinal chimera possesses distinctly different genotypes in one or more complete layers of the shoot apical meristem. Chimeras can arise whenever a spontaneous or induced genetic change occurs in an apical initial cell in a histogen of a shoot apical meristem. They may become obvious, as with the appearance of patterned variegation (20), or with a change in surface features, such as thornlessness (5). However, not all genetic changes are expressed phenotypically. Undoubtedly, chimeras exist that appear identical to their nonchimeral "parent" but differ in subtle physiological and biochemical ways. Using tissue culture, Bush et al. (3) dissociated flower petals of the chimeral cultivars of 'Indianapolis' chrysanthemums into their component genotypes. They suggested that some of the regenerated variants that arose did so because of a rearrangement of chimeral cell layers that possessed genetic differences in addition to those for color.

The interaction of adjacent histogens composed of dissimilar

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