SWEET POTATO GENETIC STUDIES

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INTRODUCTION

Few genetic studies of the sweet potato, *Ipomoea batatas,* have been reported for two chief reasons: the species is almost completely self-sterile, and it fails to flower naturally in temperate regions.

Self-fertile seedings are very rare. Takahashi (6) after extensive search was able to find only two self-fertile clones; one was a Russian variety, the other a native Hawaiian variety, Huamoa keokeo, no longer available. The former produced about fifty percent of its potential seed yield, the latter about nine percent. Wada in Japan, as reported by Miller (4) obtained some self-fertility, and made some genetic analyses, whether from crosses between self-fertile clones or from self-pollinations is not made clear. The report quotes, ". . . green stem, white skin, and white flesh are dominant to red stem, red skin, and yellow flesh respectively, and the segregation takes place according to ratios of either 3 to 1 or 15 to 1."

Open-pollinated populations occur naturally in the subtropics and tropics, but in Hawaii most clones, whether native to Hawaii or imported from the Mainland, are either self-sterile or fail to flower at all. Open-pollinated populations, in the absence of selection, tend to maintain fixed gene ratios according to the Hardy-Weinberg formula $(np + nq)^2$, hence their analysis may have some preliminary value.

Published phenotypic ratios of open-pollinated sweet potato populations for skin and flesh character inheritance (5), where the known parent had dark purple (red) skin and cream (white) colored flesh, conformed to apparently monofactorial ratios, $\frac{1}{4}$ clear flesh (cream or orange)/purple skin to $\frac{1}{2}$ clear flesh/brown skin to $\frac{1}{4}$ flecked purple flesh/purple skin. For flesh color alone the ratio was $\frac{1}{2}$ orange to $\frac{1}{2}$ cream, and for skin alone it was $\frac{1}{2}$ purple to $\frac{1}{2}$ brown. One-half purple-skinned plants had purple flecking of the flesh.

On the other hand, the hexaploid chromosome number of all known commercial clones of *Ipomoea batatas,* 45_{II}, (6, 1) suggests a species-hybrid origin, and therefore creates the expectation of more complex character inheritance. This seeming contradiction of monofactorial mendelism and complex species-hybrid origin is, nevertheless, the combination found in genetic studies with coffee reported from Brazil (2). *Coffea arabica,* 22_{II}, was shown to be most probably an amphidiploid species-hybrid between *C. canephora,* 11_{II}, and another unknown eleven paired species. In variety crosses between commercial coffees, monofactorial mendelian ratios were observed in the majority of analyses reported by Krug and Mendes (2).

The inferred origin of *Ipomoea batatas,* 45_{II}, by amphidiploidy following natural species hybridization between a 30_{II} and a 15_{II} species probably accounts for most of the observed self- and cross-sterility. The recent work of Ting and Kehr (7) shows that some male and female sterility accompanies clones which show meiotic irregularities, such as laggards at I metaphase, secondary associations between bivalents during metaphases, and other indicators of species hybridization.

Except for HES 8, all seedlings selected at the Station for promise of commercial or genetic value were derived from several crosses made about 1940 in

Louisiana between the two moist flesh varieties Nancy Hall and Porto Rico. Both parents are self-sterile but usually produce some flowers at the 600-foot elevation each winter. The former has pale yellow flesh, and produces an erratic root yield; the latter has varying shades of orange flesh, and produces a more dependable root yield. Thus, segregations from open-pollinated selections of seedlings derived from these two parents frequently produce clones of commercial as well as genetic value.

Discovery of a prolific self-fertile seedling, HES 107-C, (5) which yields seed as well by hand-selfing as by natural selfing when isolated from insect pollen vectors, presented an opportunity to test the ratios suggested from open-pollinated sources. It also permitted study of a large number of other inheritances, especially those associated with improved yield and fertility. A population of 452 selfed seedlings was obtained from 800 seeds of HES 107-C, seeded July 13, and set to the field on the University's Manoa Valley farm August 18, 1953. Seeds were scarified by treatment with concentrated sulphuric acid for 45 minutes. This treatment induces prompt and uniform seed germination but may possibly account for some of the low percentage of seed viability. Readings for genetic character analysis were made from September 15, 1953, to January 26, 1954.

Chi-square analysis for test of qualitative character independence was done in group combinations of 1, 2, 3, and 4 characters. Varying degrees of complexity in phenotypic ratios were observed, from single pairs of alleles to those probably too multiple for estimation in a 452 seedling population, and some characters (such as those expressed only on roots, or on plants which flowered) were confined to only a fraction of the whole population. Test by chi-square for independence of quantitatively determined characters was based on numbers calculated as the product of row and column totals divided by the population total. For qualitative characters the standard method was employed.

SIMPLER TYPES OF INHERITANCE

Monofactorial segregations were indicated in the two nonallelic characters: Flowering vs. nonflowering, and red stems vs. green stems. Five other qualitatively classifiable character contrasts indicated di-factorial gene segregations.

Ability to produce flowers at 80 feet above sea level (Manoa Valley) was studied according to season. The data disclosed a complex pattern from the four groups classified: A, September 15 to October 6; B, October 7 to October 23; C, October 24 to January 1; D, January 2 to January 26. After the fourth period no further flowering was expected. The observed proportion of 334 flowering, F, to 109 nonflowering, f, fitted a satisfactory 3:1 ratio. Data gathered on degree of stem pigmentation, despite many shades of red which ranged from extensive black to mere dots at nodes and junctions of petiole and blade, suggested one major pair of alleles determining inheritance of red pigmentation on leaves and stems, 344 red, G, to 101 green, g, with doubtless several factors modifying red pigment.

Gene interaction governing degree of smoothness of root surface on 239 of the 260 seedlings which formed roots was classified into an acceptable ratio of 13 ridges, N, to 3 smooth, n. These, of course, included only the 9/16 rooted, R, not the 7/16, r, unrooted plants. Relationships exhibited in this set of four characters, presumably six pairs of genes, is set forth in condensed form in table 1, which shows observed and calculated numbers in the cells and margins, with the chi-square total value at the table bottom.

TABLE 1. Test data for fitness of probable mendelian ratios governing inheritance of flowering, F, vs. nonflowering, f, (3:1); red stems, G, vs. green stems, g, (3:1); roots, R, vs. no-roots, r, (9:7); and ridged, N, vs. smooth, n (13:3).

VINE CHARACTERS		ROOT CHARACTERS				TOTAL
		R		Subtotal	r	
		N	n			
FG	O	111	24	135	106	241
	C	109.26	25.21	134.47	104.59	239.06
Fg	O	34	10	44	30	74
	C	36.42	8.40	44.82	34.87	79.69
fG	O	37	9	46	36	82
	C	36.42	8.40	44.82	34.87	79.69
fg	O	11	3	14	14	28
	C	12.14	2.80	14.94	11.62	26.56
Total	O	193	46	239	186	425
	C	194.24	44.81	239.05	185.95	425.00

Chi-square for FGRN interaction = 1.770. 11 df; $X^2_{.05}$ = 19.675

The test of goodness of fit for the postulated mendelian interactions indicated that for the entire series of 12 classifications there was very good agreement within and between classes for the assumption of clean segregation and independent assortment. Chances are better than 99 times in 100 with these four characters that upon further analysis an even smaller departure from the hypothesis will be met.

MORE COMPLEX TYPES OF INHERITANCE

The 260 root-forming seedlings were reclassified in combinations of the five characters: skin, flesh, and stem color; degrees of leaf lobing; and ridging on root surfaces. Simultaneous inclusion of three root characters reduced the population size to only 181 plants. At the outset it was evident that interaction between skin color and flesh color was neither independent nor determined by monofactorial segregations. Fractionation for a dihybrid segregation in each case indicated good fit for a 9:7 ratio of brown vs. cream skin, and 13:3 for some degree of orange flesh vs. cream flesh. Analysis of flesh color in one combination-analysis showed that orange-flesh seedlings break down to 9/16 orange and 4/16 deep orange. In another grouping, however, an excess of deep orange prevented an acceptable fit for 9:3:4, but not for the 13:3 postulation. In addition to the already considered degree of ridging on root surfaces, (13 ridged, N, to 3 smooth, n), another acceptable mendelian fit was obtained for degree of leaf margin serration, viz., 13 entire leaf margin, A, to 3 serrated margin, a.

In table 2, groupings into a two-fold table show correspondence between observation and calculation for BONGA in all 32 cells. Chi-square independence tests were made for the five major allelic segregations, B vs. b (9:7), O vs. o (13:3). N vs. n (13:3), A vs. a (13 smooth margin: 3 serrate), and G vs. g (3:1), and all ten combination character-pair segregations show at the bottom of the table.

TABLE 2. Interaction between colors of skin (9:7), flesh (13:3), and stem (3:1), together with ridging of skin (13:3) and outline of leaf (13:3). Observed and calculated frequencies are shown with chi-square values for critical probabilities.

SKIN, FLESH, AND RIDGING		STEM COLOR AND LEAF MARGIN				TOTAL
		AG	Ag	aG	ag	
BON	O	54	15	11	3	83
	C	40.96	13.65	9.45	3.15	67.21
BOn	O	10	5	2	2	19
	C	9.45	3.15	2.18	.73	15.51
BoN	O	1	1	0	0	2
	C	9.45	3.15	2.18	.73	15.51
Bon	O	0	0	0	0	0
	C	2.18	.73	.50	.17	3.58
bON	O	21	9	5	2	37
	C	31.86	10.62	7.35	2.45	52.28
bOn	O	3	2	3	1	9
	C	7.35	2.45	1.70	.57	12.07
boN	O	19	2	2	0	23
	C	7.35	2.45	1.70	.57	12.07
bon	O	7	1	0	0	8
	C	1.70	.57	.39	.13	2.79
Total	O	115	35	23	8	181
	C	110.30	36.77	25.45	8.50	181.02

X^2 BONGA $= 70.988$, df 30, $X^2_{01} = 50.892$ X^2 OG $= 3.027$, df 3, $X^2_{05} = 7.815$

X^2 BO $= 42.557$, df 3, $X^2_{01} = 11.341$ X^2 OA $= 3.497$, df 3, $X^2_{05} = 7.815$

X^2 BN $= 0.665$, df 3, $X^2_{05} = 7.815$ X^2 NG $= 1.428$, df 3, $X^2_{05} = 7.815$

X^2 BG $= .452$, df 3, $X^2_{05} = 7.815$ X^2 NA $= 1.237$, df 3, $X^2_{05} = .7.815$

X^2 BA $= .426$, df 3, $X^2_{05} = 7.815$ X^2 GA $= 0.550$, df 3, $X^2_{05} = 7.815$

X^2 ON $= .666$, df 3, $X^2_{05} = 7.815$

Each of the five pairs of major alleles fits the mendelian ratio postulated, but the ten combinations between them produce interesting information. The total chi-square value for the 32 cells, 70.988, far exceeds the 1 percent allowable value for 30 degrees of freedom, 50.892, the last value included in most chi-square tables. There is no point, therefore, in calculating tabular values for the obtained 31 degrees of freedom. All the paired-character groupings were well within their 5 percent allowable values, except the skin-flesh color ratio for 3 degrees of freedom, 42.557, which far exceeds the 1 percent allowance, 11.341. These ten chi-square values indicate that at least two loci in the two combined root character dihybrid ratios are on the same chromosome. As seen in rows 1, 2, 7, and 8, the degree of linkage produces (a) an excess of brown skin/orange flesh, and cream skin/cream flesh, and (b) from the four central rows a deficiency of brown skin/cream flesh and cream skin/orange flesh.

COLORS OF FLESH, SKIN, STEM, AND FLOWERING

Test of interaction of the three pigmented characters with the monofactorial alleles, flowering vs. nonflowering, was made in a new grouping (table 3). Again it appears that all paired combinations, except those involving skin and flesh color, are segregating independently. There was a slight nonsignificant shortage of green stem/brown skin phenotypes in the stem–skin color classification, but not enough to throw doubt on the goodness of fit. Notice from tables 2 and 3 the lack of association between colors of stem and root.

STEM COLOR, STEM LENGTH, AND LEAF MARGIN

Table 4 shows results of distributing plants in the four vine length classes according to interaction with the stem color and leaf margin phenotypes. Length of vine growth by December 1 (five and one-half months from seeding) was distributed in intervals set by the standard deviation as follows: 1, less than 15 inches; 2, 15-29 inches; 3, 30-59 inches; 4, 60-89 inches. Graphic portrayal of vine length as a frequency distribution indicates a somewhat erratic skewed figure when considered as columns in table 4, i.e., 56, 171, 206, 19. But when frequency was reclassified on 5-inch class intervals a much smoother, although still positively skewed distribution, appeared as below:

Class value:

(inches)   3   8 13 18 23 28 33 38 43 48 53 58 63 68 73 78 83 88

Frequency: 3 15 33 40 52 65 58 59 47 29 23 11   5   5   4   1   1   1 = 452

TABLE 3. Relations between phenotypes for colors of stem (3:1), root skin (9:7), flesh (13:3), and flowering propensity (3:1).

STEM AND SKIN		FLESH COLOR AND FLOWERING				TOTAL
		FO	Fo	fO	fo	
GB	O	85	1	22	0	108
	C	66.84	15.42	22.28	5.14	109.68
Gb	O	32	29	19	7	87
	C	52.00	12.00	17.33	4.00	85.33
gB	O	29	2	7	0	38
	C	22.28	5.14	7.43	1.71	36.56
gb	O	15	4	8	0	27
	C	17.33	4.00	5.78	1.33	28.44
Total	O	161	36	56	7	260
	C	158.45	36.56	52.82	12.18	260.01

$$\text{Chi-square } GBFO = 65.920, \text{df } 15, \; X^2_{01} = 30.578$$
$$BO = 46.674, \text{df } 3, \; X^2_{01} = 11.341$$
$$GB = 0.189, \text{df } 3, \; X^2_{05} = 7.815$$
$$FO = 2.436, \text{df } 3, \; X^2_{05} = 7.815$$
$$BF = 3.472, \text{df } 3, \; X^2_{05} = 7.815$$
$$GO = 3.872, \text{df } 3, \; X^2_{05} = 7.815$$
$$GF = 0.083, \text{df } 3, \; X^2_{05} = 7.815$$

TABLE 4. Test of independence between three characters: red stem vs. green stem (3:1), smooth leaf margin vs. serrated margin (13:3), and vine length (arbitrarily grouped on standard deviation into 4 classes).

STEMS AND LEAVES		VINE LENGTH				TOTAL
		1	2	3	4	
AG	O	37	108	124	9	278
	C	34.44	105.17	126.70	11.69	278.00
Ag	O	11	24	40	8	83
	C	10.28	31.40	37.83	3.49	83.00
aG	O	8	30	28	2	68
	C	8.42	25.73	30.99	2.86	68.00
ag	O	0	9	14	0	23
	C	2.85	8.70	10.48	0.97	23.00
Total	O	56	171	206	19	452
	C	55.99	171.00	206.00	19.01	452.00

Chi–square AGX $= 14.978$, df 15, $X^2_{05} = 24.996$

The HES 107-C parent of this generation, grown with this population as a vegetatively propagated clone, was classified as: red stem G, leaf margin A, vine length 3=55 inches, floral season 4.

Analysis of agreement between observed and calculated frequencies in table 4 shows complete satisfaction of the mendelian postulates for independent assortment between (3:1) (13:3) ratios for stem color and leaf margin, and also that there is no inconsistency in vine length frequency distributions caused by interaction with the AG, Ag, etc., classes. The distribution outline suggests either geometric interaction or partial dominance of genes for shortness.

Efforts to break down stem color groups among the 346 red stem plants produced a confusing proportion of: 58 restricted pigment to 138 full pigment to 150 strong red (maroon or black) over stems, petioles, and occasionally over the upper surface of leaves. Fractionating these frequencies for di- or tri-factorial mendelian ratios only emphasized the difficulty of clearly differentiating shades of red or intensity of pigment. It is clear, however, that lumping red-pigmented plants vs. green plants produces a ratio of 3:1, whether stated as 48:16 or 12:4. Furthermore the 3:1 proportion holds for the 425 plants of table 1, 181 of table 2, 260 of table 3, or 452 of table 4.

HETEROSTYLIE, VINE LENGTH, AND FLORAL SEASON

Table 5 shows the distribution of 323 plants classified simultaneously for (a) number of anthers level with or above the stigma; (b) number of plants on December 1 with (1) vine length below 14 inches, (2) 15-29 inches, (3) 30-59 inches, (4) 60–89 inches; and (c) those plants which flowered between: A, September 15 to October 6; B, October 7 to October 24; C, October 25 to January 1; D, January 2 to February 10. For greater convenience, data are arranged in two halves, each showing a paired grouping of anthers-up with one of the other two characters. Although the table shows no vine length and floral-season grouping,

TABLE 5. Relations between three quantitatively determined characters. (1) Number of anthers level with the stigma (in the rows); (2) number of vine-length types (left columns); (3) plants which flowered in four floral seasons: A, the earliest—D, the latest (right columns).

ANTHER TYPES	O/C	VINE LENGTH TYPES 1 1-14"	2 15-29"	3 30-59"	4 60-86"	TOTALS	FLORAL SEASON TYPES A 9/15-10/6	B 10/7-10/24	C 10/25-1/1	D 1/2-1/26	TOTALS
0/5	O	6	22	18	2	48	10	12	26	0	48
	C	4.76	17.83	23.63	1.78	48.00	7.13	20.95	19.32	0.59	47.99
1/5	O	11	33	42	2	88	14	40	33	1	88
	C	8.72	32.69	43.32	3.27	88.00	13.08	38.41	35.42	1.09	88.00
2/5	O	9	37	54	4	104	17	46	39	2	104
	C	10.30	38.64	51.20	3.86	104.00	15.46	45.40	41.86	1.29	104.01
3/5	O	2	19	30	4	55	5	25	25	0	55
	C	5.45	20.43	27.07	2.04	54.99	8.17	24.01	22.14	0.68	55.00
4/5	O	3	8	11	0	22	2	14	5	1	22
	C	2.18	8.17	10.83	0.82	22.00	3.27	9.60	8.85	0.27	21.99
5/5	O	1	1	4	0	6	0	4	2	0	6
	C	0.59	2.23	2.95	0.22	5.99	0.89	2.62	2.41	0.07	5.99
Total	O	32	120	159	12	323	48	141	130	4	323
	C	32.00	119.99	159.00	11.99	322.98	48.00	140.99	130.00	3.99	322.98

Chi-square total sources:: 23 df each half, $X^2_{05} = 35.172$ A, left half $= 11.530$ B, right half $= 19.163$

Vine length × floral season: (339 F to 107 f), $X^2_{05} = 22.281$, $X^2_{05} = 30.144$

Chi-square total: (19 df) $= 22.281$, $X^2_{05} = 30.144$

one was made, as shown by the last footnote to the table. Chi-square analysis for the three possible paired groupings measures the accuracy of the assumption that genes for all three characters assort independently. Table 5 shows that calculated values sustain the no-association hypothesis. Furthermore, the frequency distribution for each of these quantitative characters is either symmetrical, or only slightly skewed. Skewness toward the short end of the range suggests either geometric interaction of genes for size, or partial dominance of small size over larger size. The outline of the distribution for vine length for the completed population of 452 has already been shown. In computing chi-square for the unshown vine length $\times$ floral seasonal grouping, a total population of 446 plants was used: 339 flowering, 107 not flowering.

FACTORS AFFECTING ROOT WEIGHT

The search for a possible correlated inheritance of the two quantitative characters, root weight and vine length, on 260 root-forming plants revealed a nonsignificant interaction coefficient of $r = +.1504$. It was next desired to learn the manner in which the distribution of root weights was affected by genes for the four qualitative characters studied in table 3, i.e., colors of stem, skin, and flesh, and propensity to flower. The frequency distribution of root weight (standard deviation was approximately 0.3 pound) is grouped for convenience into 12 1-pound classes, from 0.1 to 11.0 pounds. Four exceptional seedlings, which exceeded weights for the last continuous frequency group, i.e., from 11.1 to 27.5 pounds, were grouped into a single class.

Table 6 shows 192 cells, having 156 entries for observed and calculated weights. Root weight along the abscissa and color-flowering combinations along the ordinate graphically display the outline of weight distribution. All paired combinations of GBFO, except BO, were independent (table 3). Table 6, using obtained qualitative character frequencies rather than calculated frequencies, reveals that weight distribution among the sixteen phenotypes is consistently unbiased. Calculated chi-square for deviations, totalling 103.603, is much lower than the number of degrees of freedom, 155, thus producing a negative value of -3.2, when applying Fisher's formula, $(2X^2)^{1/2} - (2n-1)^{1/2}$, to find the normal deviate. With this material, larger deviations may be expected in more than 999 times in 1000. More than half the entire population lies in the less than 1-pound weight per plant class. Two high-weight plants (a) Field No. 68, with 75 roots weighing 20.5 pounds, and (b) Field No. 252, with 65 roots weighing 27.5 pounds (figures 1 and 2) constitute apparently recessive gene combinations approaching maximum homozygosis for weight. As indicated in footnotes to table 6, No. 252, the better of the two, failed to flower and had brown skin, orange flesh, and red stems. The other flowered and had brown skin, orange flesh, and green stems. Its flower proved self-sterile when bagged in the field.

PLANT FERTILITY

As many as possible of the 334 seedlings which flowered were wrapped in cheesecloth bags in the field for tentative identification of possibly self-fertile plants. Nineteen plants, thus bagged, produced one or more seed pods, but since one was pin-heterostyled and could not possibly have set seed unaided, all were transferred as stem cuttings to a pollen-vector-free screenhouse. Two cuttings were made per plant, one to be hand-pollinated, the other to test ability to self-pollinate unaided (like parent HES 107-C in the same screenhouse).

TABLE 6. Relation of class frequencies for root weight to those for colors of stem, root, flesh, and ability to form flowers. Weight classification according to 1-pound intervals

QUALITATIVE PHENOTYPES	O/C	0.1–1.0	1.1–2.0	2.1–3.0	3.1–4.0	4.1–5.0	5.1–6.0	6.1–7.0	7.1–8.0	8.1–9.0	9.1–10.0	10.1–11.0	11.1–28.0	TOTAL
GFBO	O	47	20	6	3	2	1	3	1	0	1	1	0	85
	C	46.10	17.65	7.19	3.92	2.29	2.62	1.63	0.98	0.65	0.33	0.33	1.31	85.00
GFBo	O	0	1								0	0	0	1
	C	.54	.21	.08	.05	.03	.03	.02	.01	.01	0	0	.02	1.00
GFbO	O	19	8	2	1	1	0	1	0	0	0	0	0	32
	C	17.35	6.65	2.71	1.48	0.86	0.98	0.62	0.37	0.25	.12	.12	.49	32.00
GFbo	O	14	4	3	2	2	2	0	0	1	0	0	1*	29
	C	15.73	6.02	2.45	1.34	.78	.89	.56	.34	.22	.11	.11	.45	29.00
GfBO	O	10	4	2	2	0	1	1	0	1	0	0	1†	22
	C	11.93	4.57	1.87	1.02	.59	.68	.42	.25	.17	.03	.08	.34	22.00
GfBo	O													0
	C													0
GfbO	O	9	5	2	2	0	0	1	0	0	0	0	0	19
	C	10.30	3.95	1.61	.88	.51	.58	.37	.22	.15	.07	.07	.29	19.00
Gfbo	O	5	1	0	0	0	0	0	1	0	0	0	0	7
	C	3.80	1.45	.59	.32	.19	.22	.13	.08	.05	.03	.03	.11	7.00
gFBO	O	16	4	1	1	2	3	0	0	0	0	0	2‡	29
	C	15.72	6.02	2.46	1.34	.78	.89	.56	.34	.22	.11	.11	.45	29.00
gFBo	O	2	0	0	0	0	0	0	0	0	0	0	0	2
	C	1.08	.42	.16	.09	.05	.06	.04	.02	.02	.01	.01	.03	1.99
gFbO	O	6	5	2	1	0	1	0	0	0	0	0	0	15
	C	8.13	3.12	1.27	.69	.40	.46	.29	.17	.12	.06	.06	.23	15.00
gFbo	O	1	0	3	0	0	0	0	0	0	0	0	0	4
	C	2.17	.83	.34	.18	.11	.12	.08	.05	.03	.02	.02	.06	4.01
gfBO	O	5	2	0	0	0	0	0	0	0	0	0	0	7
	C	3.80	1.45	.59	.32	.19	.22	.13	.08	.05	.03	.03	.11	7.00
gfBo	O													0
	C													0
gfbO	O	7	0	1	0	0	0	0	0	0	0	0	0	8
	C	4.34	1.66	.68	.37	.22	.25	.15	.09	.06	.03	.03	.12	8.00
gfbo	O													0
	C													0
Total	O	141	54	22	12	7	8	5	3	2	1	1	4	260
	C	140.99	54.00	22.00	12.00	7.00	8.00	5.00	3.00	2.00	1.00	1.00	4.01	260.00

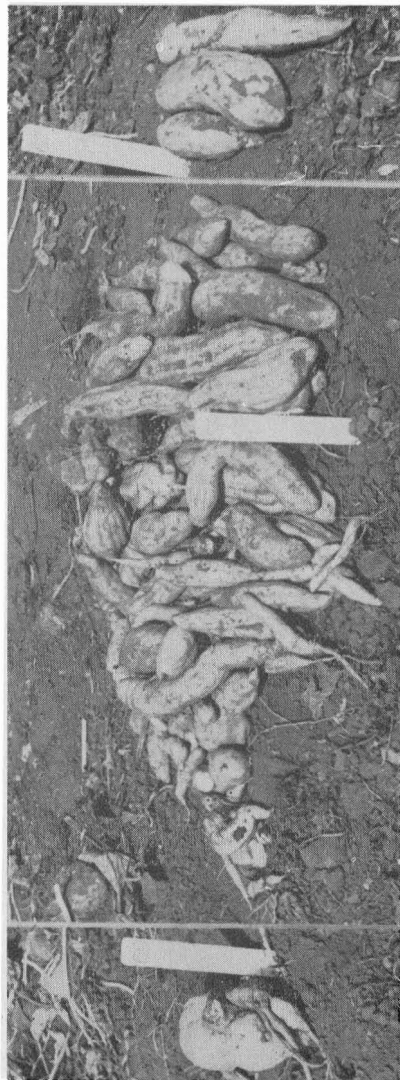*13.5 lb. †27.5 lb. ‡20.5 and 11.1 lb.

FIGURE 1. Root yield of Field No. 68 and its two adjacent siblings 67 and 69. Seedling 68 produced 75 strongly ridged roots, a total yield of 20.5 pounds. Seeded July 13, 1953; harvested January 26, 1954.

Much variation among these 19 plants was observed in floral season from A to C, as well as number of anthers-up, as shown below:

Plant Number

	5	21	27	39	44	72	168	185	194	227	246	281	305	334	336	364	413	423	451
Season	A	A	A	B	B	C	B	A	C	C	A	A	B	B	A	B	C	A	A
Anthers-up	2	3	3	5	2	2	2	1	0	1	3	2	2	2	2	2	3	1	4

Most of the 19 stem cutting clones at first failed to resume an inflorescence after taking root about February 1. But after a few weeks several produced a new floral flush, started to form buds, but dehisced before fruition. Light intensity in the screenhouse is approximately half that in the field, which doubtless contributed to flowering failure. Only one plant, No. 334, had by mid-March exhibited ability to set seed unaided, and this plant is not at present very fertile. But since HES 107-C is most fertile during the February-April flush, it is still early to estimate fertility potentialities.

FACTORS AFFECTING SEASON OF FLOWERING

Table 5 indicated lack of interaction of the four floral seasons with number of anthers-up and vine length. A study was then made of interaction of floral seasons with five qualitative characters analyzed in table 2, viz., root colors and surfaces, stem color, and leaf lobing. No interaction was indicated and tabular presentation of the data will be omitted except for observations on the method of applying chi-square analysis to the data.

Two methods were employed for computing calculated frequencies: (a) that based on the postulated mendelian proportions (9:7, 13:3, 13:3, 13:3, 3:1); and (b) that based on the obtained phenotype numbers. Method a produced a chi-square value of 138.856 for 101 degrees of freedom, which includes the previously obtained $X^2 BONGA = 70.988$ for 31 degrees of freedom between phenotypes. Method b eliminates the effect of linkage between the B-O root colors, and shows $X^2 = 50.689$ for 101 df. The former method produced a c value of 2.47, the latter produced $c = -4.14$. $C = 2.47$ indicates that the B-O linkage distortion applies also to the floral-season frequency distribution. The latter $c = -4.14$ indicates even less interaction between floral-seasons and the qualitative characters than exhibited in table 6.

DISCUSSION

Questions are raised by some today regarding the theory of the gene. Whether or not the theory is considered outmoded in certain circles, the hypothesis of mendelian ratios continues to work. Plant breeders continue to find utility in information that mono- and di-factorial segregations govern development of important morphological and disease resistant features of crop plants. If any justification is needed for the attempt to discover and test mendilizing factors in the sweet potato, there are at least three: (a) open and controlled pollinated population analyses suggest their presence, (b) knowledge of their nature would aid the breeder, and (c) little genetic information has hitherto been reported.

Discovery in May 1948 of HES 48, a prolific open-pollinated seed producer with pin-heterostyled, self-sterile flowers, initiated a series of searches for improved fertility. These from selections for increased number of anthers-up

FIGURE 2. Root yield of Field No. 252: 65 slightly ridged roots totalling 27.5 pounds. Seeded July 13, 1953; harvested January 26, 1954.

supplied, in May 1950, the first self-fertile seedling, HES 107-C, to come to our attention (5). This clone, parent of all the self-pollinated seedlings comprising this study, sets self-pollinated seed without aid at all seasons of the year, although there are two major cycles when flowering and fertility is abundant: early fall, and (the better of the two) in February-April.

Observation of what appeared to be degrees of heterostylie (pin to full homostylie), and that the self-fertile seedling had an average of three stamens level with or above the stigma, might suggest presence of *Primula*-type self-incompatibility among the sterility mechanisms observed in commercial clones of *Ipomoea batatas*. A sibling, HES 107-B, on the other hand, had 3.5 anthers-up, but proved to be entirely self-sterile, thus demonstrating that type of heterostylie was not associated with grades of fertility.

Data were gathered from mid-September to mid-February on various types of flower habit. Some of these characters have already yielded genetic information; others require study over a prolonged period, and, if associated with self-fertile plants, will serve for continuous study for several years. Nineteen plants which promised some degree of self-fertility in one or more seasons were removed as clones from the planting field to a pollen-vector-free screenhouse for continuous study. Studies embraced quite a range of factors, including the following: (a) number of anthers-up, (b) number of pods set when permitted to self-pollinate naturally or artificially, (c) number of flower flushings per year, (d) intensity of flower production in different seasons, and (e) duration of individual flushings. To illustrate the range of conditions expected from a segregating selfed generation, the following are a few extreme examples already obtained in seedling production studies: HES 110-3 is largely or entirely cross- and self-sterile, but flowers abundantly all year round at sea level; HES 107-C flowers abundantly

in two main cycles, sparingly in between, and sets seed with fair fecundity all the time; Onolena (a newly released seedling variety) usually fails to flower at all in Manoa Valley. When flowering stems of Onolena are transported from our substation at 600 feet elevation to Manoa Valley (80 feet) for reciprocal cross pollinations in a screenhouse, it usually fails as male or female parent; but at the higher elevation during most years when many varieties are in flower it sets fairly satisfactory quantities of open-pollinated seed. Finally, one-fourth of all the progeny of HES 107-C failed to flower from September to February in Manoa Valley; the picture would probably have differed had the trial been conducted above the 600-foot elevation.

Data on the foregoing analyses have been grouped and regrouped in populations of varying sizes to elucidate various character interactions. The only mendelian ratios accepted are those which are upheld after several reclassifications. It was observed that although some groupings suggested that orange flesh (13/16) could be broken down to 9/16 orange, 4/16 deep orange, others failed to conform, but all groupings upheld the 13:3 ratio. A somewhat similar observation was made for surface of root ridges. Some groupings conformed to a ¼ smooth to ½ ridged to ¼ strongly ridged, but even there the ratio better fitted a 13:3 postulate, which always gave the best chi-square values.

Wada's paper (8) is not available for study at any library in Honolulu. But his sweet potato phenotypes, reported second-hand via Miller (4), are in striking contrast to those now reported. Different researchers can be expected to use different color designations such as cream for white, or vice versa, and red for brown, but Wada's dominant alleles happen to be our recessive alleles. On the other hand, a 13 to 3 mendelizing ratio means that a dominant and a non-allelic recessive gene determine the same phenotype. Three out of seven qualitative characters now reported are of this kind. Our evidence is that we have both a dominant orange flesh and a recessive orange flesh. Comparison of Wada's data and ours might indicate a similar situation exists for stem and skin color.

Study of factors influencing degrees of self- and cross-fertility promises to be an involved one in view of the complexity in floral type regarding anthers-up number and season. Lack of association in these studies between anthers-up number and self-fertility probably indicates no *Primula*-type incompatibility, and further suggests that factors interfering with the normal alternation of generations, i.e., generational sterility, account for most or all the observed self- and cross-sterility. Meiotic irregularities already considered, together with the well demonstrated sterilities, indicate that the postulated species-hybrid origin of this hexaploid species involved sufficient karyological homology to cause the sterilities.

Perhaps the most sensational information disclosed in the foregoing studies concerns the nature of root yield in the 9/16 of the population which set fleshy roots. Two such unique seedlings as field numbers 68 and 252 out of a total of only 260 clearly indicates recessive acting genes for heavy weight and very few heterozygous root weight genes in parent HES 107-C. Seedling 252, with 65 roots weighing 27.5 pounds, promises to have commercial possibilities in yield, color of flesh, smoothness of surface, and good keeping quality compared to the parent and other heavy yielding siblings. It still requires study in field and baking trials as a clone included in tests with other commercial type clones. It should be emphasized that all plants in this study arose from a cross between the standard commercial

clones Nancy Hall and Porto Rico. Table 6 indicates the flowering and root color phenotypes, especially of the two unique seedlings numbered 68 and 252. Although the former flowered, it proved self-sterile, and the latter failed to flower at all at 80 feet above sea level.* Both plants will serve for important investigations into root weight inheritance. Stem girdling and manipulation of elevation above sea level will be employed for studying the possibility of assortative matings in case they should prove cross-fertile. The great majority of cross-pollinations attempted at this station have thus far failed. But self-pollination has demonstrated that inbreeding does not depress yield. It uncovers what appear to be recessive gene combinations approaching maximum homozygosis for increased stem length and fleshy root yield.

The cross Nancy Hall × Porto Rico, from which this population ultimately derived, is perhaps one of the most favorable now available for production of improved commercial type clones and important genetic stocks. Other crosses will uncover other ranges of character potentials, such as full range of skin colors to include purple coloration in root skin and flesh, numerous degrees of leaf margin lobing, and other proportions of high yielding roots. A hexaploid species-hybrid should produce more tendency to stable degrees of self-fertility when larger than 450 plant populations are employed.

SUMMARY

A prolific seeding self-fertile seedling of *Ipomoea batatas* arose in May 1950 during the search for self-fertile plants from several successive open-pollinations. Eight hundred seeds obtained from both artificial and natural self-pollinations in a pollen-vector-free screenhouse yielded 452 seedlings which were set to an open field for genetic character analysis. Planting at 80 feet above sea level in the late summer months permitted classification of seven qualitative and four quantitative character segregations.

Qualitative character alleles, with phenotypic ratios approved after reclassification in groupings of one- to five-character combinations, are the following:

3/4 red stem, G, to 1/4 green stem, g

3/4 flower forming, F, to 1/4 nonflowering, f

9/16 root forming, R, to 7/16 nonrooting, r

9/16 brown skinned roots, B, to 7/16 cream skinned roots, b

13/16 smooth leaf margins, A, to 3/16 slightly lobed, a

13/16 ridged surface roots, N, to 3/16 smooth surfaces, n

13/16 orange colored flesh, O, to 3/16 cream flesh, o

Chi-square analysis for independent assortment of the genes postulated disclosed evidence of independence between all alleles except the (13:3, 9:7) interaction between skin and flesh colors. This produced an excess of brown skin/orange flesh and cream skin/cream flesh, and a deficiency of brown skin/cream flesh and cream skin/orange flesh.

Quantitative character classification embraced the four characters:

a. Number of anthers level with or above the stigma, and included the full range from 0/5 to 5/5, where the parent plant clone averaged 3/5 anthers-up;

b. Vine length, classified on December 1, into five groupings, gave evidence

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*Field No. 252 is now (January) flowering abundantly and, in addition, is probably self-fertile.

of positive skewness toward the short end, suggesting dominence of genes for shortness, or geometric interaction of several pairs of alleles;

c. Season of flower production, from September 14, to January 26, suggested geometric interaction between several alleles, producing a skewed distribution toward the early end of the range;

d. Weight of fleshy roots, clearly indicated dominance of low weight over high weight. More than half the population of root forming plants produced 1 pound or less total weight, while two unique plants produced (1) 75 roots weighing 20.5 pounds, and (2) 65 roots weighing 27.5 pounds per plant.

Evidence on quantitative factor inheritance is that vigor is not depressed upon inbreeding, but that short stem length and low weight of root yield are dominant by relatively few factors over long stem length and high root yield. All four quantitive character combinations with respect to each other and the seven qualitative characters were apparently governed by independently assorting genes.

Preliminary investigations on self-fertility among 334 plants which flowered indicated that only 19 suggested any degree of self-fertility in any flowering season, and only one produced unaided self-pollinated seed when transferred from field to screenhouse.

Fertility relationships are complicated by differences in (a) number of flowering cycles, (b) duration of individual cycles, (c) intensity of flower production in different seasons, and (d) ability to flower at different elevations above sea level.

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