

Inheritance of Chlorophyll Deficiencies in *Beta Vulgaris* L.

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Introduction

The inheritance of chlorophyll deficiencies in sugar beets, including plastid inheritance, has attracted the attention of scientists because many problems in genetics and physiology of sucrose content and root yield can not be solved by studies restricted to the root.

Discussions concerning the localization and the synthesis of sucrose in beets (21, 30)² and also the forms of the mobile sugar in the vascular system rest on the new facts showing that the synthesis of sucrose is localized in leaves but not in the petiole or in the tops of the roots. In experiments where radioactive-marked carbohydrates ($C^{14}O_2$) were used for nutrition, it was indicated that when beets were exposed to light the radioactive carbohydrates appeared first in the formation of sucrose in the leaf blades. This made it possible to consider sucrose as principal mobile sugar built during photosynthesis directly in leaves, but not in the roots of sugar beets (21, 22, 30).

The intensity of photosynthesis depends upon different structures of plastids which vary during the ontogenetic development of the plants (45). The sugar beet root contains, even in the internal tissues, some colorless leucoplasts, as well as green chloroplasts (10). The function of plastids in the root tissues is unknown.

Experiments in beets (41), barley (12), and other crops showed that genes causing chlorophyll deficiency changed the size, color, and number of plastids in the leaf cells. In this way such genes also changed the intensity of photosynthesis, and in connection with this, they could acquire a pleiotropic action on the development of certain quantitative characters in beets.

In *Antirrhinum* (44), barley (13, 14, 15), and sorghum (20) certain genes which cause chlorophyll deficiency in the homozygote showed general heterosis in the heterozygote.

Different chlorophyll mutations were observed in plants after exposure to atomic radiation (17, 36).

Knowledge of the inheritance of chlorophyll deficiency in beets is necessary for the genetic and physiological study of beets as well as for breeding work, especially for the breeding of irradiated beets.

Material and Methods

The chlorophyll-deficient races studied were isolated in varietal populations of sugar and fodder beets, inbred lines, and hybrids. In this way they all represented natural mutations but not mutations stimulated by X-rays, radiation, etc.

Hybrids were obtained by exchanging pollinating paper bags. F_2 seed was obtained by selfing or from sib-matings of F_1 plants. To study the in-

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heritance of the small differences in the quantity of chlorophyll, the parental plants were propagated vegetatively. Clones were vegetatively propagated for several years, which made it possible to obtain F_1 and F_2 seed and to produce backcross hybrids.

Linkage between genes causing chlorophyll deficiency and other genes known in *Beta vulgaris* L. will not be discussed in this paper.

Experimental Results

The inheritance of albinism. The study of albinism in beets was started by Proskowetz (35). During 1885 and 1886 Proskowetz studied seventeen chimeric plants with alternate green and white sectors. He came to the conclusion that albinism was partially inherited.

Non-Mendelian inheritance of chlorophyll deficiency, *status albomaculatus*. In 1919 Stehlik (43) found a variegated seed beet which developed one green and one white branch. The seedlings grown from the seed balls collected from the white branch were yellow. He concluded "Das diese gelbe Färbung von dem in den Zellen vorhandenen Farbstoffe der chromatophoren herrührt." ("That this yellow color was caused by the color of chromoplasts located in the cells.") These plants could not develop chlorophyll and perished at an early stage. The plants derived from seed balls of the green branch gave 600 normal green plants without any trace of albinism. Stehlik was the first to state that albinism in variegated beets was inherited through the cytoplasm, as shown from studies in *Mirabilis Jalapa albomaculata* by Correns in 1909 (8).

Stehlik's conclusions that albinism in beets is inherited through the cytoplasm only, was confirmed by Murerati in 1928 and 1942 (25, 26). Murerati indicated that the chimeric variegated beets occurred in populations at the rate of one per 30,000 or 40,000 green plants. To study the inheritance of albinism, Murerati collected about 300 chimeric plants per year in commercial varieties.

The progeny consisted of white seedlings exclusively when the flowers from the white branches or green branches.

Seed collected from the green branches in the first generation, as well as in five subsequent generations, produced normal green plants independently of whether they were derived from hybridization by pollen collected from white or green branches. Therefore, Murerati concluded that albinism in beets is inherited through the cytoplasm only as it is inherited in *Mirabilis Jalapa albomaculata* (5 and 6), *Primula sinensis* (11 and 46), and in *Zea mays* (3).

In 1940 Owen and Ryser (32) also described one case of cytoplasmic inheritance of albinism from studies of the progeny from white and green branches of "partially albino plants."

I have studied many progenies of chimeric variegated plants isolated in sugar and fodder beet populations. Among these progenies only one authentic case was established where albinism was caused by a change in the nuclear gene. In all other cases the chimeric plants appeared as a result of heritable changes in the cytoplasm.

It is interesting to note that among several thousand plants known to be heterozygous for recessive genes causing chlorophyll deficiencies, I have never observed chimeric plants. Thus, chimeric variegated plants occurred

in beet populations more often as a consequence of heritable changes in the plasm rather than as a result of mutation of nuclear genes. This type of albinism, because of its comparatively frequent appearance, attracted the attention of the first investigators (25, 35, 43).

In a review of the inheritance of chlorophyll deficiencies in which a resume of all investigations conducted in all crops to 1933 was cited, H. de Haan (16) mentioned, for *Beta vulgaris*, only one type of chlorophyll deficiency—Mirabilis type (*status albomaculatus*).

Mendelian inheritance of albinism—the gene w_1 . In 1928, among seed beets of Yellow Eckendorf, I found one variegated plant (4, 41). The pollen collected from flowers of the white and of the green branches of this plant was used for pollinating normal green sugar beets. F_1 plants developed colored roots and green foliage. F_2 hybrids segregated for characters typical of sugar and fodder beets as well as the presence or absence of chlorophyll in seedlings.

In F_2 hybrids derived from pollination of normal green sugar beet plants by pollen collected from white branches of a variegated plant, there appeared 256 green and 79 albino seedlings. The color of these albino seedlings corresponded to the "maize yellow" of Ridgway (37).

In F_2 hybrids derived from pollination of green sugar beets by pollen collected from the green branches of the same variegated plant, only certain families segregated for albino seedlings in the ratio of three green to one albino. In this way the green branches of this variegated plant were heterozygous for the recessive gene causing chlorophyll deficiency.

Some F_3 lines obtained from green F_2 plants segregated again for green and white seedlings in the monohybrid ratio (Table I). Thus, the variegated Eckendorf plant was heterozygous for the recessive gene which I denoted as w_1 . This gene produced albino seedlings in the homozygote. The chimeric nature of the original heterozygous variegated Eckendorf plant was caused by the mutation of the dominant gene W into a recessive gene w .

Recessive genes causing complete albinism of seedlings are considerably rarer in beets than the other recessive genes for chlorophyll deficiencies, as for example the genes *virescens*, *chlorina*, etc.

Table I.—Mendelian Inheritance of Albinism in *Beta Vulgaris* L.

	Number of Seedlings		χ^2
	Green	White	
In F_2			
Observed	256	79	
Calculated (Ratio 3:1)	251.25	88.75	0.359
In F_3			
Observed	778	247	
Calculated (Ratio 3:1)	768.75	256.25	0.445

5% point of probability $\chi^2 = 3.84$

1% point of probability $\chi^2 = 6.64$

Sometimes the appearance of albino seedlings may be caused by some other genes, for example, by the dominant gene *Aurea* or by the action of two non-allelomorphic genes.

In F_2 hybrid lines the albino seedlings appeared sometimes in the ratio of one to 15 normal green plants. In such a case we had to deal with true duplication of genes causing albinism as described in other crops (7).

Aurea type—the dominant gene *Au*. In a population of U.S. 22/3 I found one plant which developed golden-yellow cotyledons (Baryta yellow in Ridgeway's "Color standards") and subsequent true leaves of the same color. If conditions for growth were favorable the heterozygous plants *Auau* developed normal green autumn leaves. Genetic study of the progenies obtained from this plant proved that the given type of chlorophyll deficiency was caused by the dominant gene *Au* with lethal effect in the homozygote. The homozygous seedlings were albino. A similar gene was described by Bauer (5, 6) in *Antirrhinum* and in *Pelargonium* and by Correns (9) in *Utricia wrens*. This gene is known in other crops too. Table 2 shows the data of genetic analysis of the gene *Au* during 1953, 1954, and 1955.

When normal green plants were crossed to plants of a given type of chlorophyll deficiency, the F_1 always was not uniform: green and yellow seedlings appeared in the ratio of 1:1. Selfed F_1 green plants produced, in all subsequent generations, uniformly green offspring, but the F_2 progenies from selfed yellow F_1 plants segregated for green, yellow, and albino seedlings in the ratio of 1:2:1 (Table 2).

Table 2.—Inheritance of Aurea Type in Sugar Beets.

	Generation	Year	Number of lines	Seedlings			χ^2
				Green	Yellow	Albino	
Observed	F_1	1953	8	529	522	—	
Calculated (ratio 1:1)				525.5	525.5	—	
Observed	F_1	1954	7	241	211	—	
Calculated (ratio 1:1)				242.5	242.5	—	
Observed	F_1	1955	4	111	103	—	
Calculated (ratio 1:1)				107	107	—	
Observed	F_2	1953	14	516	1129	591	
Calculated (ratio 1:2:1)				559	1118	559	
Observed	F_2	1954	7	181	343	183	
Calculated (ratio 1:2:1)				176.75	353.50	176.75	
Observed	F_2	1955	7	103	181	101	
Calculated (ratio 1:2:1)				97	194	97	

1% point of probability for F_1 generation $\chi^2 = 6.64$

1% point of probability for F_2 generation $\chi^2 = 9.21$

Lutescens type—gene *lu*. The recessive gene *lu* was isolated in hybrids between sugar and fodder beets, Red Eckendorf N 6219. The hybrids were propagated by sib-mating (41) (Table 3). In homozygous *lulu* plants the cotyledons and sometimes the first and second pair of leaves also showed normal green color. But subsequent leaves became more and more a lighter yellow. The majority of such homozygous yellow plants died. In surviving plants the root weight was reduced and did not exceed six percent of the root weight in normal green plants of the same hybrid. The F_1 plants were completely normal.

Virescens type—the genes vi_1 , vi_2 , and vi_3 . In beet races of virescens type, development of chlorophyll is delayed. Seedlings of these races are golden-yellow (Martius yellow in Ridgway's "Color Standards") because of the presence of carotene and of xanthophyll. Chlorophyll accumulates later. The first leaves are light green, but the following leaves become greener and greener under greenhouse conditions and eventually, they can not be distinguished from leaves of normal green beets.

In the species *Beta vulgaris* numerous genes of the virescens type are dispersed. These genes are distinguished by the grade of delayed action of chlorophyll accumulation and, in connection with this, in the grade of viability and of productiveness of plants.

Table 3.—Inheritance of Lutescens Type in Sugar Beets.

	Number of Plants with Second and Third Pairs of Leaves Colored as follows:		χ^2
	Green	Yellow	
Observed	270	83	
Calculated	264.75	88.25	0.416

5% point of probability $\chi^2 = 3.84$ 1% point of probability $\chi^2 = 6.64$ Table 4.—Segregation in F_2 After Crosses of Two Races of Virescens Type ($V_1 V_1 v_1 v_1$ and $V_2 V_2 v_2 v_2$) of chlorophyll deficiencies in *Beta vulgaris* L.

	Number of F_2 Plants Surviving		χ^2
	Green	Yellow	
Observed	434	290	
Calculated (ratio 9:4)	501	223	2.857

1% point of probability $\chi^2 = 6.64$ 5% point of probability $\chi^2 = 3.84$

All these genes are recessive. They belong to different loci. When two different virescens races are crossed, the F_1 seedlings are normal green in color. In F_2 dihybrid segregation was observed (41). The double homozygotes ($vi_1 vi_1 vi_2 vi_2$) were albino and perished because of their inability to accumulate chlorophyll. Plants homozygous in V_1 gene and heterozygous in gene V_2 ($vi_1 vi_1 V_2 v_2$) were also non-viable. Therefore, at the time of harvest, the segregation showed nine green to four yellow plants (Table 4).

The weight of root in these surviving yellow plants at harvest was 43.0 percent of the weight of root of the normal green plants in the same F_2 hybrids.

Every virescens gene vi , when it is separated from other virescens genes, showed mono-hybrid segregation in the ratio of three to one. In such cases there was no continual deficiency of plants with recessive genes in beets, the same as observed by Lamprecht (23) in peas.

In the past few years I isolated at the Salt Lake City station another gene vi_3 , the homozygotes of which showed a still stronger delay in chlorophyll development than the previously described genes vi_1 and vi_2 . Table 5 illustrates the inheritance of the gene vi_3 . Observations were conducted for three years. The F_1 plants were normal green. In the F_2 generation mono-hybrid segregation was observed.

Table 5.—Inheritance of Virescens Type Deficiency (gene $VisVi_3$) in *Beta vulgaris* L.

	Year	Genera- tion	Number of Popula- tions	Number of Seedlings		χ^2
				Green	Yellow	
Observed	1954	F_1	3	89	- -	
Observed	1952	F_2	1	317	103	
Calculated (ratio 3:1)				315	105	0.0507
Observed	1953	F_2	7	343	125	
Calculated (ratio 3:1)				351	117	0.729
Observed	1954	F_2	3	161	62	
Calculated (ratio 3:1)				167.25	55.75	0.9342
Observed	1955	F_2	6	218	89	
Calculated (ratio 3:1)				230.25	76.75	2.6069
Observed	1955		1	25	19	
Calculated (ratio 1:1)		backcross		22	22	0.8181

5% point of probability $\chi^2 = 3.84$

1% point of probability $\chi^2 = 6.64$

Variegated chlorophyll deficiencies—the genes v_1 , v_2 and v_3 . Variegated chlorophyll deficiencies are based on a recessive-pattern gene. A variegated gene was observed in beets by Owen and Ryser (32). Their description of this gene is as follows: "Variegated foliage, white with irregular blotches of green. Viability fair if seedlings are not crowded. Vigor not reduced in early cotyledon stage because cotyledons develop normally without chlorophyll deficiency. Leaves lack chlorophyll and plant vigor is decidedly reduced, but many v_1 plants have flowered and produced seed. Experience shows considerable instability at the v_1 locus."

The data for segregation in F_2 and in backcross hybrids given by Owen and Ryser showed a deficiency of variegated plants compared to normal green.

Abegg (1) found another variegated gene in beets v_2 , the gene which causes variegated cotyledons: "Light green to normal green sectors."

The third gene v_3 was indicated by Abegg (1): "Variegated foliage. Yellow to normal green sectors." The inheritance of this gene was not shown.

The variegated chlorophyll deficiencies which develop in the presence of a mutable gene have been described in several species (18, 19, 33, 36). Similar genes were not found in *Beta vulgaris*.

Chlorina type—genes ch_1 and ch_2 .—The genes causing chlorina type defects of chlorophyll in beets are recessive in the seedling stage. The decrease of chlorophyll is typical of the homozygotes— $chch$. The cotyledons, seedlings, and all new leaves in homozygous $chch$ beets are light green until fall (Cosse green in Ridgway's "Color Standards"). The homozygous $chch$ plants were viable, although the weight of their roots was reduced.

Table 6.—Inheritance of Chlorina Type Deficiency in *Beta vulgaris* L.

	Year	Genera- tion	Number of Families	Number of Seedlings		χ^2
				Green	Yellow	
Gene ch isolated in US 35/2						
Observed	1953	F ₂	5	198	68	
Calculated (ratio 3:1)				199.5	66.5	0.0451
Observed	1954	F ₂	3	101	40	
Calculated (ratio 3:1)				105.75	35.25	0.8534
Observed	1955	F ₂	6	294	109	
Calculated (ratio 3:1)				302.25	100.75	0.4764
Observed	1955	F ₂	7	311	112	
Calculated (ratio 3:1)				317.25	105.75	0.4925
Gene ch isolated in Great Western beet						
Observed	1954	F ₂	1	63		
Observed	1955	F ₂	9	440	135	
Calculated (ratio 3:1)				431	144	0.7101
Gene ch isolated in Kleinwanzleben beet						
Observed	1955	F ₂	1	53	22	
Calculated (ratio 3:1)				56.25	18.75	0.7511
Gene ch isolated in red mangel beet						
Observed	1955	F ₂	1	116	37	
Calculated (ratio 3:1)				114.75	38.25	0.5446

5% point of probability $\chi^2 = 3.84$

1% point of probability $\chi^2 = 6.64$

Certain chlorina-type genes differ in the grade of reduction of the weight of the root. For example, the gene ch_2 , which was isolated in the variety U.S. 35/2, reduced the yield of roots about 20 percent. Another gene ch_1 , which I found earlier (41), decreased the root weight much more.

The homozygotes ch_2ch_2 , which were isolated in the inbred line SLC 378 mm remained light green for three years. The F_1 hybrids ch_2ch_2 normal green beets as well as the reciprocal hybrids were always normal green in the seedling and rosette stages.

The F_2 hybrids between ch_2 and different sugar beet varieties showed normal monohybrid segregation in 1953, 1954, and 1955 (Table 6).

Dr. H. E. Brewbaker and Dr. R. K. Oldemeyer of the Great Western Sugar Company kindly provided some plants with light green foliage which were found at the Experiment Station in Longmont, Colorado. I crossed these beets to normal green plants and to chlorina type beets SLC 378 mm. When beets of the chlorina type, which I received from Longmont, were crossed to normal green plants, the F_1 plants were normal green and the F_2 hybrids showed mono-hybrid segregation (Table 6).

When beets of the chlorina type from Longmont were crossed to chlorina type beets SLC 378 mm, the F_1 plants were not distinguishable in color of cotyledons and leaves from the two parental types. In F_2 hybrids obtained from these crosses segregation was not observed.

Thus, the beets with light green foliage isolated at Longmont belonged to the chlorina type and their light green foliage was caused by the action of the gene of the same locus as the gene ch_2 .

In 1955 I studied also the recessive gene of the chlorina-type isolated in the inbred line SLC 1022 mm which originated from Kleinwanzleben's beets (Table 6).

Interaction between certain genes for chlorophyll deficiency. In the description of the virescens type of chlorophyll deficiency in beets, it was shown that the combination of two different homozygous genes (vi_1 and vi_2) produced non-viable homozygotes ($vi_1vi_1vi_2vi_2$) in the F_2 generation. At the same time the heterozygous F_1 plants ($Vi_1vi_1Vi_2vi_2$) were completely viable (Table 4). However, if the homozygous genes of the virescens type were combined with the homozygous genes causing another type of chlorophyll deficiency, for example, with the gene of chlorina type, then the plants carrying two homozygous genes were completely viable under greenhouse conditions. The F_1 hybrids between two homozygotes which carried the above-mentioned genes, were normal green and the F_2 progeny segregated for nine green and seven yellow-green or golden-green plants (Table 7).

Table 7.—Interaction Between Virescens and Chlorina Genes for Chlorophyll Deficiency in F_2 Generation.

Hybrids	Year	Seedlings		χ^2
		Green	Yellow	
<i>vi</i> ₁ <i>vi</i> ₁ X <i>ch</i> <i>ch</i>				
Observed	1955	97	92	
Calculated (ratio 9:7)		106	93	1.8645

5% point of probability $\chi^2 = 3.84$

1% point of probability $\chi^2 = 6.64$

Table 7 also shows that it was possible to distinguish by the color of seedlings and mature leaves the plants of the vi_2vi_2 genotype from the *chch* genotype in these hybrids.

When the gene *vi* (of *virescens* type) was combined with the gene *Au*, segregation was more complicated. In F_1 green and yellow plants were observed. F_2 offspring could be obtained only from the yellow F_1 plants, because only these plants carried the gene *Au*. These yellow F_1 plants produced, after selfing, F_2 progeny which segregated in the ratio: 3 green (1 *VvAuau* + 2 *Vviauau*): 6 yellow (4 *VvAuau* + 2 *VvAuau*): 3 golden yellow (2 *viviAuau* + 1 *vivianau*): 4 albino (1 *VvAuAu* + 2 *VvAuAu* + 1 *viviAuAu*) seedlings. The three viable classes gave F_3 families which confirmed the correctness of the accepted classification.

The effect of environment on chlorophyll formation in different chlorophyll-deficient races. Cultivation of beets belonging to the main types of chlorophyll-deficiencies such as *Aurca* (*Auau*), *chlorina* (*chch*), *virescens* (*vivi*), and albino (w_1w_1) in different environments showed that temperature and light influenced very much the formation of chlorophyll in these mutants.

Differences in the development of chlorophyll-deficient races were especially obvious when these races were cultivated in the greenhouse or under field conditions. Different development in the same races was also observed in spring and fall plantings.

Brighter light and higher temperature usually increased the depressive action of the genes *Au*, *ch*, *vi*, and w_1 on the development of the beets. The influence of environment on the development of chlorophyll-deficient types could be illustrated by the following examples:

Lethal chlorophyll mutants—*AuAu*. The albino seedlings *AuAu* died under field conditions three days earlier than in the greenhouse.

Semi-lethal chlorophyll mutants *Auau*. These heterozygous yellow seedlings developed almost normally in the greenhouse. After 60-80 days of growth under greenhouse conditions they developed green leaves and produced a fair amount of seed. The seedlings of the same mutant (*Auau*) when planted in the field in spring developed chlorotic foliage and had considerably decreased seed production.

***Virescens* type—*vivi*.** These homozygous beets developed golden seedlings. The plants grew in the greenhouse very slowly at the beginning, but later they accumulated more and more chlorophyll. In spite of this they developed under greenhouse conditions smaller roots than normal beets and produced less seed. When planted in the field, even in the fall, all homozygous *vivi* plants perished due to the loss of ability to accumulate chlorophyll.

The classification of many chlorophyll-deficient races becomes conditional because of the variation caused by the environment. The races which were denoted as "*virescens*" under greenhouse conditions, could be easily classified as "*xantha*" in field plantings. The races with yellow cotyledons which gradually turned green were denoted as *virescens*, because they were more viable than some other races with yellow seedlings which I observed

Table 8.—Interaction Between *Virescens* and *Aurea* Genes for Chlorophyll Deficiency in F₂ Generation.

Hybrids	Year	Seedlings				χ^2
		Green	Yellow	Gold	Albino	
<i>Auan X vicia</i>						
Observed	1954	93	173	97	121	
Calculated (ratio 3:6:3:4)		91	181	91	121	1.164
Observed	1955	55	88	39	73	
Calculated (ratio 3:6:3:4)		48	95	48	64	4.4897

5% point of probability $\chi^2 = 7.82$

1% point of probability $\chi^2 = 11.34$

before and from which I could hardly obtain seed even in the greenhouse, although their heterozygotes were normal green. The differences in the development of chlorophyll-deficient mutants under the influence of environment which I am discussing in beets were also described for other crops; Akerman (2) in oats, Smith (42), and Holm (17) in barley.

The grade of dominance of the genes causing chlorophyll deficiencies also varied under different conditions. Homozygous and heterozygous beets of chlorina type were as viable in greenhouse as in the field. However, the homozygotes *chch* looked much lighter in field than in the greenhouse. The heterozygotes *Chch* did not differ in the greenhouse from the normal green plants. The gene *ch* was recessive under greenhouse conditions. Another kind of behavior was observed in the field. The seedlings heterozygous for the gene *ch* were normal green while the homozygous seedlings were light green. In the late summer the heterozygous plants turned lighter and could be distinguished from the normal green plants. At the time of harvest the heterozygous plants lost still more chlorophyll and it was difficult to distinguish them from the homozygous recessive plants *chch*.

In such a way the grade of dominance changed during the vegetative period, as can be seen from the data of segregation in such hybrids. (Table 9).

Table 9.—Segregation in F₂ Chlorina Hybrids (Field Observations in 1953).

Reading in:	No. of plants with color of leaves as follows:		
	Green	Light-green	Total
July	36	11	47
October	14	33	47

Intensity of green color of leaves in sugar beets. Sugar beet plants within commercial populations differ in quantity of chlorophyll in the leaves. The differences in the quantity of chlorophyll represents the main factor causing the variation of the intensity of green color of leaves in individual beets. Many investigations (27, 28, 29, 31) showed a high correlation between the quantity of chlorophyll determined by the spectrophotometer in the leaves and the intensity of their green color. Therefore, for the determination of the intensity of a green color of leaves, color standards may be used making possible the classification of large numbers of plants in a short time.

To determine the intensity of green color of leaves the color standard of E. F. Votchall was applied. This color standard contains 16 classes for the intensity of green color, from light green to dark green. Each class is divided into four sub-classes, which do not differentiate in the quantity of chlorophyll but correspond to different shades of beet leaves. The color standard was graduated according to spectrophotometer readings and the readings of the color standards themselves showed the quantity of chlorophyll which the leaves contained (28, 31). The differences in the quantity of chlorophyll (chlorophyll *a*) between classes of this standard equaled 0.009 to 0.01 mgr. per one square cm. of the leaf blade.

Lines of sugar beets differ very much in the quantity of chlorophyll (40). Sugar beet races rich and poor in chlorophyll with dark and light foliage were obtained after selection for the intensity of the green color of leaves. A. C. Okonenko (28) was the first to start breeding for quantity of chlorophyll. He showed that plants selected for intensity of green color and propagated in isolations produced offspring with striking differences in the intensity of green color of the foliage.

I studied the inheritance of intensity of green color by using sugar beet clones (38, 39, 41). Table 10 shows the characters of the original clones and of their F_1 , F_2 , and backcross hybrids. Reading of the intensity of green color was done several times for each plant individually. The data showed the following:

1. When light green clone 37 was crossed to the light green clone 161, the F_1 hybrids were almost as light green as their parents.

2. When dark green clone 61 was crossed to dark green clone 205, the F_1 hybrids were almost as dark green as the parents.

3. When light green clone 37 was crossed reciprocally to dark green clone 66, the F_1 offspring were intermediate in color in both cases.

4. In both reciprocal F_2 hybrids populations derived from crosses of light green clone 37 to dark green clone 66, the interpopulation variability was much higher than in the corresponding F_1 hybrids.

5. When F_1 hybrids (Cl. 37 x Cl. 66) were crossed back to the light green clone 37, the offspring appeared to be lighter than the F_1 generation and vice versa when the same F_1 hybrids were crossed back to the dark green parental clone 66. The offspring were darker than the F_1 . In both cases the backcross hybrids were intermediate in leaf color between the F_1 and recurrent parents.

Table 10.—Variation in the Intensity of Green Color of Leaves in Sugar Beet Clones and Their F_1 , F_2 , and Backcross Hybrids Determined According to Color Scale of Prof. E. Votchal.*

Generation	Designation of Parents and Hybrids	Number of Plants With the Grade of Green Color as Follows:														Number of Plants	Mean	Standard Deviation	Coeff. of Variability Percent
		3	4	5	6	7	8	9	10	11	12	13	14	15	16				
Clone	P-37 with light green leaves			7	18	6	3									34	6.147	0.86	14.0
Clone	P-161 with light green leaves		4	6	16	8										34	5.824	0.94	16.1
F_1	P-37 x 161			11	39	29	11									90	6.444	0.96	14.9
Clone	P-66 with dark leaves									4	5	12	7	3		31	14.000	1.15	8.2
Clone	P-205 with dark leaves									3	3	6	15	8		35	13.628	1.20	8.8
F_1	P-66 X 205									6	8	8	21	35	19	97	13.319	1.42	10.7
F_1	P-37 X P-66					4	19	30	26	16						95	9.186	1.10	11.9
F_1	P-66 X P-37					3	9	18	6	4	3					43	9.186	1.09	11.9
Backcross	P-37 X (P-37 X P-66)			15	21	28	24	26	12	13			2			141	7.887	1.85	23.6
Backcross	P-66 X (P-37 X P-66)					5	16	20	28	16	14	19	18	18		154	11.272	2.37	21.0
F_2	P-37 X P-66			10	16	13	24	28	21	18	12	11	8	9	5	175	9.731	2.87	29.5
F_2	P-66 X P-37			6	20	25	37	36	39	30	19	17	11	15	5	260	9.896	2.68	27.1

* Intensity of green color increases with the increase of number of scale.

6. F_1 and F_2 hybrids obtained from reciprocal crosses between light green clone 37 and dark green clone 66 could not be distinguished. This was an indication that the genetic differences responsible for the intensity of green color which were observed in the usual sugar beet populations were caused mainly by the nuclear genes, but not by the elements of cytoplasm. The backcross hybrids confirmed this conclusion.

7. The genetic analysis of the F_1 and F_2 hybrids as well as of the corresponding backcross hybrids showed that the intensity of green color in beets is a quantitative character which is caused by the action of polygenes. Therefore, the inheritance of the quantity of chlorophyll in sugar beet races must be studied on the basis of methods usually applied for the study of the quantitative characters (24, 47, 34). However, the analysis of variability as well as of segregation for different grades of intensity of the green color of leaves is beyond the limit of this paper and will be elucidated later.

Summary

Genetic analysis is given for the following chlorophyll deficiencies in beets.

Albino (gene w_1), Aurca (gene Au), lutescens (gene lu), virescens (3 genes— vi_1 , vi_2 , and vi_3), and chlorina (genes ch_1 and ch_2).

The peculiarities of interaction between genes vi_1 and vi_2 as well as between genes vi_3 and ch_2 and Au are discussed.

The effect of environment on some indicated genes is shown.

Chimeric plants with variegated leaves consisting of mosaic white and green tissue sectors originated more often as a result of changes in the heritable substances of plasma than in the result of nuclear mutations.

A genetic study of different hybrids showed that the inherited differences in the quantity of chlorophyll which are peculiar to different plants within commercial varieties are determined by the nuclear inheritance, that is, by the action of polygenes. These differences in color of leaves and in quantity of chlorophyll are independent of cytoplasmic inheritance. Therefore, the heritable variability of the production of chlorophyll in beets is caused by the following factors:

- a. Variability of heritable elements of plasm or cytogenès (origin of chimeric variegated plants).
- b. Major chromo-genes which cause major changes in chlorophyll (the genes of chlorophyll deficiencies).
- c. System of nuclear polygenes which cause the polymorphism chlorophyll quantity in ordinary beet populations.

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