

SURVEY ON INHERITANCE OF SUNFLOWER CHARACTERS WHICH ARE
CONDITIONED BY A SMALL NUMBER OF GENES

By

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This paper summarizes hitherto notion on inheritance of morphological characters with sunflower. For to accomplish a most complete as possible set of characters we exploited the results of our own studies on characters which had not been investigated by other authors yet. Further on, our experimental data were contronted with those of other authors and judged from the point of view of gene interactions in the course of forming the characters. Only those characters were not included into the set, the phenotypes of which are being manifested mediately (e.g., fertility restauration, disease resistance); this was because the genetic analysis of those characters can be rather complicated by penetrance and expressivity.

In most characters a detailed evaluation of their genetic conditions was carried out; by this analysis a more complicated inheritance involving several genes, was always stated. Some characters were only designated as inherited characters, eventually their recessive or dominant relations to the standard phenotype were determined without precising the number of genes involved, and character of their inheritance.

The survey on inherited characters has been divided into two parts. The first part includes monogene inherited characters, inheritance of which could not be defined in detail. The second one comprises characters which are conditioned more complexly. With those characters following data are listed in the survey:

1) the name of phenotypical expression as related to the standard phenotype; 2) designation and the number of genes involved in the expression of the phenotype concerned; 3) the type of realization or the type of gene interaction as well as respective segregation ratio; 4) authors which studied the inheritance of the character in question.

Survey on essential data on simply inherited characters the detailed inheritance of which was not specified.

Character - phenotype expression	gene denotation	Relation to the standard phenotype	Authors
Ramification in the upper part of the plant	Br ₁	Dominant	Hockett, Knowles
Phytomelanine layer in the pericarp	P	Dominant	Anajeva; Gundajev
Striped achene	S	Dominant	Anajeva; Tavcar
Deep color of achene hypodermis	Hc	Recessive	Anajeva
White pollen color	Pa	Recessive	Anajeva; Stoenescu
Protogyny connected with spiral style	Pg	Recessive	Paun, Stoenescu
Curled leaf blade	Cu	Recessive	Clement, Diehl; Luczkiewicz
Strengthened leaf nerves	Vs	Recessive	Anajeva
Glossy brown tinge of the leaf surface	Bt	Recessive	Kovacik, Skaloud
Corky spots on the stem	So	Recessive	Kovacik, Skaloud
Fasciation of the stem	F	Recessive	Petrov; Stoenescu; Kovacik, Skaloud
Stipules on the leaf petioles	-	Recessive	Kovacik, Skaloud
Atrophy of first true leaves	-	Recessive	Stoenescu
Deformed bouquet flowers	-	Recessive	Soldatov
Globe-shaped inflorescence	-	Recessive	Soldatov
Mini-inflorescences on the bracts of the heads	-	Recessive	Soldatov
Fasciation of branches	-	Recessive	Kovacik, Skaloud
Multi-budding	-	Recessive	Kovacik, Skaloud
Dichotomic multi-heading	-	Recessive	Anascenko
Multi-heading with one additional small head	-	Recessive	Kovacik, Skaloud
Germination of achenes in unripened heads	-	Recessive	Kovacik, Skaloud

Survey on essential data on complexly inherited characters

1. Scarred stem (recessive).
 2. Two genes: Sc_1 , Sc_2 .
 3. Segregation 13: 2 = 1; dominant epistasis with intermediarity of the hypostatic gene. Double recessive condition results in decay of plants prior to their blossoming.
 4. Kovacik, Skaloud
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1. Anthocyanin color of leaf petioles (dominant).
 2. Three genes: Pc_1 , Pc_2 , Pc_3
 3. Segregation 36:18:10; complementarity between genes Pc_1 , Pc_2 and Pc_3 ; uncomplete double dominant epistasis between genes Pc_1 and Pc_2 .
 4. Kovacik, Skaloud
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1. Deep spots in the leaf sheaths (recessive)
 2. Three genes: Sh_1 , Sh_2 , Sh_3
 3. Segregation 57:7; dominantly recessive epistasis of Sh_1 over Sh_2 and Sh_3 ; complementarity of Sh_2 and Sh_3 .
 4. Kovacik, Skaloud
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1. Slitted petioles (recessive)
 2. Three genes: Sl_1 , Sl_2 , Sl_3
 3. Segregation 58:6; dominantly recessive epistasis of Sl_1 over Sl_2 and Sl_3 ; complementarity of Sl_2 and Sl_3 , the hypostatic gene Sl_3 acting as intermediary.
 4. Kovacik, Skaloud
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1. Green color of leaves (non-standard phenotype being recessive)
 2. Four genes: Cg_1 , Cg_2 , Cg_3 , Cg_4
 3. Segregations: 9 standard: 7 deep green; 13 deep green: 3 ashy green; approximately 13 standard: 13 ashy green. Standard expression is being caused by complementarity of genes Cg_1 and Cg_2 while deep green one by inhibition of the gene Cg_4 by the gene Cg_3 ; ashy green phenotype is being conditioned by Cg_4 . The relation of the standard to the ashy-green color occurs as a result of the combination of both complementarity and inhibition.
 4. Luczkiewicz; Kovacik, Skaloud
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1. Chlorotic leaf color (recessive)
 2. One gene: Cch
 3. Segregation 12:2,75; monogene recessivity; segregation ratio 3: 1 has been misrepresented by regular decay of chlorotic plants.
 4. Rudolf; Razoviteleva et al.; Kovacik, Skaloud.
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1. Mutational lack of chlorophyll (lutescens, chlorina-recessive)
 2. One gene with three alleles: Chl , $Chl1$, $Chlch$
 3. Segregation 3 green: 1 lutescens; 3 green: 1 chlorina; monogene recessivity with multiple allelism; dominance between alleles $Chl > chl1 > chlch$. Mutations causing the lack of chlorophyll are conditioned by genes which are non-allelic to genes for chlorophyll absence.
 4. Leclercq; Ljascenko, Vilor.

1. Mutational absence of chlorophyll (xantha, albina-recessive)
 2. One gene with three alleles: Cha, chax, chaa
 3. Segregation 3 green: 1 xantha; 3 green: 1 albina; monogene recessivity with multiple allelism; dominance between alleles Cha > chax > chaa.
 4. Leclercq; Skoric; Kovacik, Skaloud
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1. Spotted leaves of maculata type (white, yellow-recessive)
 2. Non-nuclear inheritance, probably of plastidic type
 4. Razoviteleva et al; Kovacik, Skaloud.
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1. Spotted leaves of variegata type (Yellow-green, brown-green - recessive)
 2. Four genes: St₁, St₂, St₃, St₄
 3. Segregation 13 standard: 3 chlorinovariegata; 55 standard: 9 brunescens-variegata. Chlorinovariegata is connected with the inhibition of the gene St₂ by St₁; brunescensvariegata is connected with the complementarity of genes St₃ and St₄, the genes St₃ and St₄ being inhibited by St₁.
 4. Kovacik, Skaloud.
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1. Crenation of leaves (non-standard slight crenation being recessive)
 2. Four genes: Cr₁, Cr₂, Cr₃, Cr₄
 3. Segregation 50 heavy crenated: 14 slightly crenated; incomplete recessive epistasis of genes Cr₂, Cr₄ over Cr₁ with double recessive epistasis. The gene Cr₄ is recessively epistatic to all other genes, namely Cr₁, Cr₂, Cr₃. Uncrenated leaf is being conditioned by the gene Cr₄.
 4. Kovacik, Skaloud
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1. Spoon-like leaf (recessive)
 2. One gene: Sp
 3. Segregation 3:1, under simultaneous presence of the gene Ms being 15:1; monogene recessivity; duplicate segregation ratio occurs as a result of interaction of genes Ms and Sp, this being a form of pleiotropic effect of the gene Ms
 4. Luczkiewicz; Kovacik, Skaloud
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1. Dense leaf nervure (recessive)
 2. Two genes: Vd₁, Vd₂
 3. Segregation 15:1; non-cumulative duplicity
 4. Anajeva
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1. Shortened leaf petioles (recessive)
 2. Two genes: Ps₁, Ps₂
 3. Segregation 9:7; double recessive epistasis
 4. Luczkiewicz; Kovacik, Skaloud
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1. Petioles joined to the stem (recessive)
 2. Two genes: Pj₁, Pj₂
 3. Segregation 13:3; inhibition
 4. Bockavoj

1. Multiple leaf whirls (recessive)
 2. Five genes: Wm_1 , Wm_2 , Wm_3 , Wm_4 , Wm_5
 3. Segregation 3:1 concerning the basic gene Wm_1 ; Wm_2 - Wm_5 are oligogene modifiers being expressed by segregation ratios: 12:3:1; 12:3:1; 1:2:1; 3:1. Wm_1 is dominantly epistatic over Wm_2 and Wm_3 . Wm_1 and Wm_2 are incompletely dominantly epistatic over Wm_4 . The gene Wm_5 is connected with the character lobed leaf.
 4. Kovacik, Skaloud
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1. Multiple cotyledons (recessive)
 2. Two genes: Cm_1 , Cm_2
 3. Segregation 12:3; inhibition. Apparently, syncotyl is not an inherited character.
 4. Kovacik, Skaloud
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1. Yellow tints of ligule flowers (standard yellow color being dominant)
 2. One gene with three alleles: L , lo , la
 3. Segregations 3 yellow: 1 orange-yellow; 3 yellow: 1 whitish yellow; 3 orange yellow: 1 whitish yellow. Monogene recessivity with multiple allelism; dominance between alleles $L > lo > la$. The genes L and lo are linked with the gene T for anthocyanin color, the linkage value being 10% (Kovacik, Skaloud)
 4. Leclerq; Stoenescu; Fick; Kovacik, Skaloud
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1. Anthocyanin color of styles (dominant)
 2. Three genes: Sa_1 , Sa_2 , Sa_3
 3. Segregation 27:27:10; double gradual complementarity; by complementarity of two genes the intermediary expression is being conditioned; complementarity of three genes results in a strong expression of the character.
 4. Luczkiewicz; Kovacik, Skaloud
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1. Anthocyanin color of the stem, leaves and hypocotyl (Dominant)
 2. Three genes: T_1 , T_2 , and Ha (for coloring the hypocotyl)
 3. Segregations 45 red: 19 green; 3 red: 1 green with red hypocotyl; 3 green with red hypocotyl: 1 green; 45 red: 3 green with red hypocotyl: 16 green. Complementarity of the gene Ha with genes T_1 and T_2 . Ha being absent, red color of stems and leaves does not occur. The gene T is linked with Ms_1 , linkage value being 1% (Leclerq)
 4. Leclerq; Velkov; Kovacik, Skaloud.
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1. Anthocyanin color of achenes (dominant)
 2. One gene: Tf
 3. Segregation 3:1. Segregation in relation to the gene T is 9:7, being realized, however, as 9:3:4; complementarity as a pleiotropic effect of the gene T .
 4. Leclerq; Velkov; Kovacik, Skaloud

1. Red color of flowers (dominant)
 2. Three genes: Fa_1 , Fa_2 , Fa_3
 3. Concerning the ratio of red to non-red individuals the segregation is 9:7 when red on the whitish-yellow basis is crossed with yellow, and 3:1 when red on the whitish yellow basis is crossed with whitish-yellow. When red on the whitish-yellow basis is crossed with yellow, segregation is as follows: 27 red:21 yellow:16 whitish-yellow. The genes involved are in a complementary relation.
 4. Anajeva; Fick; Kovacik, Skaloud
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1. Short tubulate flowers (recessive)
 2. One gene: $F1$
 3. Segregation 3:1; monogene recessivity; the gene $F1$ is linked with the gene Ms_2 , the linkage value being 20% (Stoenescu, Vranceanu)
 4. Stoenescu; Fick; Kovacik, Skaloud
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1. Long tubulate flowers (recessive)
 2. Two genes: Ft_1 , Ft_2
 3. Segregation 13:3; inhibition
 4. Aanjeva; Kovacik, Skaloud
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1. Absence of ligulate lowers (recessive)
 2. Three genes: Fd_1 , Fd_2 , Fd_3
 3. Segregation 42:22; the gene Fd_1 inhibits the effect of both the genes Fd_2 and Fd_3 ; the complementary condition Fd_2 , Fd_3 is not inhibited by Fd_1 .
 4. Clement, Diehl; Skoric; Luczkiewicz; Kovacik, Skaloud
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1. Full-blossom (dominant)
 2. Two genes: Bf_1 , Bf_2
 3. Segregation 3:6:7; complementarity of genes Bf_1 and Bf_2 with simultaneous intermediarity of the gene Bf_1 which results in partial full-blossom.
 4. Luczkiewicz; Kovacik, Skaloud
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1. Colored anthers (non-standard color being recessive)
 2. Three genes: Ag_1 , Ag_2 , Ag_3
 3. Segregation 60:3:1; dominant epistasis of genes Ag_2 and Ag_3 over the gene Ag_1 by which the brown color of anthers is being conditioned. The genes Ag_2 and Ag_3 are in duplicate relation.
 4. Stoenescu; Luczkiewica; Kovacik, Skaloud
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1. Pollen sterility (recessive)
 2. Five genes: Ms_1 , Ms_2 , Ms_3 , Ms_4 , Ms_5
 3. Segregations 3:1, 9:7, 15:1, and 13:3. The genes Ms_1 and Ms_2 are in duplicate relation; the genes Ms_3 and Ms_4 are in complementary relation; the genes of the group Ms_1 , Ms_2 are in incomplete recessive epistasis with the group of genes Ms_3 , Ms_4 . The gene Ms_5 is connected with zero-type of sterility.
 4. Putt; Heiser; Leclercq; Vranceanu, Stoenescu; Anascenko; Stojanova; Kovacik, Skaloud

1. Fascial multi-heading (recessive)
2. Three genes: Mhf₁, Mhf₂, Mhf₃
3. Segregation 63:1; non-cumulative duplicity
4. Kovacik, Skaloud

1. Palmette multi-heading (recessive)
2. Three genes: Mhp₁, Mhp₂, Mhp₃
3. Segregation 63:1; non-cumulative duplicity
4. Kovacik, Skaloud

1. Wild type of branching (dominant)
2. Two genes: Br₂, Br₃
3. Segregation 15:1; non-cumulative duplicity, branching being a dominant character
4. Hockett, Knowles; Kovacik, Skaloud

1. Wild type of branching with one main head (recessive)
2. Two genes: B₁, B₂
3. Segregation 15:1; non-cumulative duplicity, branching being recessive character
4. Putt; Hockett, Knowles; Luczkiewicz

1. Yellow color of the plant top (recessive)
2. One gene: Y
3. Segregation 3:1; monogene recessivity; the gene Y is linked with the gene Br₃, linkage value being 12%.
4. Hockett, Knowles

The given survey on inheritance of sunflower characters which are conditioned by oligogenes is not, of course, definitive. It will be necessary to determine inheritance of the other characters that were not studied yet, and to define in more detail the inheritance of characters which have been considered simply inherited. The main task, however, is to establish a collection of characters whose inheritance is known, and to determine linkages between them. Mentioned problems inclusive of the genetic research on quantitative characters, genetics of resistance and cytoplasmic pollen sterility, would become the object of activity of the Subsection for the Common International Research on Genetics in Sunflower, sponsored by FAO.