

INHERITANCE OF FIVE NEW CHARACTERS IN COLLINSIA HETROPHYLLA

J. GORSIĆ

Department of Biology, Elmhurst College
Elmhurst, Illinois 60126

ABSTRACT. Five new genetic characters of Collinsia heterophylla Buist. ($2n = 14$) are reported: (1) recessive cotyledon lethal, le; (2) replicate vernalization, re; (3) rimmed leaf, ri, displaying raised peripheral veins of the blade; (4) dentate, denticulate, crenate, and crenulated leaf margin controlled by four alleles of the Lm locus; and (5) displaced bud, db, displaying the fusion of the basal region of the lateral branches with the main stem. Physiological and morphogenetic aspects of the lethal, leaf margin, and displaced bud phenotype are briefly discussed.

For studies on genetic homologies among the 21 species of the genus Collinsia Nutt. (Scrophulariaceae) a large number of known gene loci in C. heterophylla - the most variable species of the genus - is required.

This paper adds five genetic characters to the list of 76 previously reported (Hiorth, 1930, 1931; Rai and Garber, 1960; Goršić, 1957, 1973). The seed used in this study were of the same origin as the seed used in previous studies (Goršić, 1973, 1974). Methods of cultivation and hybridization of Collinsia plants have been reported by Goršić (1957).

OBSERVATIONS AND INTERPRETATIONS

One trait reported in this paper is scored in the cotyledon stage of seedlings, three traits concern the development and morphology of leaves, and one trait represents the displacement of axillary buds.

Lethal, le (Tab. 1, Fig. 1). After emergence from the soil, the cotyledons of the homozygous le/le plants expand only to the size of about one third of the cotyledons of the wild-type plants. At the age of three weeks the cup-shaped, green cotyledons discolor brown, and the seedlings wilt and die exhibiting no plumule.

Replicate, re (Tab. 1, Figs. 2, 3). C. heterophylla has a decussate leaf arrangement. Plants of the replicate phenotype have one leaf of each pair folded backward (adaxially) in the bud. The folded leaves alternate with the non-folded leaves in two rows on one side of the stem. The replicate trait is not expressed at the lowermost nodes. The irregular folding of bracts (3 - 7 per node) of the inflorescence, ob-

served in the replicate (re/re), and in the wild-type plants, is not controlled by the re gene.

Rimmed leaf, ri (Tab. 1, Figs. 5, 6, 7). The leaves of the homozygous ri/ri plants have a rim on the upper (adaxial) side along the margin of the blade. The rim, being slightly raised above the surface of the leaf, is produced by the proliferation of the cells of the bundle sheath of the veins. The terminal branches of the peripheral veins are primarily affected. The ri, Lf (leaf form, Goršič, 1973), sn (spotted necrosis, Goršič, 1973), and Lm (leaf margin, see below) genes appear to be closely linked (Tab. 3).

Table 1. Segregation of backcrosses (BC) and F₂ generations for four characters of C. heterophylla

Character	Gene	No. of cultu- res	Segre- gation (*)	No. of domi- nants	No. of reces- sives	Expected No. of reces.	Chi-square value
lethal	<u>le</u>	8	F ₂	93	28	30.25	0.222
replicate	<u>re</u>	46	F ₂	448	144	148	0.143
		5	BC	43	43	43	--
rimmed leaf	<u>ri</u>	6	F ₂	77	26	25.75	--
		2	BC	26	22	24	0.332
displaced bud	<u>db</u>	10	F ₂	117	30	36.75	1.651

(*) Expected ratios: BC = 1:1, F₂ = 3:1

Leaf margin, Lm (Tab. 2, Figs. 4, 9, 10). The leaves of C. heterophylla vary morphologically in (1) the composition (controlled by D and F1 alleles, Hiorth, 1930; Goršič, 1957), (2) the shape of the blade (controlled by Lf alleles, Goršič, 1973), and (3) the nature of the leaf margin.

Four pure-breeding lines have been identified for the leaf margin, namely: dentate, denticulate, crenate, and crenulated (Fig. 9). On the basis of the phenotypic ratios obtained in the progenies of the hybrids between these pure-breeding lines (Tab. 2), a single locus, having four alleles, is postulated to control the leaf margin phenotypes; the four alleles being: Lm^d (dentate), Lm^l (denticulate), Lm^c (crenate), and Lm^r (crenulated, shallow crenate). These alleles interact in the hybrids producing intermediate phenotypes (Fig. 10). Some reciprocal crosses do not produce identical phenotypes (compare Lm^dLm^c and Lm^cLm^d leaves in Fig. 10). Plants of the pure-breeding (homozygous) lines having leaves with a conspicuously different margin are easy to identify but, in segregating populations composed of three or four genotypic classes, to match with certitude all observed phenotypes with the corresponding genotype is well-nigh impossible. The ri (rimmed leaf) gene which is closely linked with the Lm locus (Tab. 3) can be used in the hybridization experiments to facilitate the scoring of the leaf margin phenotypes of

Table 2. Segregation of F₂ generations and backcrosses (BC) of hybrids involving leaf margin alleles: Lm^d, Lm^l, Lm^c, and Lm^r

Parental genotype	No. of cultures	Segregation	P r o g e n y				Expected ratio	Chi-square value
			Homozygotes	Heterozygotes	Heterozygotes	Homozygotes		
<u>Lm</u> ^d <u>Lm</u> ^c	19	F ₂	91	199	--	85	1:2:1	1.548
<u>Lm</u> ^d <u>Lm</u> ^r	2	F ₂	7	20	--	6	1:2:1	1.416
<u>Lm</u> ^l <u>Lm</u> ^c	3	F ₂	15	40	--	17	1:2:1	0.999
<u>Lm</u> ^l <u>Lm</u> ^r	2	F ₂	10	31	--	11	1:2:1	1.960
<u>Lm</u> ^c <u>Lm</u> ^d x <u>Lm</u> ^c <u>Lm</u> ^c	1	BC	8	7	--	--	1:1	--
<u>Lm</u> ^c <u>Lm</u> ^d x <u>Lm</u> ^d <u>Lm</u> ^d	2	BC	26	26	--	--	1:1	--
<u>Lm</u> ^c <u>Lm</u> ^d x <u>Lm</u> ^l <u>Lm</u> ^l	2	BC	--	27	31	--	1:1	0.274
<u>Lm</u> ^c <u>Lm</u> ^l x <u>Lm</u> ^l <u>Lm</u> ^l	1	BC	6	6	--	--	1:1	--
<u>Lm</u> ^c <u>Lm</u> ^r x <u>Lm</u> ^d <u>Lm</u> ^d	1	BC	--	12	12	--	1:1	--
<u>Lm</u> ^d <u>Lm</u> ^l x <u>Lm</u> ^r <u>Lm</u> ^r	1	BC	--	9	8	--	1:1	--
<u>Lm</u> ^d <u>Lm</u> ^r x <u>Lm</u> ^d <u>Lm</u> ^d	2	BC	22	21	--	--	1:1	--
<u>Lm</u> ^l <u>Lm</u> ^r x <u>Lm</u> ^c <u>Lm</u> ^c	1	BC	--	4	4	--	1:1	--
<u>Lm</u> ^r <u>Lm</u> ^r x <u>Lm</u> ^c <u>Lm</u> ^d	2	BC	--	10	10	--	1:1	--

Table 3. Pairs of genes showing significant deviation from independent segregation ratios

Genes	Segregation*	AB	Ab	aB	ab	Total
<u>Lm</u> ^c - <u>ri</u>	F ₂	50	0	2	20	72
<u>Lm</u> ^c - <u>ri</u>	BC	26	0	0	21	47
<u>Lf</u> ^e - <u>Lm</u> ^d	F ₂	23	0	0	9	32
<u>Lf</u> ^e - <u>sn</u>	F ₂	19	2	3	8	32
<u>Lm</u> ^c - <u>sn</u>	F ₂	20	2	3	7	32

* Expected ratios: F₂ = 9:3:3:1, BC = 1:1:1:1

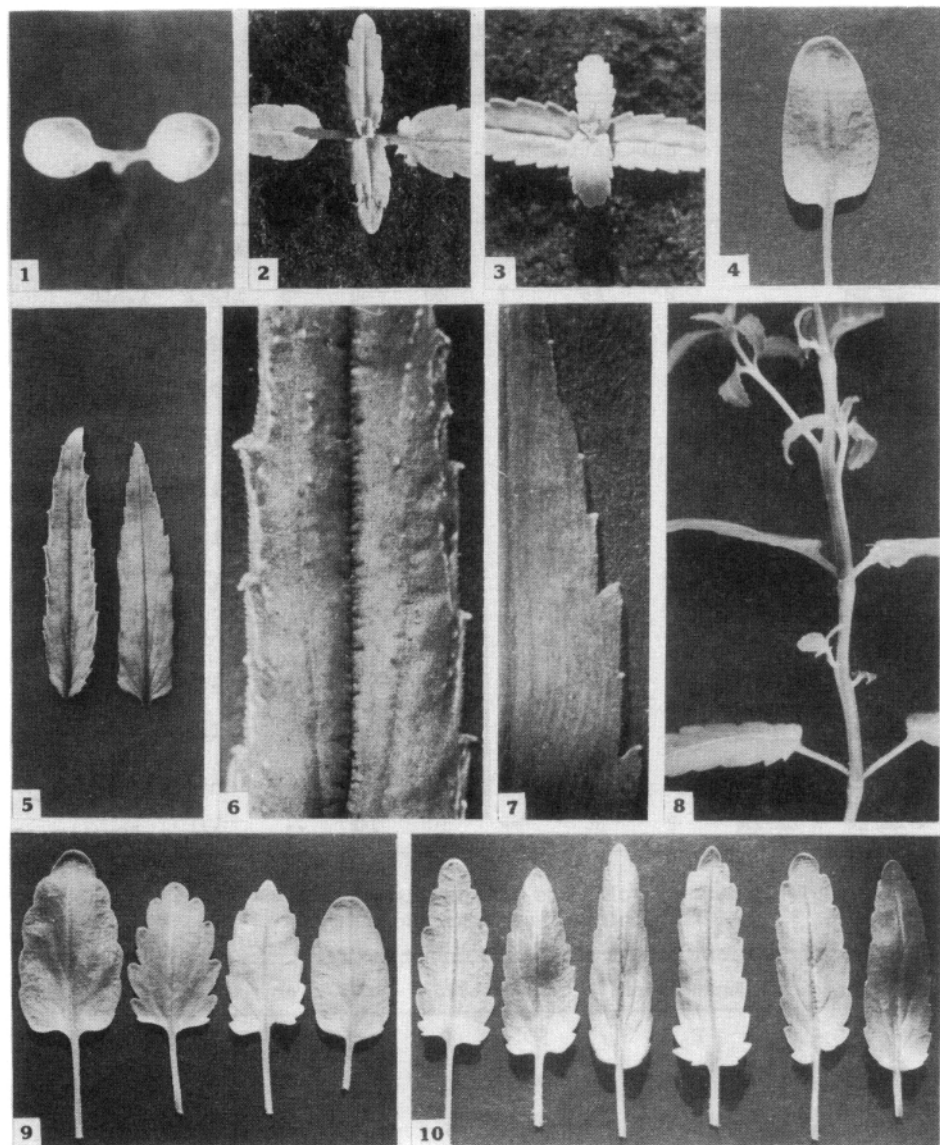


PLATE 1. Gene expression in *Collinsia heterophylla*. FIGURE 1. Cotyledon lethal, le. FIGURE 2. Replicate, re. FIGURE 3. Non-replicate (wild-type), Re. FIGURE 4. Nonserrate (zahnlos), z. FIGURE 5. Rimmed leaf, ri (left), and wild-type (right). FIGURE 6. A close-up of a rimmed (ri) leaf. FIGURE 7. A close-up of a wild-type (non-rimmed) leaf. FIGURE 8. Displaced axillary bud,

the progenies.

Additional alleles of the *Lm* locus may exist in *C. heterophylla*. The entire (smooth) margin allele of this locus has not been detected. However, the nonserrate phenotype (Fig. 4) is controlled by a pleiotropic gene *z* (*zahnlos*) of a different locus (Hiorth, 1930; Goršić, 1973).

Displaced bud, *db* (Tab. 1, Fig. 8). The lateral buds of mutant plants are displaced from the axil of the leaves upwards into the internode. In some *db/db* plants only one bud is affected, in other plants all vegetative buds of the stem and the branches are affected. The distance of the displacement of buds varies - in the same plant, and from plant to plant - but is restricted to the region of one internode. A scar may develop in the axils of leaves devoid of a bud.

DISCUSSION

In *C. heterophylla* four recessive genes (*a*, *yg*, *sl*, and *le*) are known to act lethally in the cotyledon stage of seedlings. The stemless (*sl*) gene may be considered sublethal (semilethal) because the plumule of the homozygous *sl/sl* seedlings can be induced - by surgically releasing the pressure of the fully fused cotyledons - to expand and develop into a normal stem (Goršić, 1973). Albino (*a*) and yellow-green (*yg*) genes, in homozygotes, interfere with the normal chlorophyll synthesis (Goršić, 1957). Depletion of the limited amount of food reserves in the thin cotyledons of the albino and yellow-green seedlings precludes the expansion of the plumule. - It is a common observation that the plumule of albino and yellow-green seedlings, growing from the seed with a large amount of food reserve, does expand (e. g. corn, soybean, oak, cherry, etc.). - The *le* gene, however, appears to have no deleterious effect on chlorophyll metabolism (no fading of green color in aging *le/le* seedlings was observed). Drastically reduced capacity of the *le/le* seedlings to expand may be attributed to the deleterious involvement of the *le* gene in either (1) the regulation of concentration of an auxin (its synthesis, or rate of degradation), or (2) in the induction mechanism of the cell enlargement and/or cell division.

Teeth of the dentate and denticulate leaves of *C. heterophylla* exhibit a minor vein which terminates in a protruding scar at the tooth tip (Figs. 6, 7). In the crenate and crenulated leaves the scar is shifted slightly in the basipetal direction on the tooth. These observations support the view that (1) the teeth develop from the meristematic cen-

PLATE 1. (continued) *db*, phenotype. FIGURE 9. Leaf margin types (left to right): crenulated ($Lm^R Lm^R$), crenate ($Lm^C Lm^C$), dentate ($Lm^d Lm^d$), and denticulate ($Lm^1 Lm^1$). Leaves taken from the third leaf node. FIGURE 10. Leaves of the fourth leaf node of hybrid plants (left to right): $Lm^d Lm^C$, $Lm^1 Lm^C$, $Lm^C Lm^d$, $Lm^d Lm^R$, and $Lm^1 Lm^R$ (in each pair, left allele is maternal, right allele is paternal).

ters localized along the leaf margin, and (2) the differentiation of the vascular tissue is intimately associated with these growth centers (Slade, 1957). In concurrence with this view, the nonserrate leaves (Fig. 4) exhibit no projected scars along the leaf margin.

The displaced bud (db) phenotype represents an ontogenetic deviation in the development of the lateral branches. A similar ontogenetic deviation in honeysuckle (Lonicera tatarica L.) has been studied by Vieth and Lamond (1973). Two deviations of the early stage development of the axillary bud, that may result in its displacement from the node into the internode, are suggested: (1) a precocial initiation of the lateral bud primordium would enable the apex of the axillary bud to grow in unison with the apex of the main stem, thus displacing the lateral bud upwards; (2) a decrease in the concentration of auxin (deficiency in synthesis, rapid degradation or diffusion, etc.) in the shoot apex would eliminate the apical dominance, and the lateral bud, being free of inhibition, would expand in unison with the main stem, and thus become displaced from the axil of the leaf into the internode. In either case, the closeness of the growing tissues of the main axis and the lateral bud(s) leads to the fusion of the developing organs to such a degree that the vascular bundles of the main stem and the vascular bundles of the branch(es) form a single vascular cylinder.

LITERATURE CITED

- GORŠIĆ, J., 1957. The genus Collinsia. V. Genetic studies in C. heterophylla. Bot. Gaz., 118:208-223.
- , 1973. The genus Collinsia. XXX. Further genetic studies in C. heterophylla. Bot. Gaz., 134:255-266.
- , 1974. Polycotyledony and morphogenesis of the inflorescence and flower in C. heterophylla. Ill. State Acad. Sci., Transactions, 67:105-113.
- HIORTH, G., 1930. Genetische Versuche mit Collinsia bicolor. I. Z. Induktive Abstammungs- und Vererbungslehre, 55:127-144.
- , 1931. Genetische Versuche mit Collinsia bicolor. II. Die Blatt- und Kotyledonenzeichnungen von Collinsia bicolor. Z. Induktive Abstammungs- und Vererbungslehre, 59:236-269.
- RAI, K. S. and E. D. Garber, 1960. The genus Collinsia. XI. Trisomic inheritance in C. heterophylla. Bot. Gaz., 121:109-117.
- SLADE, B. F., 1957. Leaf development in relation to venation as shown in Cercis siliquastrum L., Prunus serrulata Lindl. and Acer pseudoplatanus L. New Phytol., 56:281-300.
- VIETH, J. et M. Lamond, 1973. Contribution à la tératologie des chèvrefeuilles et au problème des fusions. Can. J. Bot., 51:517-525.