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An Example of Introgressive Hybridization Between Viola Papilionacea Pursh and V. Nephrophylla Greene

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Both *Viola papilionacea* Pursh and *V. nephrophylla* Greene are fairly common and well-known acaulescent blue violets of northeastern and midwestern United States. *V. papilionacea*, the common blue violet, is found from Maine to Minnesota and thence southward to Oklahoma and Georgia. In the midwestern prairies the somewhat smaller plants are sometimes called var. *pratincola*. *V. nephrophylla*, though not so abundant locally, is much more widespread, occurring from Newfoundland to British Columbia and southward to northern New York, Michigan, northern Iowa, North Dakota, and, in the west, south along the mountains to Arizona and southern California (Fernald, 1950). In the area about Minneapolis, Minnesota, both species occur in approximately equal concentrations. *V. papilionacea* is found either in river woods (the typical form) or in wet prairie and along the edges of wet meadows (var. *pratincola*). *V. nephrophylla* locally occupies wet, poorly drained

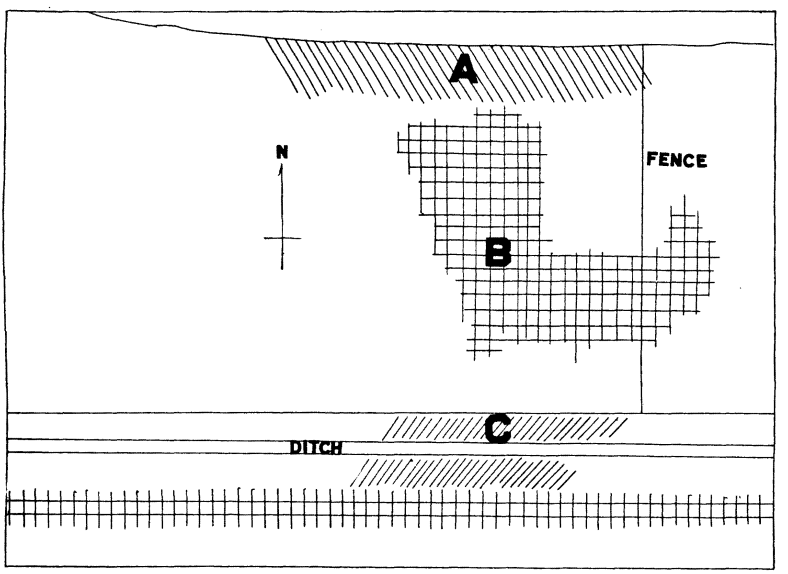

Figure 1. Sketch map of the meadow referred to in the text. Scale: 1 inch equals about 20 feet. The area studied is bounded by a floodplain creek on the north and a railroad bed on the south. A—local population of *V. papilionacea*. B—local population of *V. nephrophylla*. C—local population of *V. sororia*.

meadows, often where cattle graze. Occasionally local populations of the two species will come into contact along the edges of wet meadows. The studies to be reported upon here were made in one such location, on the south floodplain of the Minnesota River, about ½ mile north of the bridge leading from Minneapolis toward Mendota (U. S. Route 52). The sketch map (Figure 1) indicates the local distribution of the two species and in addition of a third, *V. sororia* Willd. Both the meadow and the creek bank to the north of it were grazed by cattle throughout the spring and summer during the four-year residence of the author in Minneapolis (1947-1941), and occasionally partly eaten violet plants were found. *V. nephrophylla* was fairly abundant in the meadow, several hundred plants being seen during the flowering season (early May). *V. papilionacea*, on the other hand, was not so abundant, only about 50 plants being found on the meadow border and creek bank.

According to Fernald (1950) and Brainerd (1921), *V. papilionacea* differs from *V. nephrophylla* in a number of observable characters. At maturity the leaves of *V. papilionacea* are cordate-ovate, often with somewhat attenuated apices, while the leaves of *V. nephrophylla* are, as the specific name implies, somewhat reniform, though not conspicuously so in spring, when the specimens herein described were collected. The leaves of *V. papilionacea* typically overtop the petaliferous flowers, while the reverse is true of *V. nephrophylla*. The color of the petals is a rich violet-blue in *V. papilionacea* and a light blue ("Wisteria Blue") in *V. nephrophylla*. In addition the cleistogamous fruits of *V. papilionacea* are borne on short, prostrate peduncles and are often purple, while those of *V. nephrophylla* are borne on longer, erect peduncles, are always green and are smaller than are those of *V. papilionacea*. The spurred (lower) petal of *V. papilionacea* is glabrous, while the spurred petal of *V. nephrophylla* is villous at the base. A differentiating factor in the spring is the bluish color of the underside of the young leaves of *V. nephrophylla*. The two species differ in other, less conspicuous features.

That the two species may hybridize in nature is attested to by both Brainerd (1924) and Fernald (1950). Brainerd (1924) reported upon collections of hybrids from Racine County in southeastern Wisconsin. Fernald notes only that hybridization occurs in nature. In the present instance, hybridization was suspected when the violets were first seen at the Minnesota River locality. Both species seemed at first sight somewhat atypical. In addition a number of plants apparently morphologically intermediate between the

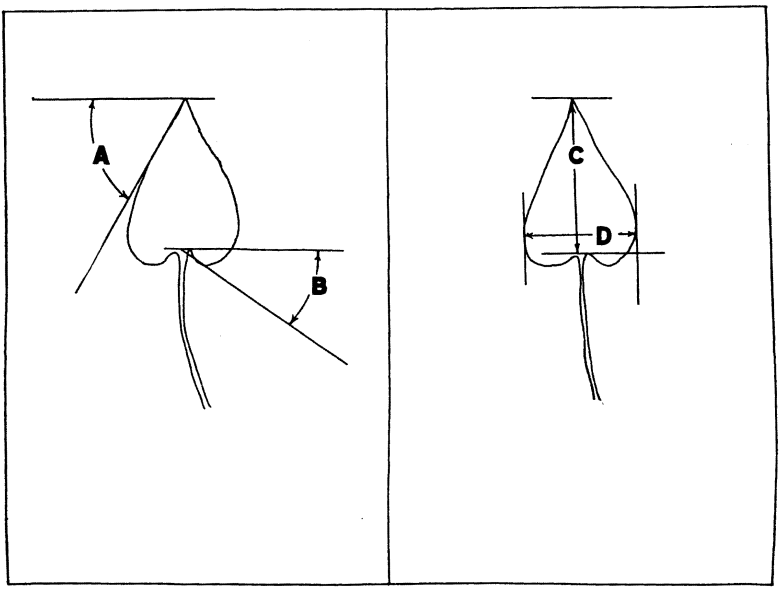

Figure 2. Lamina measurements, A—"Apical Angle", B—"Basal Angle", C—Lamina Length, D—Lamina Breadth.

two species were found especially along the zone of contact (i.e. where the ground rose toward the edge of the creek and the soil became obviously drier).

Methods

Two population samples of 25 plants each were taken. The first, designated by the collection number NR 59491, was collected from the wet meadow. The second, NR 59492, from the drier creek bank to the south. The plants were returned to the laboratory, carefully washed, pressed and dried. The following measurements and observations were then made: lamina length and breadth, length of the longest peduncle and the longest petiole, amount of pubescence on the spur petal (scored as 0 or glabrous, 1 or slightly pubescent, and 2 or very pubescent), the angle of divergence from the horizontal of the apical margin of the leaf blade (designated as "apical angle"), and the angle of divergence from the horizontal of the basal lobes of the blades (designated as "basal angle"). The leaf measurements are indicated in Figure 2.

Results

Means for the characters measured for the two populations are given in Table 1. In addition means are given here for the ratios

between peduncle length and petiole length, lamina length and lamina breadth, and apical angle and basal angle.

In Table 2 the distributions of the measurement and ratio values are shown for certain characters. The considerable morphological overlap between the two populations is clearly indicated by Table 2. From the data in this table a hybridization index (Anderson, 1936) was constructed. Four characters were considered and values assigned as follows:

	papilionacea	*intermediate*	*nephrophylla*
1. Pubescence spur petal	glabrous	few hairs	villous
score	0	1	2
2. Ratio peduncle length/ petiole length	.60 - 1.19	1.20 - 1.39	1.40 - 2.00
score	0	1	2
3. Ratio apical angle/ basal angle	1.50 - 2.70	1.10 - 1.49	.50 - 1.09
score	0	1	2
4. Lamina length/ lamina breadth ratio	.90 - 1.70		.60 - .89
score	0		2
TOTALS	0		8

Each of the plants measured was scored individually using the above index. Therefore the total score of any single plant might vary between zero and eight. If zero, it would be considered a typical plant of *V. papilionacea*, if eight, a typical individual of

Table 1.

Means of measured characters. Means for pubescence of spurred petal were based upon three values: 0 = glabrous, 2 = villous, 1 = intermediate.

Collection	Designation	Number Specimens	Length Peduncle (mm)	Petiole Length (mm)
NR 59491	*V. nephrophylla*	25	85.04	67.84
NR 59492	*V. papilionacea*	25	71.28	70.24

Collection (cont.)	Peduncle/ petiole ratio	Lamina length (mm)	Lamina breadth (mm)	Length/ breadth ratio	Apical angle (degrees)
NR 59491	1.11	23.76	25.00	0.92	41.00
NR 59492	1.05	28.32	27.52	1.04	47.56

Collection (cont.)	Basal angle (degrees)	Apical angle/ basal angle ratio	Pubescence spurred petal
NR 59491	47.16	0.89	1.04
NR 59492	30.72	1.59	0.04

Table 2.

Distribution of individual measurements of certain characters.

Ratio—length longest peduncle / length longest petiole

Collection	.60	.80	1.00	1.20	1.40	1.60	1.80	2.00
NR 59491		2	4	7	10		1	
NR 59492	3	5	12	3	1			

Ratio—lamina length / lamina breadth

Collection	.60	.70	.80	.90	1.00	1.10	1.20	1.30	1.40	1.50	1.60	1.70
NR 59491	2	6	10	7								
NR 59492	2	3	5	9	3				1			1

Apical Angle—degrees

Collection	20	25	30	35	40	45	50	55	60
NR 59491		2	3	2	6	9	2	1	
NR 59492			1	2	2	3	13	3	

Basal Angle—degrees

Collection	20	25	30	35	40	45	50	55	60	65	70	75
NR 59491			2	3	5	2	6	3	3		1	
NR 59492	1	6	10	5	3							

Ratio—apical angle / basal angle

Collection	.50	.70	.90	1.10	1.30	1.50	1.70	1.90	2.10	2.30	2.50	2.70
NR 59491	2	11	6	5								
NR 59492			3	2	4	10	2	2	1		1	

Amount of pubescence on spurred petal. 0 = glabrous, 2 = villous, 1 = intermediate.

Collection	0	1	2
NR 59491	3	18	4
NR 59492	24	1	0

V. nephrophylla. If intermediate, the plant would be considered a putative hybrid or backcross. Two of the characters, the ratios between apical angle and basal angle and between lamina length and lamina breadth, though actually both indications of leaf shape, measure two aspects of leaf shape and are thought to be complementary. In all cases the distinctions between the measurements accorded each species were based upon study of typical herbarium

material and published descriptions of the two species. The range of scores derived from each collection was as follows:

	Score									
Collection	0	1	2	3	4	5	6	7	8	Total Plants
NR 59491			3	4	5	6	2	4	1	25 (*nephrophylla*)
NR 59492	13	5	3	1	1	2				25 (*papilionacea*)

Conclusions

The mean score for collection NR 59491 was 4.64 and for collection NR 59492 was 1.12. Based upon the above method, it would seem fairly obvious that not only was hybridization occurring, but that *V. papilionacea* had introgressed markedly into *V. nephrophylla*. Whereas the mode of the *V. papilionacea* scores was 0, that of *V. nephrophylla* was 5, indicating a shift of the characters of the latter species, in this particular location, towards those of *V. papilionacea*. Introgression in the reverse direction is much less distinct, if present at all.

Admittedly, the hybridization index is but a crude measure of the effects of hybridization, particularly when used with as few characters as in the present instance. However, it has been widely used and has proved reliable in nearly every instance (Anderson, 1949). Its particular value is the rapid diagnosis of the importance of hybridization which it makes possible.

A character which was observed but not included in the measurements present above was that of lamina pubescence. Both *V. papilionacea* and *V. nephrophylla* are characterized by having perfectly glabrous laminas. However, it was noted here that 4 of the 25 measured plants of *V. nephrophylla* had laminas which were pubescent on the upper surface. On the other hand, all of the *V. papilionacea* plants were perfectly glabrous. It is possible that *V. nephrophylla* may be here hybridizing to some extent with the few plants of *V. sororia* which occur just to the south of it (see Figure 1). *V. sororia* is characterized by pubescent laminas. If this were eventually shown to be the case, it would constitute an example of a population being affected by two different introgressants. All three of the species of this local complex have diploid chromosome numbers of 54 (Gershoy, 1934), and apparently are very closely related.

The results of introgression may be various, depending upon local circumstances and also intrinsic genetic factors. In the present instance, if introgression proceeds strongly into *V. nephrophylla*, as

is indicated by the index scores, it is possible that it will be eventually genetically "swamped" by the replacement of its alleles by those of *V. papilionacea.* This would be undoubtedly an extreme result. Apparently the end result of continued very local introgression is the enrichment of the gene pools of one or both participating species; in other words additional alleles are added to those already present in the species.

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