AN EXPERIMENTAL STUDY OF HYBRIDIZATION IN THE GENUS APOCYNUM

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Introduction

In his monograph of the genus *Apocynum,* Woodson ('30) maintained a rather extreme position as to the prevalence and importance of interspecific hybridization in that genus. He classified the Apocynums of eastern North America in four species, *A. hypericifolium, A. cannabinum, A. androsaemifolium,* and *A. medium,* the last derived from hybridization between two of the others. The remaining variants, largely (according to Woodson) the result of hybridization, were allocated to some 14 varieties of these major species. Figure 2, a copy of his fig. 11, presents a graphical summary of his hypotheses as to phylogenetic relationships in the genus. To the writer these ideas, though stimulating and interesting, seemed rather in need of experimental confirmation by other than purely morphological criteria. After much friendly argument an experiment was planned and carried to completion in the experimental grounds of the Bussey Institution of Harvard University. It consisted in making progeny tests of individual plants of *Apocynum cannabinum* and *A. androsaemifolium,* and their suspected hybrid, *A. medium.* It is pleasant to report that the genetical and cytological data not only confirmed Dr. Woodson's general thesis but that they agreed exactly with several minor details of his hypothesis about which the writer had been extremely skeptical.

Methods.—Seed of *Apocynum medium* and *A. cannabinum* was collected by Dr. R. E. Woodson in a field near South Bend, Indiana, where *A. cannabinum* grows in company with a lesser number of *A. androsaemifolium* and their putative hybrid, *A. medium.* Seed was collected from five different plants of *A.*

medium and from one plant of *A. cannabinum,* the seeds from each plant being kept separate. The writer collected seeds of *A. androsaemifolium* from one of several plants growing in a meadow on the banks of the Concord River near Billerica, Massachusetts. They were sown in the greenhouse in the winter of 1934 and the resulting seedlings planted out the following spring. During the summer of 1935, when they were a year and a half old and fully mature, they were kept under careful observation by the writer. To reduce the personal equation to a minimum, counts of pollen fertility were made by Mr. Lawrence Regan, who was completely unacquainted with the history of the plants he was examining. The taxonomic determination of the progeny was equally objective. A com-

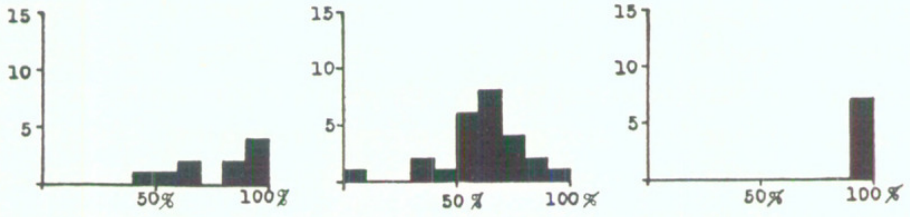

Fig. 1. *A. androsaemifolium* (left), *A. medium* (center), and *A. cannabinum* (right). Horizontal axis represents per cent of fertile pollen, vertical axis, number of individuals.

prehensive flowering and fruiting herbarium specimen was made of nearly every plant. Each was tagged with a serial number, and the specimens, completely shuffled, were handed over to Dr. Woodson for identification. To increase the objectivity he was not even informed as to the source or the specific identity or the relative amount of material grown from seed collected by the writer. The data as presented below are therefore unusually trustworthy, even for a scientific experiment.

The results of the progeny test are presented in full in table 1 and certain points are summarized in fig. 1. The progeny of each plant are listed together; for each seedling the table gives the individual record number, the percentage of fertile pollen as determined by Mr. Regan, and its probable specific identity as determined by Dr. Woodson from the herbarium specimen

submitted to him. His comments have been added in the last column since they have a direct bearing upon the problem.

Conclusions

1. Pollen fertility.—The progeny of *Apocynum cannabinum* had pollen of uniformly high fertility. Those of *A. androsaemifolium* were mostly of high fertility though a few seedlings were semi-sterile. The progeny of *A. medium* were characterized by a low average fertility. The results are presented graphically in fig. 1.

2. Genetical results.—The putative parental species, *A. cannabinum* and *A. androsaemifolium,* both bred true, though both segregated noticeably for presence or absence of pubescence. In spite of the small numbers of seedlings obtained, *A. medium* failed to breed true. Of the twenty-six seedlings of *A. medium* pressed and turned over to Dr. Woodson, eighteen were diagnosed as *A. medium,* six as *A. androsaemifolium,* and two as *A. cannabinum.* It is also significant that all the plants about whose absolute specific identity Dr. Woodson had some doubt were among these seedlings of *A. medium.* The comments in the right-hand column of table 1 give a very true picture of the comparative variability of the progeny of *A. cannabinum* and *A. androsaemifolium,* on the one hand, and of *A. medium,* on the other.

3. Apocynum medium.—This species is therefore most certainly a hybrid and might well be designated as such in botanical literature. In addition to the evidence which originally led Woodson ('30) to that conclusion, the above experiment has demonstrated that, like most hybrids, it produces variable progeny of low average fertility. Some of these progeny resemble the putative parental species so strongly that in the absence of any information as to their source, they would unhesitatingly be so identified by any one familiar with the species in question.

4. Apocynum cannabinum and *A. androsaemifolium.*—These are probably more or less self-sterile as Woodson had already suspected ('30). The existence of as much variation as was

TABLE I

RESULTS OF PROGENY TESTS OF ONE PLANT OF *APOCYNUM CANNABINUM*, ONE OF *A. ANDROSAEMIFOLIUM*, AND FIVE OF *A. MEDIUM*

(Further explanation in the text)

	Seedling No.	Per cent fertile pollen	Identification	Remarks
A. cannabinum				
No. 447—South Bend, Ind.	1	95	*A. cannabinum* var. *typicum*	
	2	93	*A. cannabinum* var. *typicum*	
	3	91	*A. cannabinum* var. *glaberrimum*	
	4	98	*A. cannabinum* var. *glaberrimum*	
	5	98	*A. cannabinum* var. *typicum*	
	6	97	*A. cannabinum* var. *typicum*	
	7	94	*A. cannabinum* var. *glaberrimum*	
A. androsaemifolium				
No. 503—Billerica, Mass.	1	60		Specimen lost
	2	89	*A. androsaemifolium*	Very typical
	3	42	*A. androsaemifolium*	
	4	99	*A. androsaemifolium*	Fairly typical
	5	86	*A. androsaemifolium*	
	6	96	*A. androsaemifolium*	Essentially typical
	7	95	*A. androsaemifolium*	Very typical
	8	95	*A. androsaemifolium*	Typical
	9	95		Specimen lost
	10	64	*A. androsaemifolium*	
	11	68		Specimen lost
A. medium				
No. 446—South Bend, Ind.	1	89	*A. medium*	Glabrous leaves
	2	63	*A. medium?*	Like a small *A. androsaemifolium*
	3	57	*A. medium*	Glabrous
	4	64	*A. medium*	Close to var. *leuconeuron*
	5	68	*A. medium*	Sparsely pubescent
	6	64	*A. medium*	Sparsely pubescent
	7	39	*A. medium*	Glabrous
	8	72	*A. medium*	Glabrous
	9	55	*A. medium*	Glabrous
	10	63	*A. medium?*	Unusually small flowers
	11	99	*A. cannabinum* var. *glaberrimum*	
No. 448—South Bend, Ind.	1	61	Probably a glabrous *A. medium*	
	2	77	*A. medium*	

TABLE I—(Continued)

RESULTS OF PROGENY TESTS OF ONE PLANT OF *APOCYNUM CANNABINUM*, ONE OF *A. ANDROSAEMIFOLIUM*, AND FIVE OF *A. MEDIUM*

(Further explanation in the text)

	Seedling No.	Per cent fertile pollen	Identification	Remarks
A. medium (Cont.)				
No. 449—South Bend, Ind.	1	77	*A. medium*	But very small flowers
	2	53	*A. medium*	Quite typical
	3	78	*A. medium*	But nearly glabrous
	4	93	*A. androsaemifolium*	
	5	98	*A. medium*	
No. 502—South Bend, Ind.	1	90	*A. cannabinum* var. *glaberrimum?*	
	2	65	*A. androsaemifolium*	But small-flowered
No. 504—South Bend, Ind.	1	58	*A. medium?*	
	2	37	*A. androsaemifolium?*	Possibly a hybrid
	3	41	*A. medium*	
	4	4	*A. androsaemifolium*	
	5	57	*A. androsaemifolium?*	Corolla rather small

exhibited between sister plants of either species indicates that intra-specific cross-pollinations must be frequent (Anderson, '28). G. Medwedewa has recently shown ('35) for *Apocynum venetum* that pollen-tubes may reach the ovary after self-pollination. She explains the lack of seed obtained in experimental selfings as due to the fact that flowers isolated in paper bags were inundated by their own nectar. There are, however, other mechanisms for self-sterility beside differential pollen-tube growth as has been shown by Stout and Chandler ('33) and others. Medwedewa's demonstration of the superior accelerating effect of foreign stigmas as compared to those from the same plant may be an indication of a deep-seated incompatibility which allows pollen-tube growth in the style but either prevents fertilization or the development of self-fertilized zygotes. As Medwedewa has suggested (loc. cit.), precise genetical tests of vicinism are really necessary for a decisive answer. The results reported above, particularly the progeny test of a plant of *A. androsaemifolium* from Billerica,

bear directly on this point. This plant was not growing in the vicinity of other species of *Apocynum* nor was there any indication of hybridity in the colony, and yet there was marked variation between its progeny. This would indicate a high percentage of out-crossing.

DISCUSSION

No one doubts any longer that inter-specific hybridization can take place in nature. There remain the determination of its comparative frequency, its taxonomic importance, and its phylogenetic consequences. The evidence reported above suggests that hybridization is of fairly frequent occurrence in the genus, and that it is largely responsible for the taxonomic difficulties encountered in classifying the species of *Apocynum* in eastern North America. These difficulties spring not from the main bulk of the genus, which is readily segregated into the chief species, but from a small percentage of puzzling aberrants. *Apocynum medium* in itself constitutes no great problem in classification, whether it be accepted as a hybrid or maintained as a species. It is rather the small percentage of specimens which are *almost* like typical *A. androsaemifolium,* or *almost* like *A. cannabinum,* or near *A. medium,* which provides a very real problem in classification. Should one deal with these variants as separate species, as was done by the late Edward L. Greene; should one ignore them more or less completely, as have many American botanists; or should one catalogue them as varieties of *A. cannabinum, A. androsaemifolium,* and *A. medium,* as was done by Woodson in his monograph? Cogent objections can be raised and have been raised to each of the above procedures. The experiments reported above give little or no information as to the best means of dealing with these puzzling variants; that is of course mainly a problem in classification. On the biological question of their origin and phylogenetic importance the evidence is, however, quite specific. Clearly, if the above results are typical, these variants are secondary hybrids one or more generations removed from the original cross between the species. They may

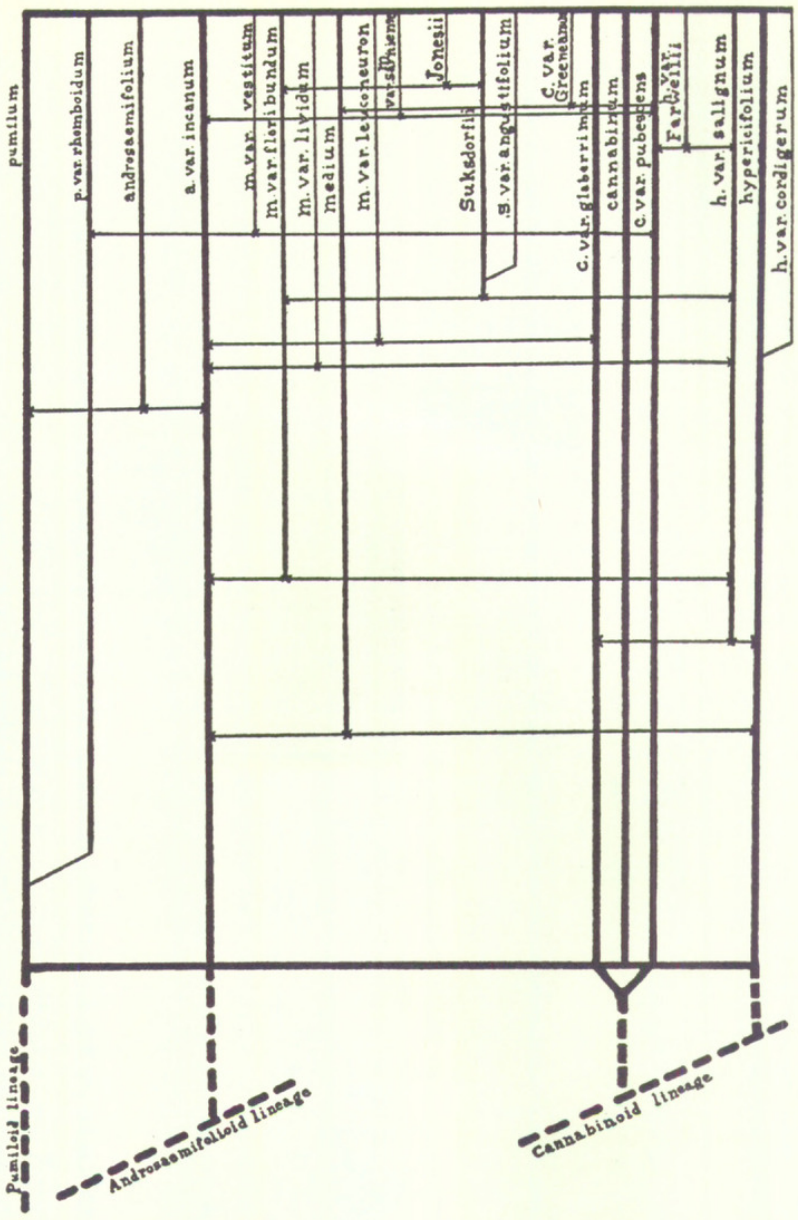

Fig. 2. Phylogenetic relationships of American species of *Apocynum* according to Woodson. Broken lines represent the hypothetical rudiments of the genus, the solid lines, the supposed relationship of the known species and varieties.

Note: According to more recent nomenclatural corrections, "*A. androsaemifolium*" in the chart should read *A. androsaemifolium* var. *glabrum;* and "*A. androsaemifolium* var. *incanum*" should be *A. androsaemifolium,* typical variety (cf. Rhodora **34**: 30–31. 1932).

be very probably crossed back to one of original parental species, at least in part, and may often resemble that species superficially. It will be remembered that the puzzling seedlings of *A. androsaemifolium* came not directly from that species, but were hybrid segregates closely resembling it. In *Apocynum,* therefore, one of the chief effects of hybridization seems to be the enrichment of the variability of the original species taking part in the hybridization.

The actual creation of a new intermediate species by that process, while certainly a possibility, does not seem to have been effected in the case of *A. medium.* That binomial may be a necessity for purposes of classification, but biologically it is still in a far different status from *A. androsaemifolium* and *A. cannabinum.* To reach that status it would require a period of isolation and the operation of natural selection to remove the variability and the semi-sterility which now characterize it. The behavior of *A. medium* No. 449 and of *A. medium* No. 446 is particularly interesting. The former must apparently have been a first-generation cross, for like such plants it is highly heterozygous. Its progeny (pl. 19, fig. 3) include everything from almost straight *A. cannabinum* to a superficially normal *A. androsaemifolium. Apocynum medium* No. 446, on the other hand, bred almost true (pl. 19, fig. 4). Most of its progeny were more or less like itself; in it the *A. medium* type is on the way to becoming stabilized and it probably represents a hybrid of the second generation or later. Given a fair degree of isolation there seems to be no reason why such an intermediate type might not in a comparatively short time reach a specific status comparable to that of *A. cannabinum* or of *A. androsaemifolium.*

SUMMARY

1. Progeny tests were made of *Apocynum androsaemifolium, A. cannabinum,* and their putative hybrid, *A. medium.*

2. *Apocynum androsaemifolium* and *A. cannabinum* bred true. *A. medium* produced a variable set of seedlings, some of them indistinguishable from *A. androsaemifolium* and *A. cannabinum.*

3. The seedlings of *A. cannabinum* had uniformly high percentages of fertile pollen and those of *A. androsaemifolium* were nearly as fertile. Those of *A. medium* were of low average fertility.

4. It is concluded that *A. medium* is certainly a hybrid.

5. The taxonomic importance and phylogenetic consequences of interspecific hybridization in *Apocynum* are discussed in the light of these results. It is suggested that the chief effect of hybridization in this genus in eastern North America at the present time is to increase variability in the parental species.

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