Rhodora

JOURNAL OF

THE NEW ENGLAND BOTANICAL CLUB

Vol. 15. October, 1913. No. 178.

INHERITANCE OF SEX FORMS IN PLANTAGO LANCEOLATA.

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In a former paper in this journal the writer[1] reported upon the first filial generation of a "second form hermaphrodite" of *Plantago lanceolata*,— a form which is structurally hermaphrodite but functionally pistillate. This F_1 generation, which resulted from unguarded wind-pollination of the 2d form mother plant by pollen from 1st form hermaphrodites, included, if certain aberrant plants are disregarded, about 60% of plants like the seed parent (called "yellows" for short, on account of the color of the anthers) and about 40% of plants like the pollen parent ("whites"). Because of the rarity of the 2d form hermaphrodite in the locality where the original mother plant was found, it is likely that the pollen parents of the F_1 generation were for the most part either whites which did not belong to any gynodioecious strain, or else members of a gynodioecious strain consisting of 1st form hermaphrodites and structurally pure pistillates. In its second flowering season the original mother plant was surrounded by its own progeny, and isolated in one of the inner houses of a long range of greenhouses from other plants of the species. Consequently, it is fair to conclude that it was this time pollinated by whites belonging to the gynodioecious strain. A second F_1 generation was therefore grown in order to determine whether or not the progeny would show the same forms as when pollinated by unrelated plants of other strains.

[1] Bartlett, H. H.: On gynodioecism in *Plantago lanceolata*. Rhodora, xiii. (1911) pp. 199–206.

Moreover, certain plants of the first F_1 generation, including both whites and yellows, were chosen as the parents of a second filial generation, and their seeds which also resulted from pollination within the gynodioecious strain, were planted in the spring of 1912. So many of the plants of the 1912 cultures failed to flower the first year that it was necessary to wait until this year to report upon the second F_1 and the F_2 generations.

It may be recalled that the first F_1 generation of 137 plants contained 13 plants which could not be classified either as typical 1st form or 2d form hermaphrodites. Some of them did not flower; others were short-spiked gynomonoecious plants. They were kept in order to see what they would be like if they flowered in the second year. Eight of them died or again failed to flower; five of them flowered.

Plant No. 7, which had abortive round spikes the first time it flowered, had long spikes about half of which were bifurcated the second season. The flowers were strictly pistillate, with the stamens reduced to mere rudiments. This plant, structurally the only purely pistillate plant of the entire culture, flowered so imperfectly in 1911, that it could only be referred to in the former paper (l. c. p. 206) as a possible exception to the rule that none of the progeny of the 2d form hermaphrodite approached the pistillate condition more closely than the mother itself. This plant, either because it was sterile or because the season was so late when it flowered that no pollen was available, failed to set seed. It died after flowering.

Plant No. 28 was short-spiked and gynomonoecious the first year. In the second year some of the spikes were as long as in the rest of the culture. The long spikes, which flowered first, had only 2d form flowers in the lower $\frac{3}{4}$ of the spike and 1st form flowers above. The shortest spikes, which were the last to bloom, had only 1st form flowers. Between the extremes there were various transitions.

Plants Nos. 41 and 53 did not flower the first year. In the second year they were typical 1st form hermaphrodites.

Plant No. 63 did not flower the first year. The second season some of the spikes had first form flowers only. Other spikes were gynomonoecious with the two flower types variously intermingled.

These records show that plants which were short-spiked the first year did not maintain this character the second year. This fact throws grave doubt upon the taxonomic validity of *Plantago lanceolata* var. *sphaerostachya*, set apart by De Candolle on account of its short

spikes, and accords with the experience of Druce,[1] who cultivated a short-spiked plant and found that it lost its distinctive character in the second year.

As a check upon the accuracy of the classification of the first F_1 generation, 18 whites and yellows, including all the individuals chosen as seed parents of the F_2 generation, were retained until they flowered a second time. They were essentially alike in both years. The original mother plant of all the cultures has likewise held perfectly to the characters which it showed the first year. It has now flowered four times and has been divided into 6 plants.

Four of the F_1 plants chosen as parents of an F_2 were yellows. Of these, two, Nos. 9 and 20 were altogether typical and quite indistinguishable from the mother plant, one, (No. 12) had the stamens of the same length and shape as the mother plant, but the anthers were slightly greener, and one, (No. 65), had the anthers just as in the mother plant, but the filaments were longer. The second form progeny of Nos. 9 and 20 reproduced the mother plant exactly. The 2d form progeny of No. 12 (50 plants) were also typical yellows with the exception of one plant, the anthers of which were slightly greenish as in the mother. Since the mother plant itself was recorded as a typical yellow in its second flowering season, its variation in the first season from the typical yellow character may have been due to some environmental factor which likewise affected the solitary one of its progeny which resembled it. If, however, the variation toward greenish anthers indicated a stronger pistillate tendency in No. 12 than in the other yellows, it is significant that the progeny of the greenish-stamened mother included a greater proportion of yellows than any other F_2. The 2d form progeny of No. 65 showed a continuous variation in the length of the filaments. In some plants they were as long as in the mother plant, in others as short as in any typical yellow, but the anthers of all were of the typical 2d form. If the long stamens of No. 65 indicated a weaker pistillate tendency than existed in the other yellows, the long-stamened character is no doubt to be correlated with the fact that the F_2 included a higher proportion of whites than the progeny of any other yellow.

[1] Druce, G. Claridge: *Plantago lanceolata* var. *sphaerostachya*. Brit. Journ. Bot. xlix (1911) p. 235. "A plant of this, which I brought back from Jersey last year, retained its short spike during the year, but has this year developed spikes indistinguishable from the type, as Dillenius says it did in the Eltham Garden. (See Dill. Herb. 97.)"

The F_1 whites which were chosen as mother plants were all alike, and typical. Their progeny consisted of both 1st and 2d form hermaphrodites, quite indistinguishable from those which were descended from yellow mother plants.

In all of the F_2 cultures a few of the whites showed a more or less pronounced gynomonoecious tendency. When only a very few flowers were of the 2d form, and the spikes were typical, the plants were counted as whites. If, however, the flowers were very aberrant, the stamens crumpled, or the perianth did not expand, and the spikes were abbreviated, the plants were regarded as "unclassified." In the following table, which summarizes all the cultures, the "unclassified" column includes both these aberrant plants and those which after being kept under favorable conditions for two years had still not flowered.

	1st form hermaphrodites (whites).	2d form hermaphrodites (yellows).	Unclassified	Total
First F_1 from original yellow.	53 = 39%	73 = 53%	11 = 8%	137
Second F_1 from original yellow.	53 = 52%	43 = 42%	6 = 6%	102
Total F_1	106 = 44%	116 = 48%	17 = 8%	239
F_2 from No. 9, yellow.	44 = 48%	47 = 52%	0	91
F_2 from No. 12, yellow.	34 = 40%	50 = 60%	0	84
F_2 from No. 20, yellow.	52 = 46%	59 = 52%	2 = 2%	113
F_2 from No. 65, yellow.	57 = 59%	38 = 39%	2 = 2%	97
Total F_2 from four F_1 yellows.	187 = 49%	194 = 50%	4 = 1%	385
Total F_1 and F_2 from yellows.	293 = 47%	310 = 50%	21 = 3%	624
F_2 from No. 46, white.	96 = 67%	36 = 25%	12 = 8%	144
F_2 from No. 49, white.	55 = 50%	56 = 50%	0	111
F_2 from No. 56, white.	51 = 50%	49 = 48%	2 = 2%	102
Total F_2 from three F_1 whites.	202 = 57%	141 = 40%	14 = 3%	357
Total F_1 and F_2 progeny of mother plant.	495 = 50.5%	451 = 46%	35 = 3.5%	981

There is no apparent explanation for the difference in constitution between the two F_1 cultures, one of which resulted from foreign pollination and the other from pollination within the physiologically gynodioecious strain. It will be noticed that the first F_1 culture agrees fairly well with the F_2 cultures from typical F_1 yellows Nos. 9 and 20. To ascribe the discrepancy between the two F_1 cultures to the source of the pollen would necessitate the assumption of a much

greater tendency to produce 2d form plants in the megaspores of Nos. 9, 12 and 20 than in the megaspores of their mother. The pollen parents of the first F_1 were of course unknown, but if it is safe to argue from the frequency of the sex forms of *Plantago lanceolata* in nature they were probably whites belonging to a non-gynodioecious strain. Would pollen from a pure 1st form strain be likely to have *less* tendency to produce whites than pollen from a strain consisting of two forms? — But in view of the small number of plants in the F_1 cultures and the relatively large number of unclassified plants which they contained, it is hardly profitable to speculate on their unexpected divergence.

As a whole, the table shows beyond doubt that in the physiologically gynodioecious strain of *Plantago lanceolata* which the writer has cultivated there are 1st and 2d form hermaphrodites in practically equal numbers in the progeny of both 1st and 2d form mothers. The mode of inheritance of the 2d form hermaphrodite in the physiologically gynodioecious strain is probably the same as that of the purely pistillate form in the structurally gynodioecious strains which have been studied by Correns.[1] This investigator has shown by pollinating the same mother plant with pollen from different plants, and, conversely, by pollinating different mother plants with pollen from the same plant, that both the seed parent and the pollen parent influence the proportion of sex forms in the progeny. The inheritance of the sex forms is not wholly determined by either parent. It should, therefore, throw some light on the mode of inheritance of the sex forms if a 2d form hermaphrodite were pollinated by a 1st form hermaphrodite belonging to a strain not only functionally but also structurally pistillate and, conversely, if a structurally pure pistillate plant were pollinated by a 1st form hermaphrodite belonging to the physiologically gynodioecious strain. Such crosses might result in a progeny in which one could distinguish by their morphological characters between those pistillate plants which had inherited the pistillate tendency through the pollen parent and those which had inherited it through the seed parent. In this connection attention may again be called to the one aberrant structurally pistillate plant (No. 7) which occurred in the first (open-pollinated) F_1 generation. Of 451 functionally

[1] Correns, C.: Die Rolle der männlichen Keimzellen bei der Geschlechtsbestimmung der gynodioecischen Pflanzen. Ber. d. deutch. bot. Ges. xxvia, pp. 686–701. 1908.

pistillate descendents of the original 2d form mother plant only this one transgressed the limits of what may fairly be interpreted as the limits of fluctuating variability of the 2d form hermaphrodite. It must either be interpreted as the result of chance pollination by a 1st form hermaphrodite belonging to a structurally gynodioecious strain through which it inherited the purely pistillate character, or else as a mutation.

Since 1910, the writer has been on the lookout for 2d form hermaphrodites in nature. Although many of them have been found in the region about Washington, they constitute but a negligible proportion of the total Plantago population. This seems not to be the case in some parts of France, where the yellow 2d form hermaphrodite is very common and has recently been described as *Plantago lanceolata* var. *androxantha*, a new variety, by Biau[1] and Lemasson. Of course these authors would not have accorded taxonomic standing to a sex form if they had recognized its true nature.

Typical plants from the cultures described in this paper have been turned over for cytological study to Dr. A. B. Stout of the New York Botanical Garden. It is to be hoped that his investigations will show whether there can be discovered a cytological basis for the inheritance of these forms.

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[1] Biau, A.: Nouveautés phytographiques. Bull. Soc. Bot. France, 4e ser. xii, pp. 711–716, 1912. (Feb. 1913).

"*Plantago lanceolata* L. var. *androxantha* Biau et Lemasson.

A *Pl. lanceolata* differt *antheris lutescentibus* vel viridi-lutescentibus, multo *angustioribus*; filamentis bis aut ter *brevioribus*; calycis carina *valde ciliata*, etc.

Ce Plantain est remarquable par ses anthères jaunâtres, lui donnant à la floraison un facies tout particulier, ce qui permet de le reconnaître à distance et de le distinguer très aisément du type à anthères blanches avec lequel il croît pêle-pêle.

Très commun dans les Vosges, aux environs du Bruyères et dans toute la vallée de la Vologne, où il nous a paru presque aussi répandu que le type.

Doit exister ailleurs, mais il faut le rechercher au moment de sa floraison, en mai de préférence, car ensuite il est difficile à distinguer du *Pl. lanceolata*; nous l'interprétons d' ailleurs comme une simple variété d'accord avec l'abbé Coste qui nous a fait l'honneur d'examiner quelques échantillons de cette nouvelle forme."— *p. 713.*