Mutants and Hybrids of the Oenotheras.

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PLATE I.

Cultures of Oenotheras in the New York Botanical Garden.

Onagra lamarckiana at left in second row; *O. argillicola* in foreground, first row; *O. rubrinervis*, center second row; *O. lamarckiana* × *O. biennis* at right (2.24, 2.32, and a young plant of 2.1 emerging from the rosette stage).

Mutants and Hybrids of the Oenotheras

By D. T. MacDougal

Assisted by A. M. Vail, G. H. Shull,† and J. K. Small

PURPOSE AND SCOPE OF INVESTIGATIONS.

The more important features of the investigations of De Vries in which lines of descent were seen to originate, which embodied new qualities and groupings of characters, constant and fully transmissible, are now so familiar to all naturalists that no rehearsal is necessary in the present paper. Early in 1902 the senior author received seeds of the Lamarck's evening-primrose, and these, with seeds of various species obtained directly from their native habitats in North America, were cultivated in the New York Botanical Garden, in which the conditions of soil and climate are, of course, widely different from those of the botanical garden at Amsterdam, Holland.

Among other primary purposes of the cultures it was deemed of great importance that the mutants should be tested as to their stability when grown as biennials after the predominant habit of the genus. The results of this test, together with detailed descriptions of three of the mutants, have already been given in an article in which occasion was taken to set forth briefly the principal tenets of the mutation theory as propounded by De Vries (MacDougal, 1903). It was found that the mutant forms were not only physiologically differentiated, but were also easily separable from one another and from the parental type when tested by accepted taxonomic criteria, and by an examination of the features of their life-histories. Furthermore, all the forms came true to their newly assumed groupings of characters without reversions, and

*The contents of this paper were presented before the weekly botanical convention at the New York Botanical Garden, October 19, 1904.

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exhibited only fluctuating variations of ordinary amplitude, although the last-named feature was not examined by statistical methods. An investigation of this feature is described in the present paper.

During the earlier cultures, plans were formulated for a somewhat inclusive investigation of the genetic relationships of the various members of the genus, and of the variations, or mutations, which might be found to occur in *O. lamarckiana* in America, and in the other species of the group. To this end correspondence was established with collectors in various parts of America and Europe, and material was obtained from such distant points as New Zealand, Mexico, Holland, and Japan. A supply of paraffined paper bags was furnished by Professor De Vries, and later those manufactured for the Station for Experimental Evolution at Cold Spring Harbor were used for inclosing the inflorescences, by which absolutely pure crops of seeds of the species, as well as of the various hybrids, were obtained. All sowings of seeds were made in soil sterilized in an autoclav for three or four hours. A number of the parcels of earth treated in this manner were moistened and kept under proper conditions, but in no instance were any germinations of other oenotheras seen. In order to economize time it was found most convenient to grow the evening-primroses as annuals, which may be done by germinating the seeds in a propagating house and then transplanting them to the experimental grounds early in May. The earlier cultures were begun about January 1, but it was found that ample time for the entire development of the plant was obtained if the sowings were made late in February or early in March.

The portions of the general investigation in which such progress has been made as to warrant the publication of the present paper are as follows:

(1) Determination of the ancestral habitat and dissemination of *Onagra* (*Oenothera*) *lamarckiana*.

(2) Description of such species of *Onagra* (*Oenothera*) as have been kept under cultivation for one or two seasons in order to facilitate observation of possible mutants.

(3) Analysis of the relationship between *O. lamarckiana* and other species of the genus by means of hybridizations.

(4) Estimation of the dominance of parental characters in hybrids of *O. lamarckiana* × *O. biennis* and *O. lamarckiana* × *O. cruciata*.

(5) Determination of the recurrence and stability of mutants of the oenotheras; description of *O. gigas* as cultivated in the New York Botanical Garden.

(6) Estimation of the fluctuating variability of some of the characters of *O. lamarckiana*, *O. nanella*, and *O. rubrinervis*.

Large-flowered Evening Primrose, figured in Barton's Flora of North America, resembling Onagra lamarckiana.

DERIVATION OF ONAGRA (OENOTHERA) LAMARCKIANA.

As a result of the earlier examination of material in a few herbaria in Europe and America no specimens of *O. lamarckiana* were found that had been grown in America, and it was suggested that it might have been originally native to a restricted range in Virginia from which it had been exterminated. The inquiry upon this phase of the investigation has been continued however, with the result that many historical records, as well as some fairly well authenticated material, have been found.

Barton (1821) describes an oenothera under the name of *O. grandiflora* in his Flora of North America, which, with the accompanying plate, well represents *O. lamarckiana*. (Pl. II.) This plant is described as "native in the woods and fields, and about habitations, in Carolina and Georgia, flowering from May to August." The fact is recalled by Barton that Elliott restricted the habitat of this form "to the vicinity of habitations in South Carolina and Georgia, remarking that it is certainly not indigenous in the low country."

Pursh (1814) had previously described an *O. grandiflora* similar to that mentioned by Bartram, as "in woods and fields of Carolina," and with "flowers larger than any other of the North American species, and of an agreeable scent."

The Floral Magazine for 1862 gives a plate of *Oenothera lamarckiana* with some notes on the species from which the following is quoted: The one now figured was grown by Messrs. Carter & Co., the well-known seedsmen of High Holborn and of the Crystal Palace nursery, Forest Hill. To them we are indebted for the following particulars (Dombrain, 1862):

> We received, about four years ago, some seed from Texas unnamed. When we had flowered it we sent some blooms to Dr. Lindley, who pronounced it to be *Oenothera lamarckiana,* a species we believe introduced into England by Mr. Drummond. Its height is between 3 and 4 feet; it blooms the first year, is a very hardy biennial, and is superior to any other *Oenothera* in the size and number of its blossoms, which measure 4 inches in diameter.

A reproduction of the same plate is to be found in L' Illustration Horticole for 1862, together with a discussion of the origin and relationships of the various species and a citation of the statements quoted above. (Lemaire, 1862.)

A specimen in the Gray Herbarium of Harvard University was examined which agrees perfectly with *O. lamarckiana*. From the inscription, which is in Dr. Asa Gray's handwriting, it appears that this plant was grown from seed in the botanical garden at Cambridge, Mass., in 1862. The sheet also bears the note, "Said by English horticulturists to come from Texas," and also "*Oe. lamarckiana*," all by Dr. Gray. It is to be noted that the date of the above culture agrees with that of the Drummond plants in England mentioned above.

The second phase of the effort to trace *O. lamarckiana* to its original habitat was directed to an examination of the material to be found in the American herbaria and to excursions to some of the historical locations. Several specimens of prime interest were encountered. A specimen collected by A. W. Chapman in Florida, and sent by him to Europe, becoming a part of the Meissner herbarium which was afterward purchased by Columbia University, was thought by Professor De Vries to be *O. lamarckiana*, and the mark on the sheet shows that it was used by Chapman (1860, 1872, 1884) in making up the description of *O. biennis* in the editions of his southern flora, in which *O. grandiflora* Ait. was given as a synonym in the editions of 1860 and 1862, but does not appear in the later edition of 1897. In the description he says: "Varies greatly in pubescence and size of flower," while the habitat is given as "Fields and waste places." The elimination of the synonym from the last edition of the book can not be accounted for, although the plant was presumably growing in a wild condition. A duplicate of the specimen mentioned above is reported by Mr. C. D. Beadle to be in the Biltmore Herbarium at Biltmore, N. C. A similar specimen is to be found in the herbarium of the Missouri Botanical Garden.

During the visit of Professor De Vries to America in the summer of 1904 he joined in the quest for specimens of *O. lamarckiana* and called attention to a sheet of material in the herbarium of the Philadelphia Academy of Sciences, collected by C. W. Short near Lexington, Ky., which he considered as *O. lamarckiana*, and which was grown wild in the locality recorded.

The co-operation of a number of botanists in various parts of the supposed range of the species was secured and a thorough search was made in the vicinity of Nashville, Tenn., by Prof. Geo. A. Martin; in the vicinity of Knoxville, Tenn., by Prof. S. M. Bain; in the vicinity of Lexington, Ky., by Prof. H. Garman; and in the vicinity of Courtney, Mo., by Mr. B. F. Bush. Up to the present time, however, no living plants have been found that might be included within the descriptions of *O. lamarckiana*.

The above evidence makes it fairly conclusive, however, that the large-flowered evening-primose which formed the basal material for the experimental researches of De Vries is, or was, a component part of the flora of North America and has been seen in the Carolinas, Florida, Kentucky, and Texas during the last century, and that material from Texas examined by Lindley fairly represents the species. The main line of descent has endured practically unchanged for a period of 116 years in European gardens, and was first observed to exhibit mutations resulting in the production of new elementary species as early as 1887, although but little doubt exists that this was by no means the beginning of its period of mutability.

REDISCOVERY OF O. GRANDIFLORA (AIT.) VAIL IN AMERICA.

During the course of the investigation of the records it became evident that one or more large-flowered evening-primroses not recognized in local floras had been found in southern United States at various times. One of the most interesting of these discoveries was that of Bartram referring to a locality on the east bank of the Alabama River above Mobile and between that place and the junction of the Alabama and Tombigbee rivers. He says:

> Early one morning, passing along by some old uncultivated fields, a few miles above Taensa, I was struck with surprise at the appearance of a blooming plant, gilded with the richest golden yellow; stepping on shore, I discovered it to be a new species of the *Oenothera* (*Oenothera grandiflora,* caule erecto, ramoso, piloso, 7, 8 pedalis, foliis semi-amplexi-caulibus, lanceolatis, serratodentatis, floribus magnis, fulgidis, sessilibus, capsulis cylindricis, 4 angulis,) perhaps the most pompous and brilliant herbaceous plant yet known to exist. It is an annual or biennial, rising erect seven or eight feet, branching on all sides from near the earth upwards, the lower branches extensive, and the succeeding gradually shorter to the top of the plant, forming a pyramid in figure; the leaves are of a broad lanceolate shape, dentated or deeply serrated, terminating with a slender point, and of a deep full green color; the large slender flowers that so ornament this plant, are of a splendid perfect yellow color; but when they contract again before they drop off, the underside of the petals next the calyx becomes of a reddish flesh-color, inclining to vermilion; the flowers begin to open in the evening, are fully expanded during the night, and are in their beauty next morning, but close and wither before noon. There is a daily profuse succession for many weeks, and one single plant at the same instant presents to view many hundred flowers. I have measured these flowers above five inches in diameter; they have an agreeable scent.
>
> After leaving these splendid fields of the golden *Oenothera,* I passed by old deserted plantations and high forests, etc.

Bartram's expedition was undertaken "At the request of Dr. Fothergill, of London, to search the Floridas and the western parts of Carolina and Georgia, for the discovery of rare and useful products of nature, chiefly in the vegetable kingdom. In April, 1773, I embarked for Charleston, South Carolina, on board the brigantine, Charleston Packet, Captain Wright," etc. (Bartram, 1793, pp. 404–405.)

Seeds of the above plant were evidently sent to Fothergill, and the following is the original description of the plant by Aiton, made from specimens grown at Kew. He says "grandiflora 2. Oe. foliis ovato-lanceolatis, staminibus declinatis, caule fruticoso, L'Herit.

stirp. nov. Tom. 2. tab. 4. Great-flowered *Oenothera*, Nat. of North America. Introd. 1778 by John Fothergill, M. D. Fl. July and August" (Aiton, 1879).

It being deemed very important that a visit to the locality mentioned by Bartram should be made, Prof. S. M. Tracy, of Biloxi, Miss., generously undertook to make the search. In accordance with arrangements he proceeded up the Alabama River on August 16, 1904, and five days later came upon the plant not far from the original locality. Professor Tracy has kindly prepared the following report:

The locality for this plant, as given by Bartram, was "a few miles above Taensa." The country immediately about Tensaw is mostly the dry, pine hills common in that section, and a careful search for several miles about the town did not reveal a single plant belonging to the Epilobiaceæ. Fort Mimms, 5 miles from Tensaw on the bank of the Alabama River, was doubtless Bartram's headquarters while he was in that part of the State, but a careful search of the river for some miles failed of results. Dixie Landing, 25 miles above Fort Mimms by river, and 13 by road from Tensaw, was the first place where the plant was seen. Immediately below the steamboat landing there is quite a stretch of abandoned fields covered with a dense growth of *Chamaecrista robusta* from 4 to 5 feet in height, and those plants are thoroughly tangled with *Bradburya virginiana*, which makes walking exceedingly difficult. The evening-primrose was found as an occasional plant in this growth, the first plants being seen about a quarter of a mile below the landing, and others being found more or less abundantly for more than a mile down the river. When growing in the thick weeds the plants were mostly erect, with simple stems, a few of which were beginning to branch at the top. A few plants were found immediately on the river bank, and even on the sides of the almost perpendicular bank, which is about 20 feet high, and when growing in that location were, as Bartram describes them, "Rising erect 7 or 8 feet, branching on all sides from near the earth upwards, the lower branches extensive, and the succeeding gradually shorter to the top of the plant, forming a pyramid in figure." The largest plant found measured 8 feet 9 inches in height. No small plants were found, and from the root and stem characters the plant is doubtless an annual. No plants were found more than 200 yards from the bank of the river, and only a few plants were found in the shade of trees. Hundreds of plants were examined, but no mature seed could be found.

A visit to Earle's Landing, 5 miles below Dixie Landing, showed the plant to be fairly abundant there also. In nearly all cases they grew on alluvial soil, which was sandy rather than heavy, and none was found near wet or marshy places. The river bank was examined nearly the whole of the distance from Dixie to Earle's Landing, and the plant was not rare on open ground covered with *Chamaecrista*, but was not seen in any other location. All of the region examined was on the east bank of the Alabama River. A gentleman owning land immediately opposite Dixie informed me that it grew in one place on the west bank.

A large number of herbarium specimens were prepared by Professor Tracy, all of which were forwarded to the New York Botanical Garden for examination, and from which seeds were obtained suitable for cultures which promise to be of great service in comparisons with the other large-flowered species of the evening-primroses.

Fig. 1. Rosette of Onagra biennis five months old.

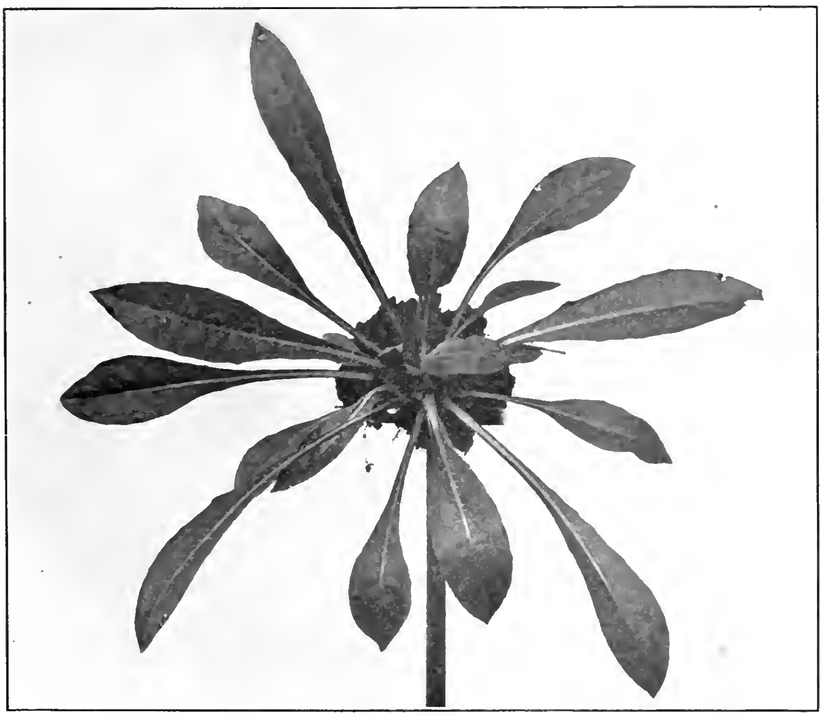


Fig. 2. Rosette of Onagra cruciata five months old.

ONAGRA (OENOTHERA) BIENNIS (L.) Scop.

Many collectors and taxonomists include a number of elementary species in *Onagra biennis* and attribute to it an extremely wide range of fluctuating variability. On the other hand, workers who have carried on cultural experiments with individuals representing a typical elementary species describe it as fluctuating between very narrow limits. The actual inclusion of the species is not so important, in connection with the present investigation, as the degree of constancy of the various strains grouped around the species and sometimes included in it.

In order to carry on observations on these points, and upon "the changes produced by cultivation," upon which some systematists lay so much stress, a number of plants of *O. biennis* (in the strictest sense), growing in uncultivated land in the New York Botanical Garden in 1903, were selected to form the basis of a pedigree-culture in 1904. Seeds were duly harvested at the end of the season and sown in the propagating house early in January. The plantlets were transferred to the experimental grounds late in May and began to bloom early in July. The species was thus grown as an annual during a season of about nine months in soil rich with fertilizers. Furthermore, the individuals were placed in rows, over a meter apart, and were kept free from the competition of weeds. Briefly stated, it may be said that in no single feature, nor in any instance, did these plants transgress the measurements, or show different forms of organs, from those of wild specimens in the vicinity. The size of the leaves, the amount of the pubescence, the size of the flowers and capsules, and the formation of the branches are capable of modification by soil-moisture, humidity, intensity of illumination, and competition, as in thousands of other well-defined species, but these modifications did not bring the species nearer in aggregate character to any of the closely allied forms. Exact records and observations were kept during the entire life-histories of the individuals, by the aid of which the following description has been prepared:

Seedling about two months old.—Leaves nearly glabrous; blades oval to oblong-oval, the larger ones about 10 mm. wide, obtuse at the apex, each rather gradually narrowed into a petiole (fig. 1).

Seedling five months old.—Rosette open; leaves rather copiously fine-pubescent; blades oblong to elliptic, the larger ones fully 2.5 cm. wide, quite approximately repand-denticulate, with the teeth more pronounced at the base, acute at the apex, each narrowed into a short petiole. (Pl. III, fig. 1.)

Mature rosette.—Leaves ample, rather copiously fine-pubescent, the larger ones about 27 cm. long, 6 to 7 cm. wide; blades oblong to elliptic, or slightly broadened upwards, unevenly repand-denticulate and mostly rather jagged-toothed near the base, the petioles relatively stout.

Adult plant (Pls. IV and V).—Plant luxuriant, mostly 1 meter tall, or less. Stem slightly uneven, but scarcely channeled, hirsute, with spreading-ascending somewhat rigid hairs, copiously branched throughout, the lower branches decumbent, the upper ones spreading or curved upward;* leaves very numerous, 1.5 to 2 dm. long near the base of the stem; blades elliptic-oblanceolate to elliptic-lanceolate; shallowly but rather prominently toothed, and often jagged-toothed near the base, acuminate, those of the upper cauline leaves mostly elliptic, acute, sessile, or nearly so; bracts mainly lanceolate, narrowed or rounded at the base; conic portion of the bud 14 to 18 mm. long, finely pubescent, the free tips of the sepals about 2 mm. long; hypanthium 2 to 3 cm. long, 5 to 6 mm. wide at the mouth, nearly terete, sparingly pubescent or glabrate; sepals 15 to 20 mm. long, much shorter than the tubular portion of the hypanthium, the free tips 4 to 5 mm. long; petals rather delicate, 12 to 16 mm. long, truncate or slightly emarginate at the apex; filaments 8 to 10 mm. long; anthers 7 to 8 mm. long; pistil shorter than the stamens; stigmas 4 to 5 mm. long; capsule 3 to 3.5 cm. long, 7 to 7.5 mm. in diameter at the thickest point, finely pubescent, slightly curved, markedly narrowed at the apex. (Pl. VI.)

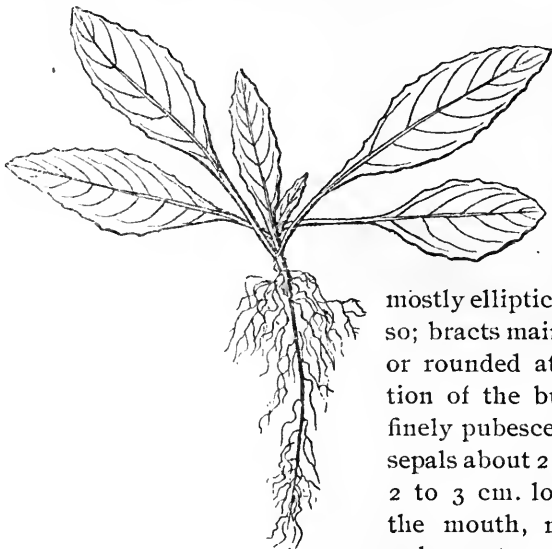


Fig. 1.—*Onagra biennis* seedling three months after germination.

It is to be seen from the above description that *O. biennis* is capable of self-fertilization by reason of the superior length of the stamens, a fact that was demonstrated in the experimental grounds. To secure purely fertilized seeds it was only necessary to inclose the inflorescence in a parchment bag during the opening of the flowers.

*Plants growing in thickets are more spindling and have the lower branches suppressed, while the young rosettes are luxuriant, with broader leaves, under such circumstances.

Onagra biennis, wild specimen, grown in competition with other meadow plants.

PLATE V.

Onagra biennis in bloom, showing method of branching when free from competition, and growing in the open.

After an examination of material in the field in America in the summer of 1904, Professor De Vries informs the authors that the *O. biennis* used in his breeding experiments at Amsterdam differs from the foregoing, and is to be included with a form usually termed *O. biennis grandiflora* by collectors. The exact relationship of the two has not yet been carefully determined.

ONAGRA ARGILLICOLA MacKenzie.

Within the last year a new wild species of evening-primrose has been brought to notice from the mountains of Virginia and West Virginia, being described by Mr. K. K. MacKenzie as "one of the most noticeable and common plants on the line of the Chesapeake and Ohio Railroad on both sides of the boundary line between Virginia and West Virginia." It has also been collected by Mrs. L. F. Ward, at "Alleghany," W. Va., and by Mr. and Mrs. E. S. Steele at Sweet Springs, W. Va., and the cultures in the New York Botanical Garden were begun with seeds from the latter locality. The following description has been compiled from observations on living plants of the resultant cultures:

Seedling about two months old.—Leaves minutely pubescent, copiously so near the base; blades oblong or elliptic-oblong, the larger ones less than 1 cm. wide, obtuse, each gradually narrowed into a copiously pubescent petiole.

Seedling five months old.—Rosette relatively lax; leaves minutely pubescent; blades spatulate to narrowly linear-spatulate, the larger ones over 25 cm. long, 2 to 2.5 cm. wide, repand, more distantly so and with more pronounced teeth near the base, each gradually narrowed into a long petiole.

Mature rosette.—Leaves numerous and conspicuously elongated; glabrous, or nearly so, except the sparingly ciliate margins, the larger ones over 40 cm. long, 2 to 2.5 cm. wide; blades broadly linear to linear-spatulate, sinuate, the teeth slightly more pronounced near the base; petioles relatively stout.

Adult plant.—Plant rather luxuriant, depressed in habit. Stems suppressed or very short, the branches radiate, decumbent, not channelled, somewhat tortuous, mainly 6 to 12 dm. long, puberulent and pubescent, with few spreading or ascending hairs; leaves very numerous, 10 to 15 cm. long on the lower part of the branches; blades undulate, or repand-denticulate, those on the lower part of the branches broadly linear to narrowly linear-oblong, acute or short-acuminate, each narrowed into a semi-terete petiole, those of the upper cauline leaves similar to those of the lower, but relatively shorter and broader, and sometimes inclined to be linear-lanceolate, sessile or short-petioled; bracts lanceolate, truncate at the base, shorter than the hypanthium; conic portion of the bud about 4 cm. long, glabrous, the free tips of the sepals subulate, approximate at the base, but ascending; hypanthium 4 to 5 cm. long, about 6 mm. wide at the mouth, ridged, glabrous; sepals 34 to 47 mm. long, shorter than the tubular portion of the hypanthium, the free tips about 6 mm. long; petals rather firm, 4 to 4.5 cm. long, truncate or broadly emarginate at the apex; filaments 21 to 23 mm. long; anthers 12 to 13 mm. long; capsule 2.5 to 3 cm. long, about 7 mm. in diameter at the thickest point, glabrous, strongly curved, narrowed from the base to the apex. (Pl. VII.)

O. argillicola is to be distinguished by the fact that it is well adapted to securing cross-fertilization. When the flower-buds come to the morning of the day on the evening of which they will open, the pistil takes on a greatly accelerated rate of growth and pushes out of the flower-buds to a length of 3 or 4 mm., bearing the unfolded stigmas in a position in which they may readily receive pollen carried by the wind from neighboring flowers. It is not actually known, however, whether pollination is secured in this manner, or whether insects are of some aid in the matter. A similar behavior of *O. lamarckiana* near the close of the season is reported in Holland. The decumbent or non-ascendant branches of *O. argillicola* form a dense cluster which gives it a very striking appearance. The main bud of the central stem appears to remain dormant.

The great size of the flower of this species doubtless accounts for some of the reports of the presence of *O. grandiflora* in the Virginias and Pennsylvania, while the habit of the plant may have also suggested some of the notions prevalent as to the variability of *O. biennis*, with which it may have been confused.

ONAGRA CRUCIATA (Nutt.) Small.

A number of roots and some seeds of *O. cruciata* were obtained from Sandy Hill, N. Y., near Lake George, at the close of the season of 1902, and early in the spring of 1903 were divided into two portions, one of which was sent to Professor De Vries at Amsterdam, Holland. Only about a dozen plants were brought to maturity in the New York Botanical Garden during 1903, attention being directed principally to the observations on *O. lamarckiana* and its mutants.

A letter was received from Professor De Vries under date of September 19, 1903, in which he said:

> Until a few weeks ago, and before flowering, the plants were a very uniform lot, with the characteristic reddish crowns and nutating tops. But now they are no longer uniform. There are two very distinct types, only differing in the

PLATE VI.

Onagra biennis.

1, leaf from young rosette; 2, leaf from rosette four months old; 3, leaf from lower part of mature rosette; 4, leaf from upper part of mature rosette; 5, stem-leaf; 6, bract; 7, unopened bud; 8, flower with petals removed; 9, petals of maximum size; 10, mature capsule. 1 to 5, one-half natural size; 6 to 10, natural size.

PLATE VII.

Onagra argillicola.

1, 2, leaves of young rosette; 3, leaf from adult rosette; 4, stem-leaf; 5, flower with petals removed; 6, bract; 7, flower-bud; 8, flower-bud immediately previous to opening, with stigma exposed; 9, petal; 10, capsule. 1 to 4, one-half natural size; 5 to 10, natural size.

PLATE VIII.

Onagra cruciata, showing capsule, buds, and slender hypanthium, photographed in 1903.

flowers and flower-buds. Both types are to be found in the plants coming from the seeds, as well as in those grown from the roots you sent me. The differences are slight, but striking, absolutely individual, and without transitions. Most of the individuals have broader linear petals and comparatively more rounded flower-buds. The others have narrower and therefore more strictly linear petals, and thicker buds.

I have also sown seed I got from Prof. B. L. Robinson, of Harvard University, gathered at Jeffrey, N. H., under the name of *O. cruciata*. They are wholly different from yours, being more slender, less nutating, and with a strikingly longer calyx-tube.

The same facts are given in "Species and Varieties: Their Origin by Mutation" (De Vries, 1905, p. 589), in which it is also stated that "It seems not improbable that *O. cruciata* includes a group of lesser unities, and might soon prove to comprise a swarm of elementary species, while the original strain might even now be in a condition of mutability."

The cultures of 1904 included over sixty specimens of *O. cruciata* which reached the adult stage, and included not only the two forms which he had observed to arise from the seeds and roots sent him from this place, but also the third obtained only from material from New Hampshire. It is obvious, therefore, that one form arises spontaneously from one of the other two forms suddenly, and dried specimens from the crop of 1903 in the New York Botanical Garden show that it originated in this manner here in the first year of cultivation, although the second half of the same lot of seeds sent to Professor De Vries failed to give rise to it in Amsterdam.

The evidence at hand therefore seems to confirm the suggestion as to the mutability of the species, but nothing may be said as to which of the types constitutes the parent. The characters of the forms are as follows:

No. 1 (Pl. VIII).—Adult plant robust and luxuriant. Stem 1 to 1.5 meters tall, copiously branched, the branches spreading, sparingly hirsute, the hairs rather ascending, 1.5 to 2.5 dm. long on the lower part of the stem; blades narrowly spatulate, finely toothed near the apex, coarsely and somewhat doubly toothed below the middle, each narrowed into a short semi-terete petiole, those of the upper cauline leaves oblong-lanceolate to lanceolate, sessile, all more or less pubescent about the veins beneath; bracts oblong-lanceolate, about one-half as long as the hypanthium, truncate at the base; conic portion of the buds slender, 16 mm. long, or somewhat longer, sparingly pubescent, the free tips of the sepals 4.5 to 5 mm. long; hypanthium slender terete or nearly so, 30 or 32 mm. long, becoming glabrous, about 4 mm wide at the mouth; sepals 17 to 20 mm. long, linear-lanceolate, about one-half as long as the tubular portion of the hypanthium, the free tips 4 mm. long; petals delicate, linear or nearly so, 10 to 15 mm. long, obtuse; filament 9 to 10 mm. long; anthers about 5 mm. long; style shorter than the stamens; stigmas about 4 mm. long; capsules 2 to 2.5 cm. long, 6 to 7 mm. in diameter at the thickest point, nearly glabrous, mainly longer than the bracts. (Pl. IX, fig. 1.)

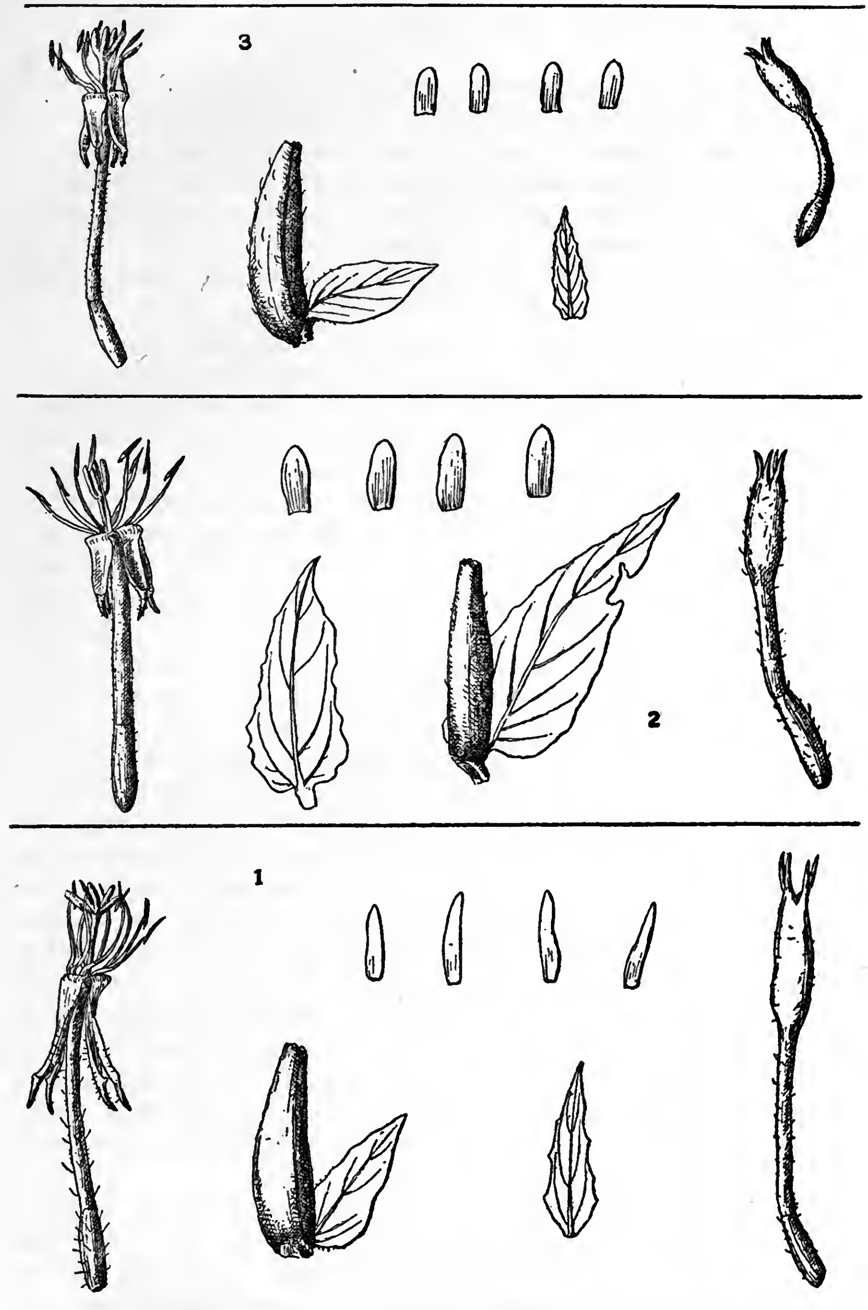
This form included about 52 of the individuals grown during 1904. The other two forms may be characterized as follows:

No. 2.—Bracts broadly lanceolate or ovate-lanceolate, round-truncate at the base, about as long as the hypanthium; conic portion of the bud sparingly pubescent, 15 mm. long or less; hypanthium stoutish, nearly terete, 28 to 30 mm. long, sparingly pubescent, abruptly dilated at the top, and about 5 mm. wide at the mouth; sepals 14 to 15 mm. long, linear-lanceolate, about one-half as long as the tubular portion of the hypanthium, the free tips about 5 mm. long; petals firm, broadly linear or linear-oblong, 8.5 to 10 mm. long, obtuse; filaments 8 to 9 mm. long; anthers 6 mm. long; style shorter than the stamens; stigmas 6 mm. long; capsules 2.5 to 3 cm. long, 7 to 8 mm. in diameter at the thickest point, with few scattered hairs, slightly curved, narrowed to the apex. (Pl. IX, fig. 2.) Seven individuals of this type were found in the cultures.

No. 3.—Bracts oblong or ovate-oblong, narrowed at the base, shorter than the ovary or slightly longer; conic portion of the buds stout, 9 to 11 mm. long, with few scattered short hairs; hypanthium slightly ribbed, stoutish, 25 to 27 mm. long, becoming glabrous, rather gradually dilated at the top and about 4 mm. wide at the mouth; sepals 9 to 10 mm. long, much less than one-half as long as the tubular portion of the hypanthium, the free tips 3 to 3.5 mm. long; petals broadly linear-oblong, 6 or 7 mm. long, obtuse; filaments 6 mm. long; anthers 4 mm. long; style shorter than the stamens; stigmas 3 mm. long; capsules about 2.5 cm. long, 7 to 8 mm. in diameter at the thickest point, with few scattered hairs, slightly curved, narrowed to the apex. (Pl. IX, fig. 3.) Six individuals were seen, all of which completed their seasonal development much earlier than the other two forms.

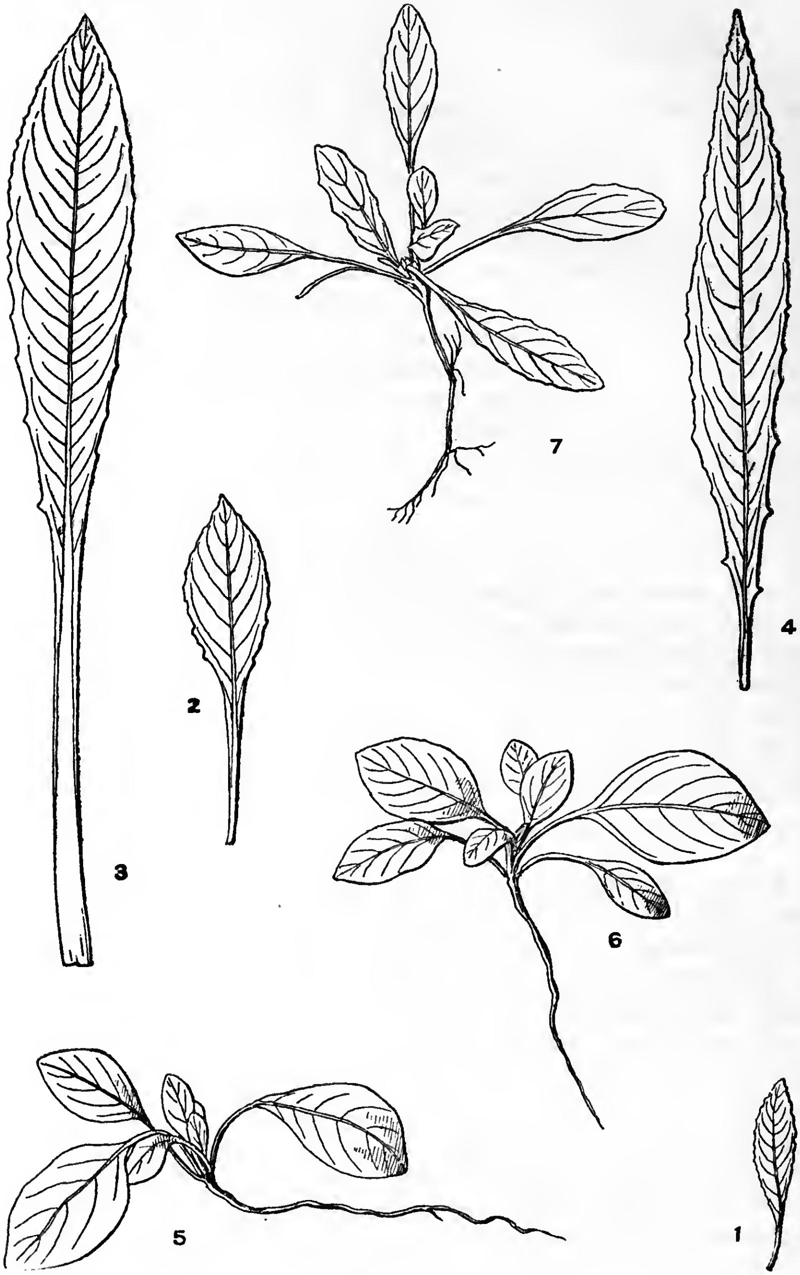
In the observations made during the earlier part of the development of the plants nothing was recorded by which the three forms might be distinguished, and hence the following characters may be taken to apply to the entire lot, although it is probable that most of the descriptions were made from mutant individuals.

Seedling about two months old.—Leaves very sparingly pubescent; blades oblong, elliptic or oval, the larger ones 8 to 11 mm. wide,



Onagra cruciata: Buds, bracts, capsules, flowers, and petals of the three elementary forms. Natural size.

PLATE X.



Onagra cruciata.

1, leaf from young rosette; 2, leaf from lower part of mature rosette; 3, leaf from upper part of mature rosette; 4, stem-leaf; 5, rosette five months old; 6, rosette two months old; 7, rosette nearly five months old, with narrower leaves. 1 to 4, half natural size; 5 to 7, natural size.

undulate, obtuse or merely acutish at the apex, each rather gradually narrowed into a petiole. (Pl. X, fig. 6.)

Seedlings five months old.—Rosettes not dense; leaves glabrous or nearly so, except the ciliate margins; blades spatulate, some of them narrowly so, the larger ones 2 to 2.5 cm. wide, shallowly repand-denticulate, mostly acute, as long as the petioles or longer. (Pl. III, fig. 2.)

Mature rosette.—Leaves conspicuously elongated, obscurely fine-pubescent, the larger ones about 26 cm. long, 25 to 30 mm. wide; blades narrowly spatulate, repand-dentate, more distantly so and with prominent teeth near the base, petioles relatively slender.

All of the forms included in, and arising from, *O. cruciata* are capable of self-fertilization when the inflorescences are inclosed in bags. So far as present information goes the species of the evening-primroses native to northeastern America may be said to have comparatively small flowers and to be capable of self-fertilization, although visited frequently by flying insects. The species ranging to the southward have larger flowers, and by reason of the superior length of the pistils are adapted to cross-fertilization, although it is not definitely known that self-fertilization does not ensue. In *O. argillicola* the early protrusion of the stigmatic surfaces from the unopened flower-bud has the appearance of a positive adaptation for securing pollen from other flowers, by the agency of wind, gravity, or insects.

HYBRIDS.

Among the crosses made in the New York Botanical Garden during 1903, that of *O. lamarckiana* × *O. cruciata* and the reciprocal were attempted. The first only was successful, as the castration of the flowers of *O. cruciata* was not accomplished sufficiently early to prevent self-fertilization. Likewise the removal of the stamens of *O. lamarckiana* was not done in such manner as to exclude the action of its own pollen and the pistil-parent appeared as a pure strain in the cultures.

O. lamarckiana × *O. cruciata.*—A detailed study of the hybrids obtained by the pollination of *O. lamarckiana* by *O. cruciata* was made by De Vries, but the pollen-parent was evidently a highly variable hybrid race which bore the general vegetative characters of the true *cruciata*, but which showed a fluctuating variability in its flowers, from an atavistic obcordate form of petal to others of the slender *cruciata* type. The form in question is known in Europe as *Oenothera cruciata varia* and is held by De Vries to be probably a hybrid of *O. muricata* and *cruciata*. (De Vries, 1903, pp. 100–110, 593–633.)

The individuals of the hybrid as made in the New York Botanical Garden in 1903 were seen to be furnished with narrower leaves in the earliest stage of the seedlings, all of which but one were destroyed by insects before the main axis was formed. The plant was recognizable at some distance throughout its entire existence by its light yellowish-green color. The leaves of the young rosettes were ovate-lanceolate, obscurely and remotely repand-denticulate, blunt at the apex, with the laminae extending down the petioles to the bases in the form of wings 1 to 2 mm. in width. (Plate XII.)

The leaves of the mature rosette were narrowly lanceolate-oblong, being broadest above the middle and tapering to both ends, with the petioles winged. The laminae were approximately denticulate in the apical portion and irregularly so in the basal half. All of the leaves of the rosette and stem were minutely pubescent.

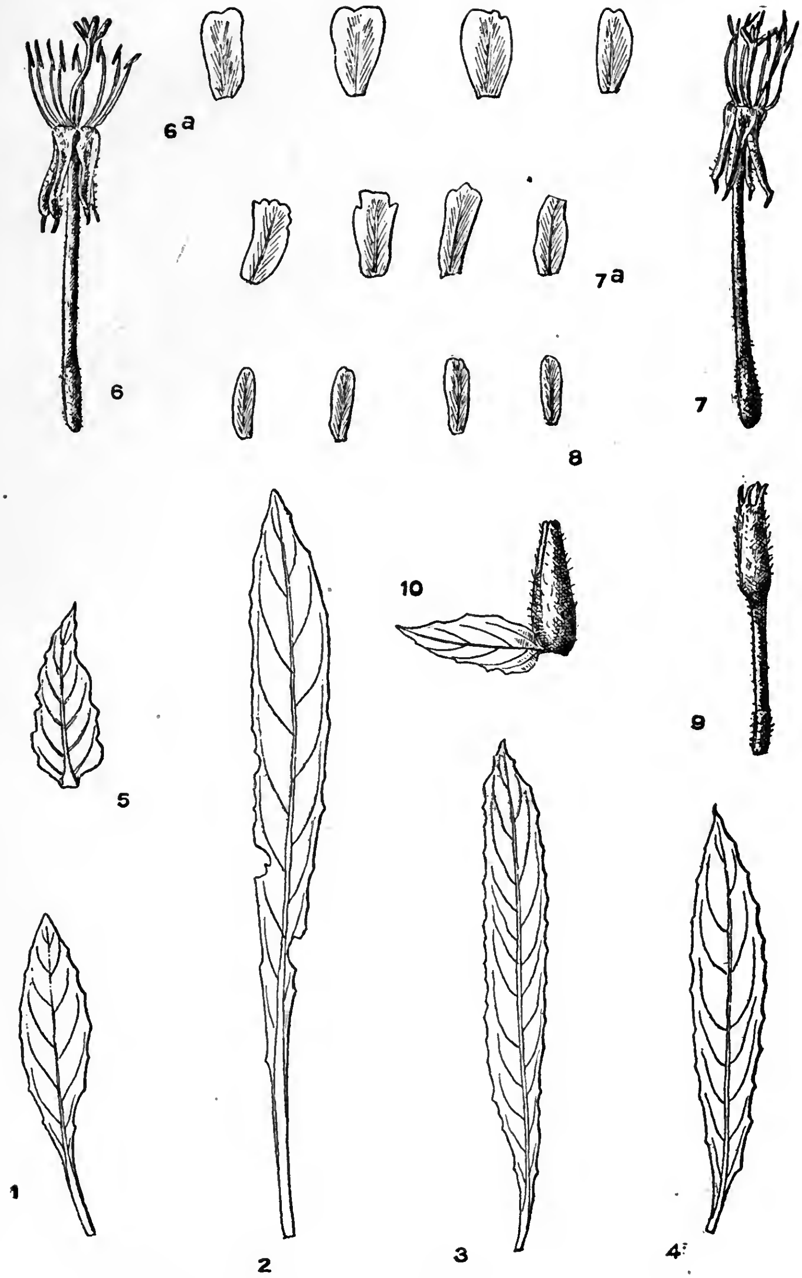
The stem attained a height of about 55 cm. and bore a number of short, spreading branches arising from the base of the main stem and reaching half of its length. Numerous shorter branches arose from the entire stem from a short distance above the base. The apical portions of all branches were tinged with red. The stem leaves were narrowly oblong-lanceolate, tapering to both ends and acute at both ends; 9 to 11 cm. long, and 14 to 17 mm. wide. The terminal rosettes were dense, close, symmetrical, and spreading. The first flower was shown on August 12, about six weeks later than the beginning of the blooming of either parent.

The petals were recurved after the manner of *O. cruciata* and were from 9 to 11 mm. long, varying from linear-oblong to irregularly obcordate or truncate, being entire, obscurely emarginate or irregularly notched near the apex. Furthermore, these various forms might be illustrated in a single flower (see Plate XII, figs. 6*a*, 7*a*, and 8). The definite tips of the calyx-segments were spreading in the bud and were 3 to 15 mm. long. The stamens varied in length, being shorter than the pistils in some flowers, and longer in others. The ovaries were about 9 mm. long, slightly hirsute, and the hypanthium was glabrous. The bracts were lanceolate-acuminate. The calyx-segments were much shorter than the hypanthium. The hypanthium showed a purplish tinge and the petals were flesh-color, except at the tips. The capsules were rounded, obscurely angled, 20 mm. long and 4 to 5 mm. in thickness, tapering from near the base to the tip, and bearing a few spreading hairs. (Pl. X.)

This hybrid agrees quite well with *O. cruciata varia* as described by De Vries, which he thought was a hybrid between *muricata* and *cruciata*. Whether it is actually identical with this form can not be

Adult specimen of the hybrid Onagra lamarckiana × Onagra cruciata (No. 3.21).

PLATE XII.



Onagra lamarckiana × Onagra cruciata (No. 3.21).

1, leaf from young rosette; 2, leaf from median portion of mature rosette; 3, leaf from upper portio of mature rosette; 4, stem-leaf; 5, bract; 6, flower with petals removed (see 6a); 7, flowe with petals removed (see 7a); 8, petals of mininum size; 9, unopened flower-bud; 10, capsule 1 to 4, one-half natural size; 5 to 10, natural size.

definitely stated, since no living material of the latter has been examined. The only characters of the hybrid clearly derived from the pistil-parent are the relative length of the main axis and the general habit of branching. It is to be said on the other hand that the *cruciata* characters to which the general aspect of the plant is largely due are without exception more or less modified. The relative length of the stamens and pistils was seen to vary so that some of the flowers were capable of self-pollination, while in others the chance of pollination without the aid of external agencies was extremely small, so that it might be said that in some branches of the plant the *lamarckiana* character was dominant, while in others the *cruciata* self-fertilizing capacity was shown. A similar range of partial variability will be described in one of the hybrid races of the *O. lamarckiana* × *O. biennis.*

O. lamarckiana × *O. biennis.*—The results of the crosses made in the New York Botanical Garden were much more diversified than those made by De Vries, who obtained what he designates as a typical unilateral hybrid as a result of fertilization of *O. lamarckiana* by *O. biennis grandiflora.* He says (De Vries, 1903, p. 31):

> The hybrid of *Oenothera biennis* (*O. biennis grandiflora*) and *O. lamarckiana* resembles the first so strongly that they can hardly be distinguished from one another. I have made this cross partly in 1894 and partly in the summer of 1899, and in the last-named year partly with *O. lamarckiana* from my own cultures, and partly from the same species grown from purchased seeds. In all cases I used *O. lamarckiana* as the mother. The stamens were taken from flowers of plants in the open (from unopened buds), and from plants of my own cultures in the last-named period. The bastards were of a single type, and were interchangeable with *O. biennis* (*O. biennis grandiflora*), not only in the rosettes, but also in the flowers and ripe fruit. I had about 50 flowering plants in 1895, and about 70 + 60 in the two series in 1899, making altogether about 180 specimens in bloom in addition to some with young stems and rosettes only (biennials). Some differences were seen, but they were not so marked or so important that a description could be made of them.
>
> I harvested some seeds in 1895, which were secured by artificial pollination, and the second generation was grown from these in the summer of 1896. These repeated, in the 50 specimens coming into bloom, only the characteristics of the first-named parent (*biennis*).

Similarly the pollination of *O. lamarckiana* by *O. muricata* resulted in a monotypic unilateral hybrid which approximated the pollen-parent.

Four distinct types were distinguishable in the hybrid in New York, and the different forms could be recognized in a very early stage of the seedlings. All of the individuals were easily seen to be grouped around the types mentioned, and no intermediate or intergrading forms were found. The number of individuals brought to maturity was comparatively small, and the possibility is not excluded that a culture of several hundred plants might include still other forms. In fact, the very differences between the results of the hybridizations, as carried out in Amsterdam and New York, suggest that the manner in which the various qualities in the two parents are grouped in the progeny might be capable of a wide range of variation. Many indications lead to the suggestion that the dominancy and prevalency, latency, and recessivity of any character may be more or less influenced by the conditions attendant upon the hybridization; the operative factors might include individual qualities as well as external conditions.

In addition to the hybrid individuals several specimens of the pistil-parent, *lamarckiana*, and one of its mutants appeared in the cultures, indicating that self-fertilization was not entirely prevented. This might be accounted for in two ways. Castration might not have been performed early enough to prevent the action of pollen being scattered from a bursting anther upon a mature stigma while the operation was being performed. Then, again, the possibility was not wholly excluded that pollen from the bursting anthers which fell upon the bracts inclosed in the parchment bags might have been carried to the stigmas by currents of air caused by the compression or expansion of the parchment bags. At any rate, the appearance of individuals of the pistil-parent type may be taken as presumptive evidence that such self-pollination occurred by some method, although the appearance of individuals of the parental type in hybrids is well known.

(I) A type represented by individual No. 2.1 (Pl. XIII, fig. 1) showed a rosette of deeply dull-green leaves, more or less crinkled and irregular in form and margin. In all about twelve plants of this type were seen, although but five reached a stage sufficiently advanced to send up a central stem. The rosettes were sparse and the leaves thick and fleshy, and almost glabrous, except that some were minutely pubescent on the veins beneath. The leaves of the rosettes varied from narrowly linear in the earlier stages to linear-lanceolate with obtuse apices, and to oblong-spatulate, broadest above the middle, and acutish in some individuals. The laminae were revolute and irregularly denticulate and formed narrow wings nearly to the base of the petioles.

The main axis of the hybrid individuals reached a height of 15 or 20 cm., at which stage in the development elongation ceased and the lateral branches became very active; in some instances no noticeable elongation of the main axis occurred. Branches of this were more rounded in outline and bore leaves of a structure somewhat more

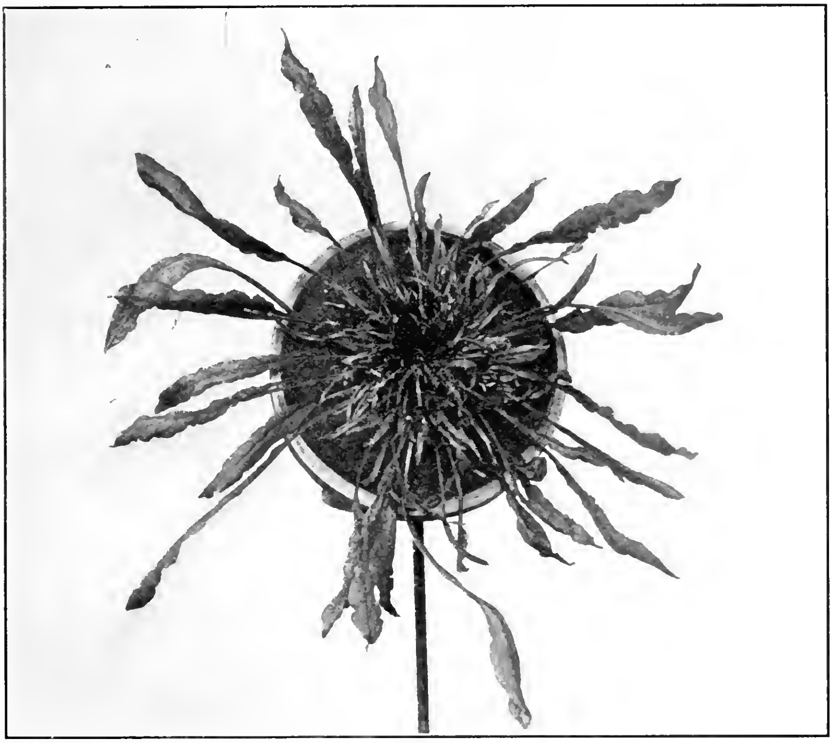


Fig. 1. Rosette five months old of No. 2.1 of the hybrid Onagra lamarckiana × Onagra biennis.

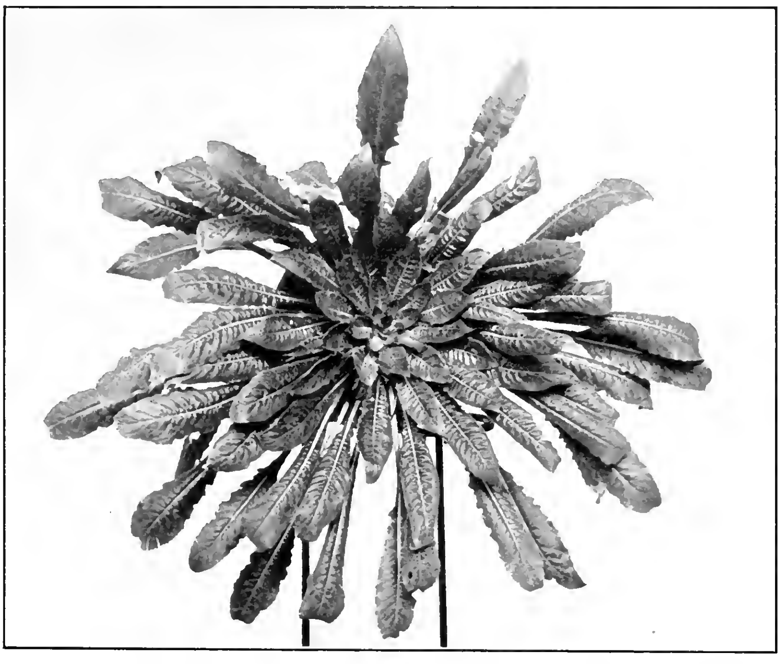


Fig. 2. Rosette five months old of No. 2.27 of the hybrid Onagra lamarckiana × Onagra biennis.

nearly conforming to normal types in a manner comparable to that of the parent, as noted above. These leaves were ovate-denticulate, abruptly acute, slightly crinkled, and were minutely pubescent. The terminal rosettes were dense and symmetrical and flower-buds were developed, the first of which opened on August 12. About this time some large rosettes were formed from lateral buds near the bases of the stems, which were composed of oblong-lanceolate leaves, slightly crinkled and denticulate and tapering to both ends. The entire plant was tinged with red, and most deeply so in the upper branches. (Pl. XVII, fig. 4.)

The petals were deeply emarginate, 28 to 30 mm. long and 30 to 35 mm. wide, being broader than long in all instances. The segments of the calyx were 30 mm. in length, being less than half the length of the hypanthium, which measured about 38 mm. The ovary was 10 mm. long and, with the hypanthium, bore a number of scattered hairs. Perhaps the most noticeable feature of this type was the variability of the relative length of the stamens and pistils. The pistils were fairly constant in length, but in some flowers the stamens were shorter and therefore not adapted to self-fertilization, while in others the anthers were above the stigmas, thus insuring self-pollination. No correlated structures were observed.

The capsules were about 2 cm. long, 5 to 6 mm. wide below the middle, oblong, tapering from near the base, obscurely angled and channeled, sparingly pubescent with both long and short scattered hairs.

The exceptional forms of leaves exhibited by this type were found to be accompanied and probably caused by the presence of a fungus, which seemed to attack this type only of the hybrid progeny. Similar effects in *O. lamarckiana* have not yet come under observation, but young rosettes of *O. biennis,* together with mature plants coming into bloom, were found growing wild in some waste park-land near the New York Botanical Garden on August 21, 1904. The leaves of these plants were closely similar to those of the pathological hybrid individual in general appearance, and furnished the curious parallel of showing a partial return to the normal form near the upper ends of the branches. Rosettes of the type described were transplanted to pots in the experimental house and the terminal portions of the leaves cut away in accordance with garden practice. Within a few days several leaves were seen to show an abundance of yellowish spermagonia, which appeared to belong to *Aecidium peckii* De Toni, although aecidia were not found.

(II) A second type was represented by individual No. 2.27, in which the leaves of the rosettes were finely pubescent on July 1; the rosettes were widely spreading and the leaves finely pubescent in specimens examined on that day. The laminae were lanceolate-oblong acute at the apex and broadest above the middle, gradually narrowing to the broad petiole and decurrent upon it to its base; approximately denticulate, crinkled between the secondary veins, more or less spotted with reddish areas. (Pl. XIII, fig. 2.)

Stems were sent up, which, upon examination on July 13, showed leaves of a dark bluish-green tinge, the laminae becoming convex upwardly owing to the unequal growth of the midrib. The stems were dotted with the reddish bases of the hairs. The apices of the main stem and of its branches formed close and symmetrical rosettes, in approximation of the structures shown by *lamarckiana*.

The general habit of the shoot was much like that of *biennis*, the basal branches being long. The central stem, however, was irregularly compressed and was of a zigzag form.

The flowers exhibited the following characters: Corolla-segments 2.2 cm. long, 2.5 to 3 cm. broad; calyx-segments 2.7 cm. long, more than half the length of the hypanthium; hypanthium 3.5 cm. long, slightly pubescent with scattered spreading hairs; ovary 6 mm. long, also pubescent with scattered spreading hairs; anthers and stigma as long as corolla, included, stigma variously 4 to 6 lobed. Bracts nearly as long as the hypanthium.

Capsules about 13 mm. long, with greatest diameter 6 to 7 mm., the greatest length being about twice the thickness; ovoid-oblong, tapering in upper portion to obtuse apex; not angled; slightly channeled; sparingly pubescent with appressed hairs. (Pl. XV, fig. 2.)

(III) The third type of the hybrid was represented by individual No. 2.24, in which the rosette was easily recognizable in the early stages and was dense, with the leaves lying flat on the ground when examined on July 1. The leaves were finely pubescent, with broadly ovate laminae, the laminae more or less crinkled, acutish or obtuse at the apex, broadest in the middle, more or less abruptly narrowed into the broadly margined petiole, which is narrowly winged at the base. These organs were approximately denticulate toward the apex, and irregularly dentate at the base, with reddish petioles and the laminae sparingly spotted with red. (Pl. XIV, fig. 1.)

The basal branches were nearly as long as the main axis. A portion of the stem immediately above the base was devoid of branches. The upper part of the stem bore numerous erect branches. The stems were deeply channeled and of a reddish color in the lower portions,

Fig. 1. Rosette five months old of No. 2.24 of the hybrid Onagra lamarckiana × Onagra biennis.

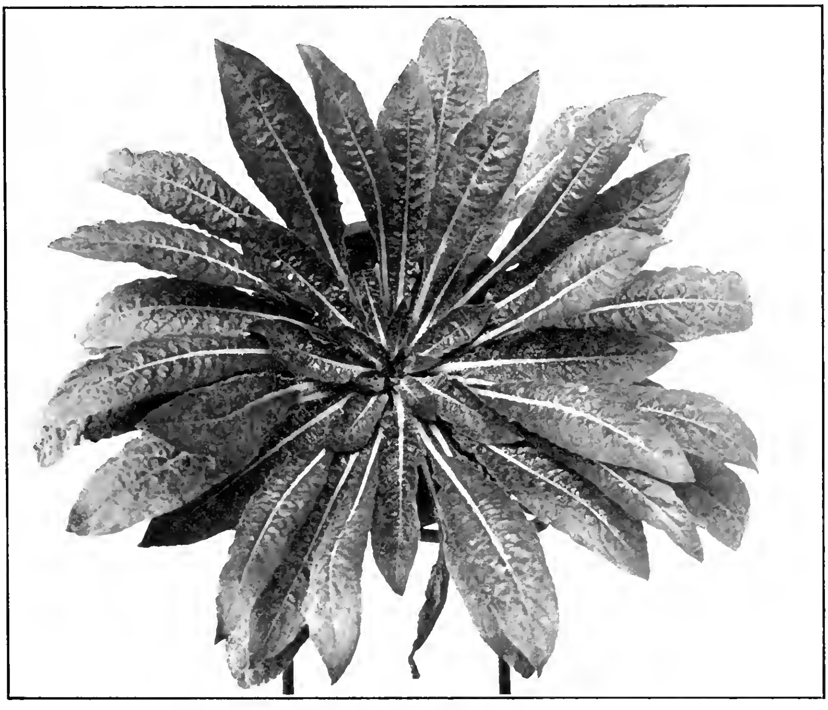


Fig. 2. Rosette five months old of No. 2.32 of the hybrid Onagra lamarckiana × Onagra biennis.

Fig. 1. Adult plant of 2.1 of the hybrid Onagra lamarckiana × Onagra biennis, showing basal rosette, pathological leaves, normal leaves on upper part of stem, buds, and flowers.

Fig. 2. Onagra lamarckiana × Onagra biennis No. 2.24 at left, No. 2.27 at right.

being distinctly paler in the terminal parts, which were of a yellowish-green color. All of the stems and branches were terminated by tufted rosettes. The following characters were exhibited by the flowers (Pl. XVII, fig. 5):

Petals 27 to 31 mm. long and 27 to 33 mm. wide, deeply emarginate; calyx-segments 30 mm. long, being more than half the length of the hypanthium, which was 48 mm. in length, slender, and glabrous, except for a few scattering hairs; ovary 12 mm. long, glabrous, except for a few scattered hairs; stamens nearly as long as the pistil. The capsules were 29 to 32 mm. long, 6 to 7 mm. in thickness, being about four times as long as broad, distinctly four-angled, and shallowly channeled; oblong and narrowed in the apical region; sparingly appressed pubescent. This type was noted as producing perfect seeds in apparently smaller numbers than the other types of the hybrid, although some branches bore several well-filled capsules. (Pl. XV, fig. 2.)

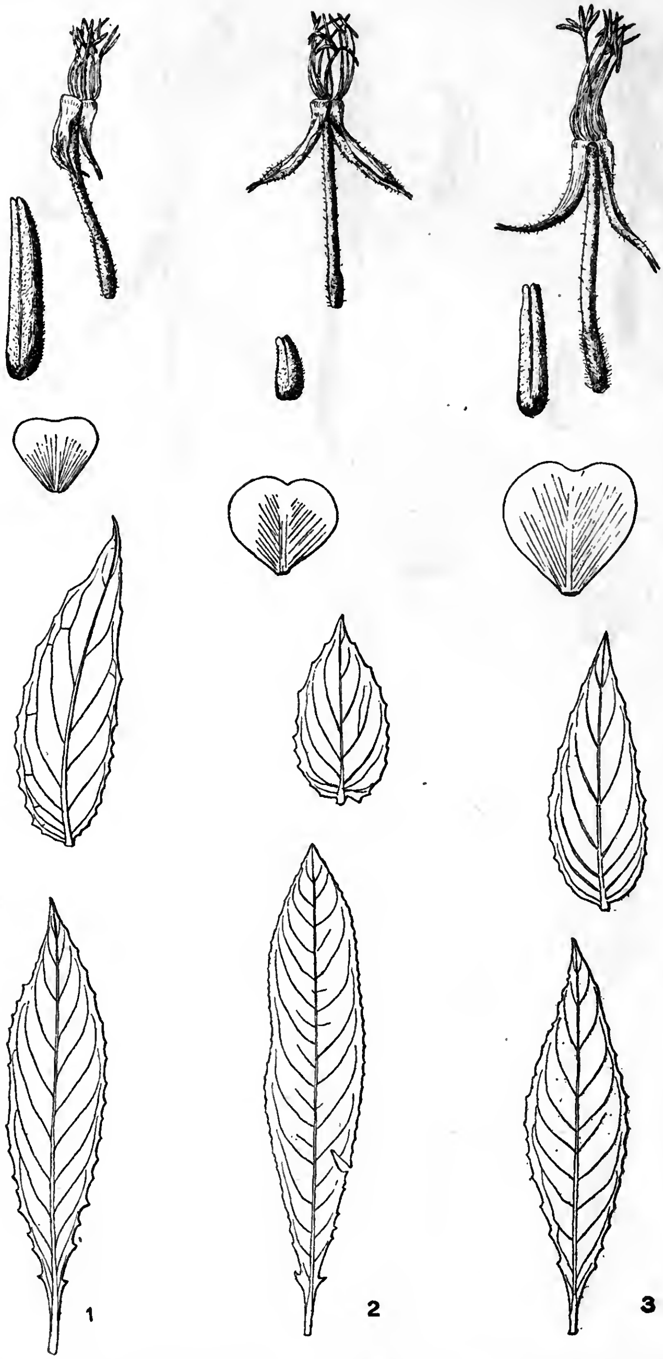
(IV) A fourth type was represented by individual No. 2.32, which was not recognized in the rosette stage, although the leaves are much narrower than in *O. biennis,* and are not so deeply toothed in the basal portion. The aspect of the adult plant (Pl. XIV, fig. 2) is very marked, however, and it is easily recognizable. The lateral branches are numerous and nearly as long as the main axis, with the stems deeply channeled. The larger leaves of the rosette are narrowly oblong-lanceolate and yellowish-green, with prominent reddish mid-veins. The stem leaves are lanceolate and broadest about the middle and deeply toothed. The entire plant is pubescent and shows a tinge of reddish color even when young, which becomes much intensified with age. (Pl. XIV, fig. 2.)

The bracts are oblong-ovate, the hypanthium longer than its segments; the petals are about 20 mm. long and 24 mm. wide, with wedge-shaped bases. The stamens, pistil and petals are about of the same length. The green capsules are about 26 to 27 mm. long and 6 to 7 mm. thick, oblong, tapering from near the base to the narrow apex, and shining green, being only sparingly pubescent. The general outline of the capsules is irregular; in cross-section they appear distinctly four-angled. (Pl. XVI, fig. 3.)

Seven individuals of this type were brought to maturity and all conformed, with only minor divergences, to the above structures.

The hybrid progeny in the cultures made in the New York Botanical Garden and in Amsterdam was thus seen to include a series of types which ranged, in the aggregate of characters included, from those

PLATE XVI.



1 2 3

Stem leaves, bracts, petals, capsules, and flowers of Onagra biennis and of two of the four hybrid types of Onagra lamarckiana × Onagra biennis.

1, *Onagra biennis*; 2, No. 2.27; 3, No. 2.32. **Stem-leaves one-fourth natural size; remainder of figures five-eighths natural size.**

PLATE XVII.

Stem-leaves, bracts, petals, capsules, and flowers of Onagra lamarckiana, and of two of the four hybrid types of Onagra lamarckiana × Onagra biennis.

4, No. 2.1; 5, No. 2.24; 6, *Onagra lamarckiana*. Stem-leaves one-fourth natural size; remainder of figures five-eighths natural size.

representing pure strains of both parents through goneoclinic forms to intermediates in which the parental characters were more or less equally apparent.

Although the great difficulties attendant upon a valuation of the characters occurring in hybrids were appreciated, it was concluded that such an estimation expressed in tabulated form would be the best method of expression of the dominance of the various characters.

Hurst selected twenty anatomical characters which were assigned equal value, and included such features as the habit of growth, and form and shape of the leaves and other organs, and upon the prevalence of these characters the degree of relationship of the hybrid to the parent was estimated. (Hurst, 1900.)

Peter made a tabulated list of the external characters of the hybrids of the hawkweed, in which these characters were classed as unilateral, goneoclinic, or intermediate with respect to the corresponding features of the two parents. The dominance of any given character was calculated from its occurrence in the entire list of plants examined. (Peter, 1884.)

Mathematical expressions of the dominancy of qualities are in themselves misleading unless based upon actual physical measurements taken by statistical methods from a number of individuals to eliminate errors. Then, again, the estimation of the development of a paired character presents one of the greatest difficulties encountered in the study of hybrids. Authors are by no means agreed as to what constitutes absolute dominance. Until within the last few years a character was regarded as dominant by most writers only when it appeared in the hybrid as an exact reproduction of the parental quality. The most recent discussion upon this subject that has come to notice is that of Correns, who takes the ground that a character apparently representing the parental quality to 75 per cent of its full power may be considered as dominant, when occurring to the extent of 25 to 75 per cent as intermediate, and below 25 per cent as recessive. (Correns, 1903.)

This author calls attention to the fact that fully dominant characters occur but rarely, and cites examples of *Hyoscyamus* and *Bryonia*.

The comparatively small number of individuals (33) of the hybrid between *O. lamarckiana* and *O. biennis* which were brought to maturity did not give extended opportunities for statistical work, and the number of characters taken into account included many not susceptible of direct physical measurement. It was decided, therefore, to express the descriptions in taxonomic terms arranged in tabulated form to serve as a graphic illustration of the general complexion of the types embraced by the hybrid. In this scheme it was found most convenient to apply the terminology generally used to designate the aspect of an individual to that of the separate characters, and qualities which were fully dominant and accurate representations of the parental forms were placed under the heading of "unilateral;" those which approximated the type of one parent closely, but did not represent it sufficiently to be identical with it in ordinary descriptive work, were classed as "goneoclinic" to that type, while those in which an average of the paired characters was apparent were placed under "intermediate." It is evident that the "intermediate" of Correns would embrace both the "intermediate" of the above classification and the goneoclinic departure from it on either hand. Goneoclinism may well be the extreme of fluctuating variability instead of a modification of a group-quality. The scheme used below has been found most convenient for this special discussion, but it is not urged as the best method for the general estimation of hybrids.

Tabulated analysis of the characters occurring in the various types of the hybrid Onagra lamarckiana × *Onagra biennis.*

No. 2.1.

	Unilateral.	Goneoclinic.	Intermediate.	Goneoclinic.	Unilateral.
	To lamarckiana.			To biennis.	
Rosettes	....	....	....	....	Leaves dull-green, fleshy, narrow, with irregular outlines, affected by parasite.
Stems and leaves.	Leaves crinkled. Terminal rosettes symmetrical.	Upper leaves ovate, denticulate.	....	....	Lower leaves thick, waxy, affected by parasite.
Flowers and fruits.	....	Capsules tapering to near apex, short, and thick.	Relative length of stamens and pistils variable.	....	Calyx-segments shorter than hypanthium.

The notable feature of the structure of this type consists of the forms of leaves exhibited by the stem. The rosettes and leaves of the stem which are attacked by the fungus are almost exact counterparts of those of *O. biennis,* while the upper portions of the shoot bear foliage-organs, very similar to those of *O. lamarckiana.* The tendency to being attacked by the fungus seemed confined wholly to this type, which is entirely unlike the remainder of the progeny in characters not affected by the parasite.

Tabulated analysis of the characters occurring in the various types of the hybrid Onagra lamarckiana × *Onagra biennis*—Continued.

No. 2.32.

	Unilateral.	Goneoclinic.	Intermediate.	Goneoclinic.	Unilateral.
	To lamarckiana.			To biennis.	
Rosettes	Leaves crinkled.	....	Leaves erected..	....	Leaves narrow, not deeply toothed.
Stems and leaves.	Stems channeled.	....	....	....	Leaves narrow, deeply toothed.
	Terminal rosettes symmetrical.	....	....	....	Branches long and numerous.
Flowers and fruits.	Ovary sparingly pubescent.	....	Capsule oblong, tapering at apex. Hypanthium of average length of parents. Petals wider than long.	Capsule four-angled and tapering at apex.	Relative length of hypanthium to calyx-segments 31:41. Bracts oblong-ovate; petals wedge-shaped at base. Stamens as long as pistils; pistils as long as petals.

Entire plant becoming deeply tinged with red when mature.

No. 2.24.

Rosettes	Leaves crinkled.	Young leaves broadly ovate, acutish or obtuse at apex.	Mature rosettes dense, spreading. Leaves broad, rounded at apex.	Young leaves denticulate. Basal portion of older leaves irregularly denticulate, tapering to petiole.	
Stems and leaves.	Leaves crinkled, hanging down, densely arranged. Upper branches erect, spreading.	....	Stems reddish...	Leaves ovate-lanceolate, denticulate throughout.	Basal branches as long as main axis.
Flowers and fruits.	Bracts subcordate, oblong-lanceolate, acutish, or acuminate.	Capsule nearly glabrous, tapering from near base, slightly channeled.	Petals intermediate in size and in relation of length and breadth.	Hypanthium thin.	Terminal rosettes tufted. Relative length of hypanthium and calyx-segments as in biennis. Relative length of stamens and pistil as in biennis. Capsule distinctly four-angled.

Among the characters noted above, all may be traced to the influence of one or other of the parents directly, except that of the excessively long and thin hypanthium. This organ sustains the proportions of some of the large-flowered relatives of *O. lamarckiana.*

Tabulated analysis of the characters occurring in the various types of the hybrid Onagra lamarckiana × *Onagra biennis*—Continued.

No. 2.27.

	Unilateral. To lamarckiana.	Goneoclinic. To lamarckiana.	Intermediate.	Goneoclinic. To biennis.	Unilateral. To biennis.
Rosettes	Leaves crinkled.	Mature rosettes dense, leaves with long petioles.	....	Young leaves oblong-lanceolate, tapering at base.	Leaves spotted with red. Leaves of mature rosettes, lanceolate-oblong.
Stems and leaves.	Leaves crinkled. Terminal rosettes dense and regular, leaves deeply green.	....	Length of stem-leaves average of parents.	Leaves of mature rosette not so deeply and regularly denticulate as in biennis. Basal branches not as long as main axis.	
Flowers and fruits.	Basal portion of petals rounded.	Bracts ovate, acute, irregularly denticulate, rounded or obscurely cordate at base. Capsule ovoid..	Petals with length greater than width. Superficial extension average of parents. Capsule pubescent, obscurely channeled.	....	Stamens and pistils of same length; capable of self-fertilization.

The stems were irregularly compressed with a zigzag outline, in a manner reminiscent of those of *O. rubrinervis*. The upper leaves of the rosettes and of the stems were strongly convexed upwardly, due to the unequal growth of the laminae and midrib. The calyx-segments were relatively shorter than in either of the parents. The entire shoot of the adult plant was deeply tinged with red.

It is to be seen from the foregoing that the hybrid *O. lamarckiana* × *O. biennis* obtained from the crosses made in New York includes four distinct and separate forms, none of which are identical with the unilateral monotypic hybrid obtained in the same cross in Amsterdam. In the last-named form the qualities of the pollen-parent were fully dominant throughout, while in the four types the qualities of the two parents exhibit diversified mosaics of dominancy and latency of the parental characteristics.

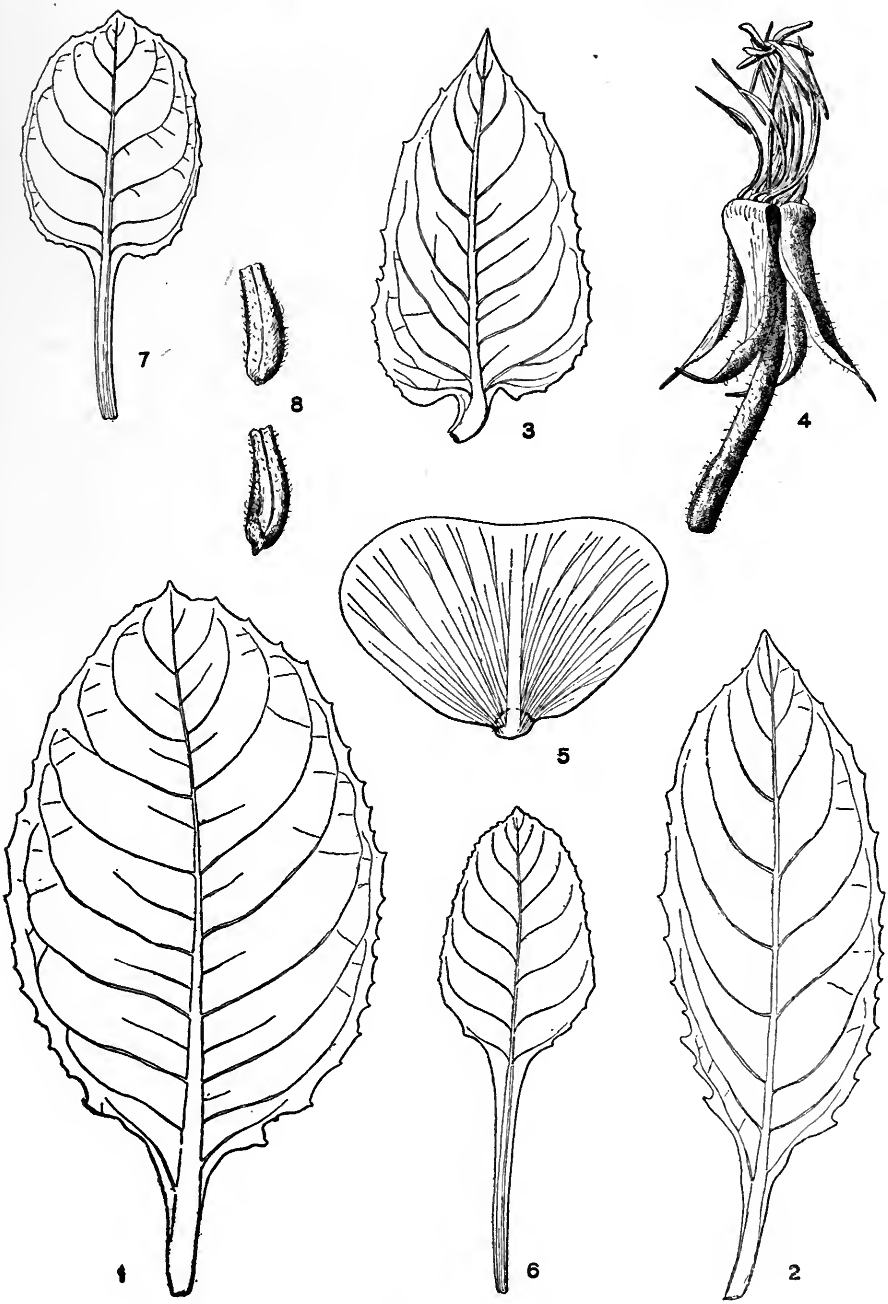
One of the American types, No. 2.1 (Pl. XVII, fig. 4), was characterized by a predisposition to the attacks of a fungal parasite, *Aecidium peckii*. The portions of the plant affected exhibited structures quite similar to those of the pollen-parent when affected by the same organism. Organs not directly attacked by the fungus showed such distinctive form as to make it certain that the diseased plants were not simply pathological individuals of one of the other types, but that the hybrid included a strain incapable of resisting the attacks of the fungus. The entire crop of seeds obtained by the cross in the previous year were sown in a single seed-pan, and this strain was seen to be affected even in the first foliage-leaf, while all of the others were found to be wholly immune. The whole pathological effect may be said to be due to the dominance of qualities of *biennis*. Leaves not directly attacked by fungus, on the other hand, exhibited a predominance of qualities characteristic of *O. lamarckiana*. The variable length of the stamens and pistils may, however, most reasonably be ascribed to the pathological condition.

A second form, No. 2.32 (Pl. XVI, fig. 3), reproduces the *biennis*-characters of the bracts, relative dimensions of the pistils, stamens, and petals quite exactly, and shows only slight departures from this parent in the habit of branching and form and margins of the leaves. The relative measurement of the hypanthium and of the petals are alike in the parents and remain the same in the hybrid. Only one character seems to have been transmitted unchanged from the *lamarckiana* parent, while the stems are channeled something after the manner of this parent, and some crinkling of the leaves is present. In this instance the qualities of *biennis* predominates strongly in the hybrid, and the qualities inherited from the other parent are of comparatively minor physiological importance. It is notable, however, that the general aspect of this plant is very different from that of *biennis*, although the taxonomic analysis yields so little actual anatomical divergence. This is partly due to the unusual reddish color present in the leaves and stems.

A third type, No. 2.24 (Pl. XVII, fig. 5), was characterized by the combination of parental qualities in such manner as to constitute intermediates. The characters of the form, size, and structure of the stems and leaves made a mosaic of modifications from both parents, in which it would be difficult to assign greater importance to one over the other. The hypanthium exhibited a length greater than that of either parent, while the ovary was less pubescent than either. The amount of red color present in the stems and branches was much greater than that of either parent and is only duplicated among some of the related species of the genus.

The form and structure of the bracts and the crinkling of the leaves were transmitted unchanged to the individual; the size and form of the petals were intermediate, and the relative length of the calyx-segments and hypanthium of *biennis* were found. It was notable

PLATE XVIII.



Onagra gigas.

1, leaf from middle of main stem; 2, leaf from main stem; 3, bract from one of the lowermost flowers; 4, flower with petals removed; 5, petal; 6, leaf from lower part of rosette five months old; 7, leaf from upper part of rosette five months old; 8, capsules. 1, 2, 3, 4, 5, and 8, five-eighths natural size; 6 and 7, one-fourth natural size.

that the spread of foliar surfaces and the density of arrangement of the leaves was similar to *lamarckiana*, while the form, incisions in the margin, and arrangement at apices of branches were similar to *biennis*. In the same manner the capsule was nearly glabrous, but was found to be distinctly four-angled.

A fourth type, No. 2.27, bore flowers not easily distinguishable from the pollen-parent, being capable of self-fertilization, but with the parts of the flower of greater size. From the other parent the unequal growth of the leaves, which results in the crinkling of the laminae is shown with a modification which causes convexities and concavities.

The symmetrical terminal rosettes are also a *lamarckiana* character of the entire laminae. An analysis of the remaining characters show that nearly all are combinations of parental qualities. Perhaps the most remarkable feature of this type is the appearance of qualities usually exhibited only by species allied to the parents and not by the parents directly. Among these may be mentioned the zigzag formation of the stem and the red coloration of the shoot.

In view of the above results it is evident that a repetition of the crosses between the mutant derivatives of *O. lamarckiana* and *O. biennis* would yield much of interest. De Vries has repeatedly called attention to the fact that the prevalency of the parental types in crosses of mutants with each other and with the parental form may be altered by nutritive conditions, and it may well be supposed that a similar state of affairs may be found to exist in the hybrid described above.

It will be of interest to trace the dominancy of the separate characters of the two parents throughout the hybrid considered as a whole. Of these the one that may be seen earliest in the development of the plantlets is the density of the rosettes due to the rapidity with which the leaves on the shortened internodes of the young stems appear, and their duration. Every individual in the hybrid, without exception, showed a heavy rosette composed of about 12 to 20 leaves, after the manner of *lamarckiana*. Plantlets of *biennis* of a similar age never bore more than half that number. The character in question depends upon the activity of the internode; the dominant character entails a more rapid succession of development in these members, as no difference could be detected in the duration of the individual leaves. While the character itself would be classed as meristic in its nature, yet it is really seen to rest upon a real and constant physiological quality. In addition to the rate of growth, it is not improbable that the greater density of the dominant rosette may be due in part to the development of a greater number of internodes before the elongated flowering shoot is sent up.

The leaves of all rosettes of the hybrid showed laminae variously crinkled, caused by the unequal growth of the mesophyllary and fibro-vascular tracts of the laminae, a character which is well marked and constant in *O. lamarckiana*, but which was not seen in *O. biennis* in any of the cultures, although it has been seen in a few wild specimens which were growing luxuriantly. Furthermore, the crinkling of the leaves was exhibited in the stem-leaves of the entire hybrid. In one type, that illustrated by 2.27 and consisting of two individuals, a further lack of correlation in the growth of the tissues of the leaf was exhibited, which consisted in an excess growth of the midrib over that of the wings of the laminae, giving it an upward convexity which might easily be converted into the reverse form. This was present in both the rosette and stem-leaves.

The forms of leaves were so diversely intermediate that it is not possible to point to any important dominancies in this respect, except such as are found in the types of terminal rosettes exhibited by stems and branches. One, a regular, flattened, and symmetrical rosette, characteristic of *lamarckiana*, was dominant in all individuals except those of 2.24, which bore tufted rosettes in the five individuals included with it.

The branching habit of *O. biennis*, by which secondary members were borne on all parts of the main axis, decreasing in length upwardly, showed exactly the complementary prevalency, being present in all individuals with terminal rosettes of the pattern of *O. lamarckiana*. Type No. 2.24, which bore *biennis* rosettes, gave off large basal branches, and the upper part of the main axis was more densely branched than in *O. lamarckiana*, so that the habit of the pistil-parent in this particular was not exhibited in pure form by any member of the hybrid.

Stems of rounded cross-section were found to be more prevalent than those with deep channeling, the latter occurring on only five individuals of the hybrid.

The capacity for self-fertilization as indicated by the relative length of the stamens and pistil was dominant in all types, except that of 2.1, or in about 29 out of the 33 individuals examined. A sharp separation with regard to this character may be detected in securing pure fertilizations. In order to obtain capsules with pure seeds it is but necessary to inclose the inflorescences of *O. biennis* in the parchment bags and the pollen will fall on the stigmatic surfaces without the intervention of any agency whatever except gravity. On the other hand, *O. lamarckiana* rarely sets seeds unless pollen is transferred to the stigmas by insects or by hand, although in the open air the same purpose is sometimes accomplished by the wind.

The calyx-segments are relatively much shorter than the hypanthium in all individuals of the hybrid showing a dominance of a character of *O. biennis*, although the actual length of the latter is greater in some individuals than in either parent. The other features of the flowers were variously intermediate. The elongated capsule was present in all of the individuals of the hybrid, except in the two included in the type of No. 2.27.

OCCURRENCE OF MUTANTS.

Among the progeny arising from the cross between *O. lamarckiana* and *O. biennis* were two individuals which, as early as July 1, were seen to be separable by the variously erect leaves with long petioles in the rosettes. The rosettes were sparse, and the leaves were oblong-lanceolate, obtuse at the apex, broadest about the middle, and more or less abruptly narrowing to the petiole, upon which the narrow wings of the laminae extended nearly to the base. The basal portions of the leaves were deeply and irregularly denticulate. The members of the rosette were minutely pubescent. On July 13 these plants had sent up shoots which soon bore the characteristic leaves, bracts, and flowers of *O. rubrinervis*, a mutant which was originally observed by De Vries in 1887.

The occurrence of mutants in hybrids in which one of the parents appears as a pure strain has long been known and has been described at length by Professor De Vries as occurring at numerous times in his cultures. He found that about 1 per cent of the hybrid progeny of *O. lamarckiana* × *O. nanella* was composed of mutants, and that about 2 per cent of the hybrid progeny between various older species were mutants in a series of tests made in 1896–1900. (De Vries, 1903, pp. 425, 426.)

O. rubrinervis was observed by De Vries to arise in the hybrid progeny of *O. lamarckiana* × *nanella*, *O. lata* × *nanella*, *O. lata* × *lamarckiana*, *O. lata* × *brevistylis*, *O. nanella* × *brevistylis*, *O. scintillans* × *nanella*, and *O. lamarckiana* × *scintillans*, to which must be added the experience related above, by which this species was also found in the descendants of *O. lamarckiana* × *biennis*.

The facts recorded by De Vries indicate that the mutability of the various forms of the evening-primrose is not modified by crossing in any manner. It is a matter of interest in this connection that he has also established the conclusion that the number and amplitude of fluctuating variations exhibited by parental forms are not increased or materially modified in the hybrids.

The designation of an individual from a hybrid progeny as a mutant is unsafe, unless, as in the evening-primroses, the characters of the mutants have been established by previous observations. It is quite possible that mutants may have appeared in hybrids at various times, thus giving basis for the assumption that new qualities were seen to appear as a result of the hybridization.

A second occurrence of *O. rubrinervis* as a possible mutant was noted in a lot of plantlets grown from seeds obtained from the botanical garden at Upsala early in 1904. The seeds were sown in germinating pans on March 28, 1904, and four individuals were transplanted to the experimental grounds on May 28 and began to send up shoots early in July. Of these, two were undoubted types of *O. rubrinervis*, corresponding to this form in all particulars.

In reply to the inquiry as to the derivation of the seed from which the above plants were grown, Prof. F. R. Kjellman, director of the botanical garden at Upsala, replied as follows under date of August 8, 1904:

> The seeds of *Oenothera lamarckiana*, which you received from this botanical garden, were gathered from plants grown in a cool house from seeds obtained from Professor De Vries. Some oenotheras of other species were growing near these plants, upon which account the possibility of hybridization was not excluded. Pure seeds of the new species of *Oenothera* may, in my opinion, only be obtained from Professor De Vries.

In view of the above record, therefore, it may only be said that the specimens of *O. rubrinervis* in this culture owe their origin either to an actual mutation, or to the pollination of *O. lamarckiana* by *O. rubrinervis*. Professor Kjellman did not state whether or not any of the new species were included in the lot growing near *O. lamarckiana*, although the negative presumption seems warranted.

Still a third occurrence of the same species is to be noted, for which all explanation is lacking at the present time. A package of seeds under the label of "*Statice Japonica*" were received from the botanical garden at Tōkyō, in 1903. After germination, four of the seedlings were transplanted to small pots in accordance with the usual custom with new accessions to the New York Botanical Garden. Attention was not called to the peculiar appearance of these plants until early in May, when they formed rosettes 2 dm. in diameter, and were unmistakably *O. rubrinervis*. I was not able to trace the history of the seed-package and learn whether all of the seeds were of the same kind or not. If by mistake a package of seeds of *Onagra* had been sown under the above label, the *rubrinervis* which was with it would have germinated first, as the seeds are very easily awakened from the dormant condition, and a half dozen of these would have been transplanted to small pots by the gardener and the remainder would have been destroyed in accordance with the usual custom. A still further possibility lies in the fact that ordinary seeds are sown in mixtures of potting soil that has not been sterilized, and might have contained some seeds of this species from the cultures made in the New York Botanical Garden for the previous year.

The chief purpose of the earlier studies of the senior author of the present paper was to make comparative studies of the parent-form with its mutant derivatives, and also to test the stability of all of the types concerned when cultivated under climatic conditions widely different from those under which the mutants arose. Previously to the cultures of 1904 less than a dozen of the various forms were brought to maturity, and no attention was given to the possible occurrence of mutants among the seedlings, although many might have been present. Thus De Vries found 600 mutants in 50,000 seedlings from *lamarckiana*, although he has pointed out that it would be possible to have extensive plantations of seedlings which included no divergent forms. Still another factor in the matter consisted in the inexperience of the experimenter. The discovery of the mutants in the seedling stage when only two or three small leaves are present is difficult for the first time, although after becoming accustomed to the typical forms and learning the aspect of the things to be looked for it is comparatively easy to recognize the better-known mutant types. Even then the mutants previously seen are much more readily distinguished than those known only by descriptions. This matter of practical observation depends greatly upon the plain mechanical fact that the selection of the various forms is generally done in the seed-pans in which germination occurred in order to save the labor necessary in transplanting them to small pots.

After the major ends of the cultures had been reached in the summer of 1904, and the newly-grown crops of seed were nearly mature, the chances of losing any of the forms under cultivation by accident was reduced to a minimum, and all of the seeds remaining on hand were sown in pans of sterilized soil in order to make separate observations upon the occurrence of mutants. Several thousands of seeds of *O. lamarckiana* of the crop of 1901 from the botanical garden of Amsterdam, and of the same species of the crop of 1903 from the New York Botanical Garden, were germinated in the above manner. In addition, a few hundred seeds of *O. gigas* of the crop of 1903 from the botanical garden of Amsterdam were sown

The seedlings of the last-named species show a wide divergence in the juvenile leaves, which is partially continued even in the foliar organs of the mature plant, although it is not believed that these divergences may be grouped in separate strains of the species. Consequently several selections were made from the cultures which, however, were soon found to be well within the limits of the type.

The results obtained from *O. lamarckiana* were of much greater interest. Mutants were found in the seedlings grown directly from the seeds from the garden at Amsterdam, and also from those of 1904 from the New York Botanical Garden. As early as October 1, 1904, *O. albida, O. elliptica,* and *O. scintillans* were recognizable in the plantlets grown from seeds produced in New York and Amsterdam. Later, *gigas*, *nanella*, *oblonga*, and *subovata* were found. In addition to these seven known mutants which had been seen to originate previously in Amsterdam, seven other forms could be distinguished which could not be identified with any forms heretofore observed by Professor De Vries or the authors. It is therefore justifiable to say that so far as present information goes the range of mutability of the parent-species has been extended under the conditions under which it has been cultivated in America. A comparative examination of the cultures in the two localities brings out the fact that the plants grown in New York were much more vigorous and active than those in Amsterdam, and the suggestion lies close at hand that whatever the causes may be that induce changes in the qualities of a species, the actual environment in which such mutative alterations ensue is one that has a majority of the factors favorable to vegetative development as well as to plentiful seed-production. The limited number of facts brought to light by the mutation cultures certainly support the suggestion in question, which, it is to be noted, is in direct opposition to the conclusion of Darwin that new types arise most plentifully in response to adverse circumstances.

In conjunction with the foregoing it is to be recalled that seeds of *O. lamarckiana* obtained from Vilmorin-Andrieux et Cie., in France, by De Vries, produced some *O. nanella* when sown in the botanical garden at Amsterdam in 1899. (De Vries, 1903, p. 459.)

It is to be seen, therefore, that *O. lamarckiana* is still in a mutable condition in various portions of its widely extended range. The results of the more recent cultures made in the botanical garden at Amsterdam leads, however, to the conclusion that *O. lamarckiana* has lost the capacity for producing *O. lata, laevifolia*, and *brevistylis.* De Vries also found that the capacity for mutability inherited by *rubri-*

Fig. 1. Onagra lamarckiana and Onagra nanella in bloom.
Photographed at 6 a. m., August 9 1904.

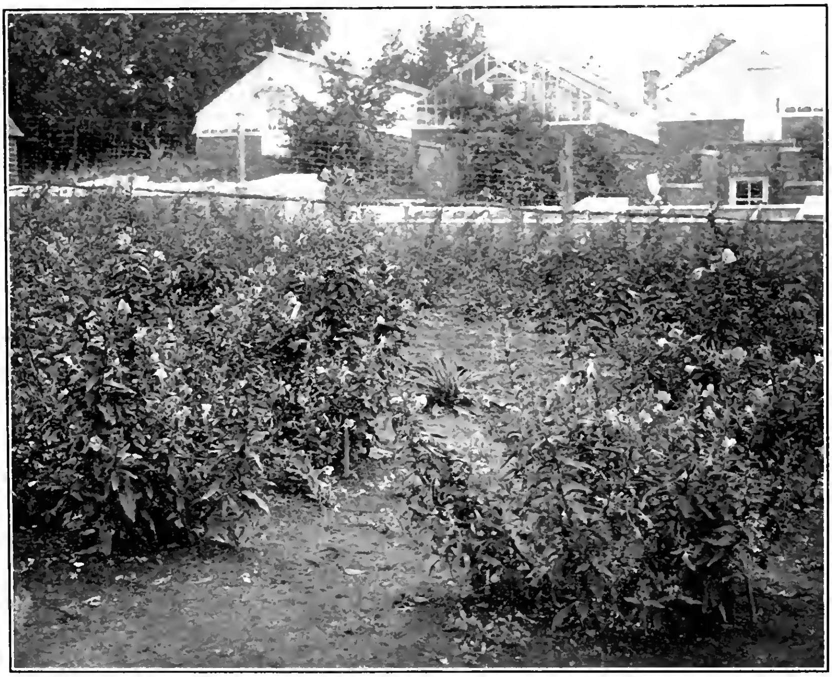


Fig. 2. Onagra lamarckiana × Onagra biennis.
No. 2.32 at left and right in foreground; No. 2.24 in center.

nervis, by which it was able to give rise to *nanella,* no longer exists. The loss of mutability has been noted to be accompanied by an acquisition of the Mendelian procedure in the hybridization of these two forms. (De Vries, 1903, pp. 458, 460.)

The discovery of single plants presumably derived from an ancestral mutation, or of a few plants as mutants from a parent, suggest that in some instances the period of mutability of a species may include only a single season, and these brief periods may recur at intervals concerning which information is totally lacking. In the case of oenotheras, however, the first mutants in bloom were found in 1887, which shows that the parents from which they were derived perfected their seeds in 1885. The recurrence of various mutants has been noted in every succeeding year, including 1904, and it is to be seen, therefore, that this species has been in a mutable condition for twenty years. How much earlier mutants have been formed than the date given above cannot be surmised. The continuance of the capacity for mutability is open to actual observation, however, and it may be possible within the next few years for the botanist to actually witness the closing of the mutative period in this plant which has furnished material so rich in practical and theoretical results. The procedure of *O. lamarckiana* is supposed by De Vries to be similar to that which has been followed by *Draba* and *Viola* in the productions of the swarms of species now recognized. (De Vries, 1905.)

During the cultures of 1902-1903 *O. lamarckiana*, *O. nanella*, and *O. rubrinervis* were grown as biennials for purposes of comparison with the behavior of other species. During 1904, however, seeds were sown in the propagating houses about the first of the year and the plantlets, after being properly transferred from smaller to larger pots, were placed in the soil in the experimental grounds in the latter part of May. No marked difference between the two series could be detected. It was noted that *O. gigas*, however, has more thoroughly established itself in the biennial habit and that not half of the plants grown as annuals actually produced flowers or seeds in 1904.

The estimation of the general hardiness or fitness of the parental form and of the mutants, with a view to the determination of their relative value if thrown into a competitive struggle for existence, is not to be too lightly made. *O. lamarckiana* has not spread over any part of North America having the climate of New York, and its cultivation in this locality must bring into contact many factors inoperative in its natural habitat. Tests made under such conditions must be accepted most guardedly. A general description of some of the more striking characteristics of the various forms will be of some value, however.

The rosettes of *O. lamarckiana* and *O. rubrinervis* which failed to send up flowering shoots in 1903 endured the following winter, which was of maximum severity, and began growth in a normal manner in the spring of 1904, but were uprooted to make room for a new series of experiments.

No actual difference has been found in the power of producing pollen among the parent-form, the mutants grown in the New York Botanical Garden, and the other American species. All produce an abundant crop of pollen, and show many faulty grains. *O. rubrinervis* was found to produce a greater number of capsules, and the seeds germinated more readily than those of the parent-form, the plants reaching maturity earlier than *O. lamarckiana*. *O. gigas*, on the other hand, grows more slowly than the parent-form, as stated above, although it

FIG. 2. Seedlings of *Onagra gigas*, about five weeks old, showing variations in forms of leaves.

produces seeds abundantly, which show a high percentage of germination. Both species are supposed by De Vries to be quite equal to the parental type in vigor, or perhaps to excel it. The latter suggestion is supported by the marked reproductive capacity of these forms in hybridizations When crossed with the parental form or with other mutants, the dominance of the characters of *O. gigas* and *O. rubrinervis* is especially marked, most so in the case of *O. gigas*.

In continuation of the work carried on in previous cultures observations of *O. gigas* were made for the purpose of placing on record an exact description of its characteristics as grown in America. The formal descriptions of the parental type and *O. rubrinervis* and *O. nanella* have already proved useful in the various phases of the present investigation. (MacDougal, 1903.)

Fig. 1. Onagra gigas in bloom.
Photographed at 7 a. m., August 9, 1904.

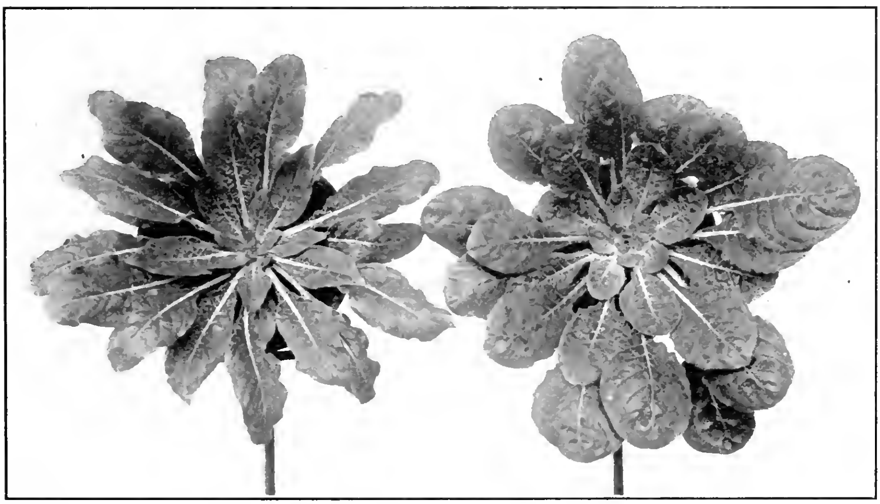
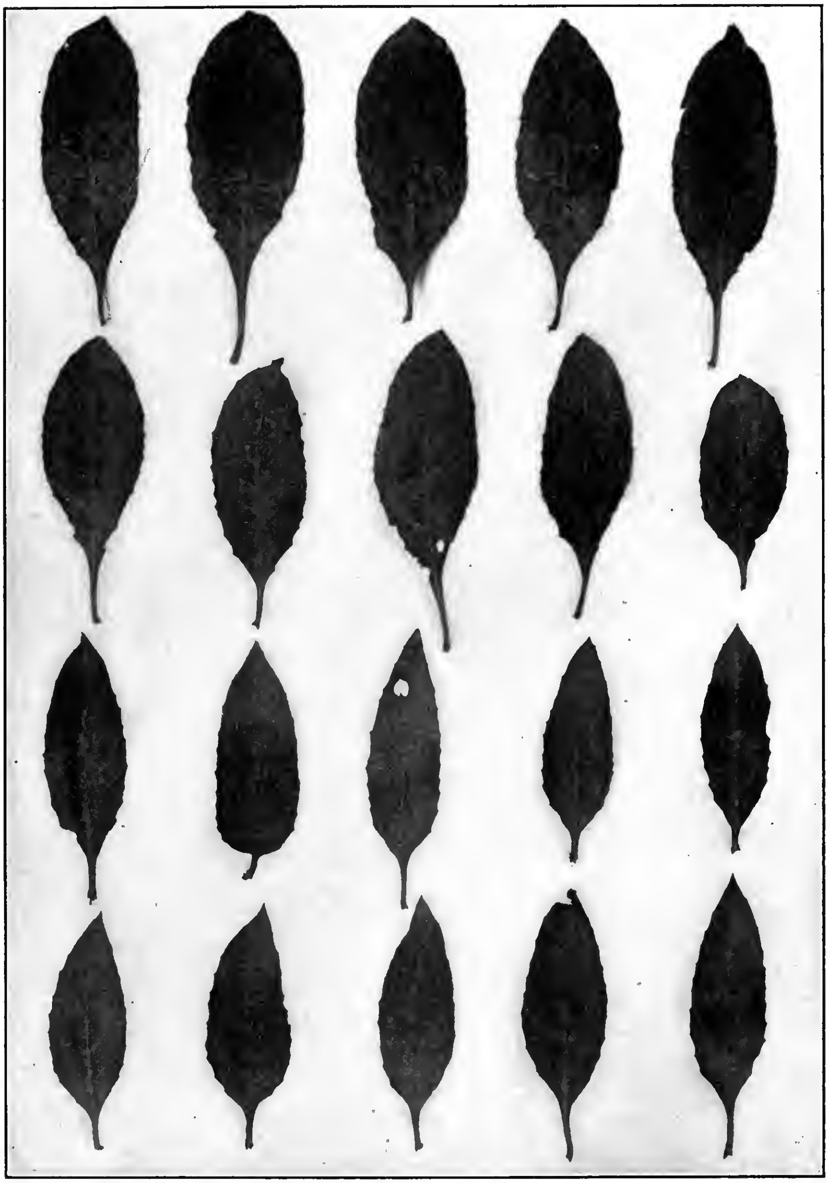


Fig. 2. Rosettes of Onagra gigas six months old, showing diverse forms of leaves.

Onagra rubrinervis.
Photographed at 6.30 a. m., August 9, 1904.



A series of leaves taken from near the middle of the basal branches of Onagra lamarckiana and Onagra rubrinervis, illustrating the nearest approach to identity in leaf-form. The two lower rows are Onagra rubrinervis; the two upper Onagra lamarckiana.

ONAGRA (OENOTHERA) GIGAS.

Seedling about two months old.—Leaves finely but rather copiously pubescent; blades various; those of the earlier leaves narrowly or broadly oblong, those of the later leaves broadly oval, suborbicular, or ovate-orbicular, mainly 3 to 4 cm. wide, abruptly narrowed at the base, or truncate, longer than the petiole.

Seedling five months old.—Rosettes rather dense; leaves copiously fine-pubescent; blades broadly oblong, oval, or ovate, varying to obovate, the larger ones 2.5 cm. wide, distantly denticulate, obtuse or nearly acutish at apex, markedly longer than petiole. (Pl. XX, fig. 2.)

Mature rosette.—Leaves ample, finely pubescent all over, the larger ones about 28 cm. long, 9 to 10 cm. wide; blades ovate and prominently glandular-denticulate, or with an ovate terminal lobe and several large basal teeth, or tooth-like lobes, with petioles very stout.

Adult plant.—Plant very stout and luxuriant. Stem channeled, branched near the base, and mainly below the middle, the branches assurgent or ascending, like the main stem hirsute, the hairs commonly widely spreading; leaves finely pubescent, 1 to 2 dm. long, on the lower part of the stem, numerous; blades shallowly and rather remotely toothed, those of the lower cauline leaves oblong-spatulate to oblong, acute at the apex, each narrowed into a semi-terete, margined petiole, those of the upper leaves broadly oblong to oblong-ovate, acute or abruptly short-acuminate, sessile or nearly so; bracts ovate-lanceolate, cordate or subcordate at the base; conic portion of the bud about 3.5 cm. long, finely pubescent, with short, spreading hairs, the free tips of the sepals 6 to 7 mm. long; hypanthium 4 to 4.5 cm. long, about 7 mm. wide at the mouth, slightly ribbed; sepals 4 to 4.5 cm. long, about as long as the tubular portion of the hypanthium, the free tips 8 to 9 mm. long; petals firm, 4.5 to 5 cm. long, truncate or slightly emarginate at the apex; filaments 18 to 20 mm. long; anthers 15 to 16 mm. long; pistil longer than the stamen; stigma 6 to 7 mm. long; capsule about 2 mm. long, 7 to 8 mm. in diameter at thickest point, finely pubescent all over, scarcely narrowed at apex. (Pl. XVIII.)

STATISTICAL COMPARISONS OF ONAGRA (OENOTHERA) LAMARCKIANA WITH TWO OF ITS MUTANTS.*

So general is the experience in garden practice that a variety which has been improved by selection rapidly loses its improved character upon the cessation of the selective process that the stability of any modification which is discovered either in nature or under cultivation demands the fullest possible proof. The mutation-theory is so diametrically opposed to Galton's law of ancestral heredity that it needs especial investigation from the same standpoint and by the same methods by which this law was established. According to Galton's law the offspring shows a certain definite degree of inheritance from each generation of its ancestors, one-half from its parents, one-quarter from its grandparents, one-eighth from its great-grandparents, and so on. (Galton, 1889.) As a consequence of this law the children of extreme parents are on the average less extreme than their parents, because their preparental ancestry is on the average more mediocre. The departure of the offspring from the mean condition of the race to which it belongs toward the extreme condition of its parents has been designated "regression." One of the most serious criticisms which has been made upon De Vries's conclusions has been that of Weldon, who points out that no satisfactory evidence has been presented to prove the completeness of regression, in the Galtonian sense, in the *Onagra* mutants. For, unless such regression is complete, these mutants could not maintain themselves distinct from the parental type except through the agency of man in guarding pollination and in selection, a fact which would deprive them of all significance in the explanation of evolution. (Weldon, 1902.)

To test quantitatively the continuity or discontinuity of a few of the differential characters of the *Onagra* mutants, and to begin the work which, when continued for several years, will forever set at rest the question of the completeness of Galtonian regression, the investigation the results of which are reported in this section were undertaken. The number of specimens available for study was not sufficient for the most satisfactory statistical work, but the results offer a number of suggestive lines for future investigation.

As all the characters chosen for this investigation are notably affected by the physical conditions to which the plants are subjected, it should be pointed out that all these specimens were grown near each other in an experimental garden which presents nearly uniform conditions throughout, and that they were planted at the uniform

*Prepared by G. H. Shull.

FIG. 3. Variations in statures of *Onagra nanella* (left) and *O. lamarckiana* (right). *O. nanella:* Range, 7-35 cm.; M., 22.81 ± 1.02 cm.; σ, 7.26 ± 0.72 cm.; C. V., 31.84 ± 3.16 per cent. *O. lamarckiana:* Range, 77-96 cm.; M., 88.68 ± 0.55 cm.; σ, 4.76 ± 0.39 cm.; C. V., 5.37 ± 0.44 per cent.

distance from each other of one meter, thus allowing each specimen sufficient space to express its characteristic physiological nature unmodified by complex interrelations with other plants.

The stature of Onagra nanella.—The character which most strikingly differentiates *O. nanella* from its parent-form, *O. lamarckiana*, is that from which it has so appropriately received its name. The great difference in height between these two species may be seen in the photograph (Pl. XIX, fig. 1), which represents a typical specimen of each. The results of measuring 23 specimens of *O. nanella* and 34 of *O. lamarckiana* are seriated in the form of curves of equal area in fig. 3. It will be observed in this figure that not only are the two curves quite distinct, but that they are separated by a wide gap. The discontinuity is tremendously in excess of the probable errors, the distance between the means of the two curves being more than forty times the sum of the probable errors of the means. The heights of *Onagra nanella* group themselves about the mean value 22.81 ± 1.02 cm., with a range from 7 cm. to 35 cm., and those of *O. lamarckiana* about the mean value 88.68 ± 0.55 cm., with a range from 77 cm. to 96 cm. The other constants present quite as interesting differences. Although the mean height of *O. nanella* is only one-fourth as great as that of *O. lamarckiana*, the standard deviation, σ, is considerably greater, being 7.26 ± 0.72 cm. in the former and only 4.76 ± 0.39 cm. in the latter. As the mean and the standard deviation are combined in the formula $\frac{100\sigma}{M}$, to form the coefficient of variability, the latter constant shows an even more remarkable difference between these two forms than do the means. The coefficient of variability in the height of *Onagra nanella* is notably high, 31.84 ± 3.16 per cent., while that in *O. lamarckiana* is quite as notably low, 5.37 ± 0.44 per cent. This is particularly interesting, as will be seen later, in its agreement with the fact that in most of the characters chosen for this study the mutant is significantly more variable than the parent-form.

The branching habit of Onagra rubrinervis.—The nature of the branching of *O. rubrinervis* as compared with that of *O. lamarckiana* is such as to give it a very characteristic aspect. On the average about twice as many of the axillary buds develop branches and these branches have a greater average length. In both species there is a whorl of long lateral branches surrounding the base of the main axis. In *O. rubrinervis* the central axis bears numerous branches roughly correlated with their position on the axis in such a way as to give the plant as a whole a distinctly conical form. In *O. lamarckiana*, on the other hand, the branches arising from the central axis are less numerous, shorter, and evidently less closely correlated with their position on the axis, but show a tendency to group themselves somewhat above the base, so that the plant resembles the framework of an inverted umbrella. (Cf. Pl. XIX, fig. 1, and Pl. XXI.)

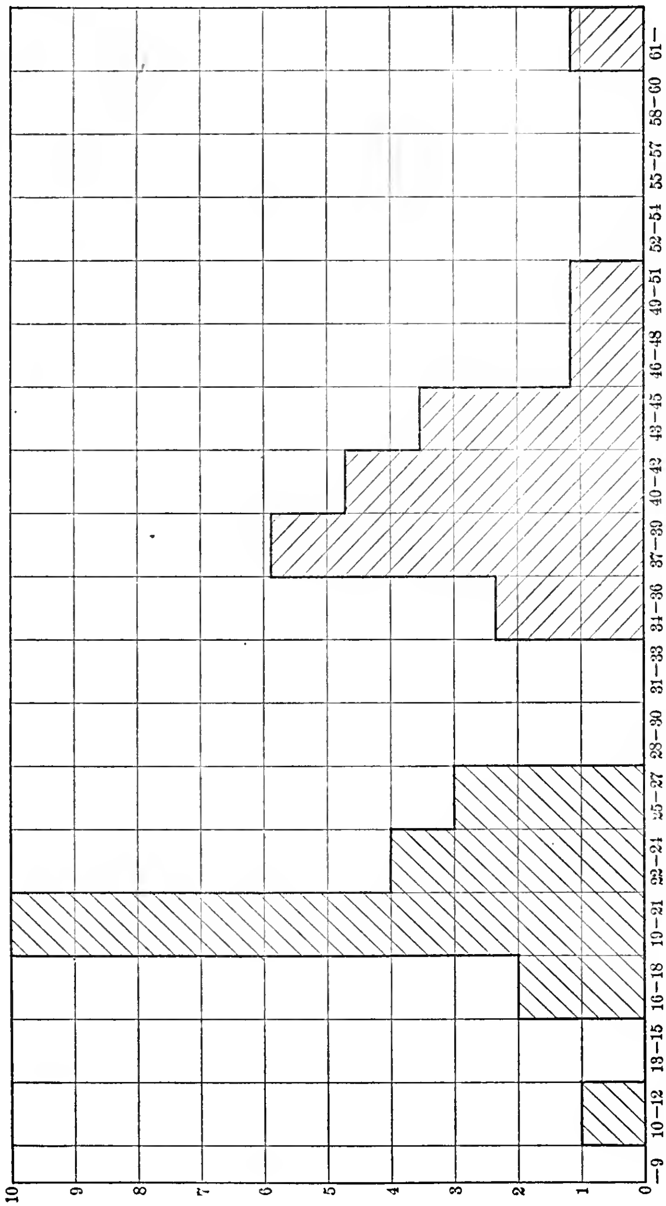


FIG. 4. Variation in number of lateral branches in *Onagra lamarckiana* and *O. rubrinervis*. Curve for *O. rubrinervis* shaded with lines rising to left. *O. lamarckiana*: Range, 11 to 25; M., 20.70 ± 0.49; σ, 3.24 ± 0.35; C. V., 15.7 ± 1.7 per cent. *O. rubrinervis*: Range, 34 to 62; M., 42.35 ± 1.04; σ, 6.34 ± 0.73; C. V., 15.0 ± 1.7 per cent.

Although such a character as this is too largely influenced by the individual physiological vigor to be of any value as a diagnostic character, the difference of aspect between the lots of plants of these two species was so striking that it was thought interesting to give it quantitative expression. A comparison of the number of lateral branches shows complete discontinuity between the two species in this regard, the range in *O. lamarckiana* being from 11 to 25, and in *O. rubrinervis* from 34 to 62. Curves of equal area representing the variation in the number of branches of 17 specimens of *O. rubrinervis* and of 20 specimens of *O. lamarckiana* selected by lot, are shown in fig. 4. The constants of these curves are as follows:

	Mean.	Standard deviation.	Coefficient of variability.
	Meters.	*Meters.*	*Per cent.*
Onagra lamarckiana........	20.70 ± 0.49	3.24 ± 0.35	15.7 ± 1.7
Onagra rubrinervis	42.35 ± 1.04	6.34 ± 0.73	15.0 ± 1.7

If, instead of the number of branches, we consider the total branch-length, the results are in some respects more striking still, for in general the branches are longer in *O. rubrinervis* than in *O. lamarckiana*. This did not prove invariably true, however, and the discontinuity which should have been increased by this difference in average length is lost through the occurrence of a specimen of *O. rubrinervis* having a total branch-length of only 7.79 meters, though it had 39 branches. This is well within the range of total branch-length of *O. lamarckiana*, which varied in this respect between 3.65 meters and 8.41 meters. The greatest length of branches observed in any specimen of *O. rubrinervis* was 29.98 meters. The variability in regard to total branch length is presented graphically in fig. 5. The constants of these curves are as follows:

	Mean.	Standard deviation.	Coefficient of variability.
	Meters.	*Meters.*	*Per cent.*
Onagra lamarckiana..............	6.68 ± 0.20	1.35 ± 0.14	20.2 ± 2.2
Onagra rubrinervis...............	18.19 ± 1.30	7.95 ± 0.92	43.7 ± 5.1

This comparison shows a remarkable difference throughout, the most important feature probably being the fact that the coefficient of variability in total branch-length is more than twice as great in *O. rubrinervis* as in *O. lamarckiana*.

The size and shape of the leaves of Onagra rubrinervis.—Much more important taxonomically than stature and branching are the leaf-characters, and it is just here that statistical study encounters the most serious obstacles in seeking a satisfactory basis. In the first place, some of the leaf-characters are incapable of quantitative expression, such as the degree of crinkling of the leaf, which is a striking, though not an absolutely distinctive feature of the leaf of *O. lamarckiana*. Some leaves of *O. rubrinervis* are also crinkled, but it is a gen-

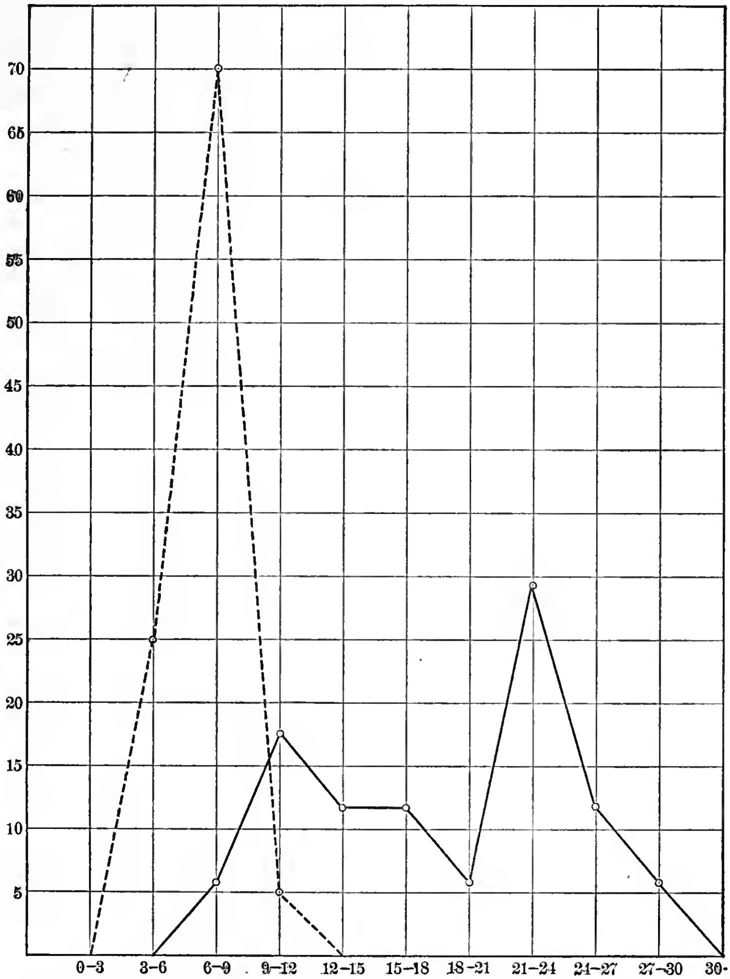


FIG. 5. Variation in total branch-length of *Onagra lamarckiana* and *O. rubrinervis*. *O. lamarckiana:* Range, 3.65 to 8.48 meters; M., 6.68 ± 0.20 meters; σ, 1.35 ± 0.14 meters; C. V., 20.2 ± 2.2 per cent. *O. rubrinervis:* Range, 7.79 to 29.98 meters; M., 18.19 ± 1.30 meters; σ, 7.95 ± 0.92 meters; C. V., 43.7 ± 5.1 per cent.

eral character of the leaf of *O. lamarckiana* and only occasional in *O. rubrinervis*. Other characters, although measurable, present technical difficulties incommensurate with the value of the results, as, for instance, leaf-thickness and degree of pubescence. The leaf of *O.*

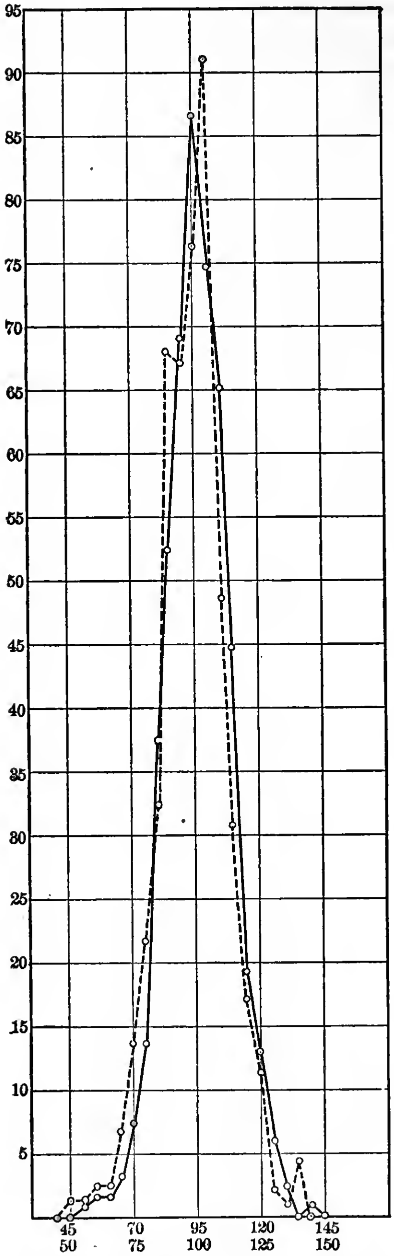


FIG. 6. Variation in leaf-length of *Onagra lamarckiana* and *O. rubrinervis*. *O. lamarckiana*: R., 49 to 137 mm.; M., 96.85 ± 0.42 mm.; σ, 13.08 ± 0.30 mm.; C. V., 13.60 ± 0.31 per cent. *O. rubrinervis*: R., 53 to 142 mm.; M., 97.99 ± 0.34 mm.; σ, 12.37 ± 0.24 mm.; C. V., 12.62 ± 0.24 per cent.

lamarckiana is noticeably thicker than that of *O. rubrinervis*. So-called qualitative differences are usually compounds of several measurable characters, any one of which is a wholly unsatisfactory measure of the quality, while only one, two, or several at most of these measurable characters can be dealt with mathematically at a time. Leaf-form is a character of this kind. Not only is the relation of length to breadth important, but the relative position of the widest part of the leaf, the angles of apex and base, and indeed the curvature of the margin at every point from petiole to apex, enter as essential features of leaf-form, and no tangible mathematical expression can be devised to represent it. Confining ourselves to a single measurable character, such as leaf length or breadth, there is still another difficulty which must be met. The leaf is a differentiated organ and there is no exact homology between any two leaves. In a plant which has but few leaves this is strikingly evident, and no leaf on a stem which has ten leaves corresponds exactly to any leaf on another plant of the same species which carries but nine leaves. In plants with numerous leaves, as in the various species of *Onagra*, the degree of differentiation between adjacent leaves is so slight that they may be treated as homotypic without appreciable error, provided as nearly as possible the corresponding parts of the various specimens are used as the source of leaves for the study.

The leaves chosen for this comparative study were taken from a point about two-fifths of the distance from the proximal toward the distal end of the long lateral branches mentioned above as forming a whorl about the base of the main axis. The number of such branches borne by each specimen allowed the collection of a sufficiently large number of leaves by taking them from a very short section of each branch, so that the error due to differentiation is insignificant compared with the "chance" variation. From 20 to 30 leaves were taken from each of 20 specimens of each species, and the width, and the length from the base of the petiole to the apex, were measured in the fresh condition. The length and width were then combined for each leaf in the ratio, width ÷ length, this being the simplest possible approximation to a satisfactory mathematical expression for leaf-form. The curves shown in figs. 6, 7 and 8 compare graphically the results of these measurements. It will be noted on reference to fig. 6 that the length of the leaves in the two species is almost identical, while fig. 7 shows that with respect to the width of leaf they are quite different, though not discontinuous. In consequence of the approximate identity in leaf-length the ratio representing leaf-form corresponds closely with the leaf-width in the character and degree of overlapping of its curves, as will be seen on comparing figs. 7 and 8.

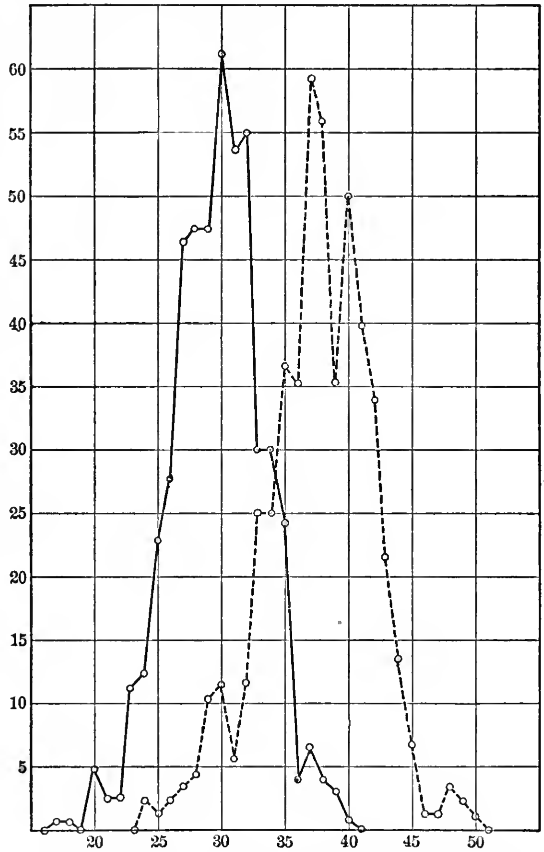


FIG. 7. Variation in leaf-width of *Onagra rubrinervis* and *O. lamarckiana*. *O. rubrinervis*: R., 17 to 40 mm.; M., 29.736 ± 0.098 mm.; σ, 3.589 ± 0.069 mm.; C. V., 12.07 ± 0.23 per cent. *O. lamarckiana*: R., 24 to 50 mm.; M., 37.617 ± 0.137 mm.; σ, 4.248 ± 0.097 mm.; C. V., 11.29 ± 0.26 per cent.

The constants of these curves, which represent the variations of the two populations, each taken as a whole, are as follows:

	Mean.	Standard deviation.	Coefficient of variability.
Variation in length of leaf:	*Millimeters.*	*Millimeters.*	*Per cent.*
Onagra lamarckiana	96.15 ±0.42	13.08 ± 0.30	13.60 ± 0.31
Onagra rubrinervis...........	97.99 ± 0.34	12.37 ± 0.24	12.62 ± 0.24
Variation in width of leaf:			
Onagra lamarckiana	37.617 ± 0.137	4.248 ± 0.097	11.29 ± 0.26
Onagra rubrinervis...........	29.736 ± 0.098	3.589 ± 0.069	12.07 ± 0.23
Variation in the ratio between width and length:	*Per cent.*	*Per cent.*	
Onagra lamarckiana	39.964 ± 0.123	3.811 ± 0.087	9.53 ± 0.22
Onagra rubrinervis...........	30.077 ± 0.084	3.098 ± 0.056	10.30 ± 0.20

Considering the great variability of leaves, it would not be expected that two species so closely related would exhibit complete discontinuity in size of leaf or in the ratio between width and length. It is not so much the extreme types of leaves which give to a plant its characteristic appearance and appeal to the systematist, as the type to which the majority of the leaves belong. The mean values of the various leaf-characters for each individual would much more nearly represent the conditions as seen by the descriptive botanist. For this reason it seemed important to compare the means of length, width, and form of leaves in the individual plants of the two species. The results are represented in figs. 9, 10, and 11, and show that there is approximate identity in the mean length of the leaf, but complete discontinuity in both mean widths and the mean ratios of width to length. The constants were not determined for these curves, as an inspection of the curves together with a statement of the ranges will sufficiently indicate the nature and degree of discontinuity present.

The ranges of mean values of the leaf-characters in the individual plants were as follows:

	Length.	Width.	Width÷length.
	Millimeters.	*Millimeters.*	*Per cent.*
Onagra lamarckiana....................	88.42–112.32	33.74–41.64	34.62–44.41
Onagra rubrinervis......................	86.28–107.15	25.93–32.53	25.30–32.54

It will be noted that the break between the mean values of leaf-width and that between the mean ratios of width to length are slight but sufficient. If a larger number of specimens had been used the range would have been extended somewhat and it is not improbable that they would overlap some, and yet the unsatisfactory character of the ratio of width to length as a measure of leaf-form would not allow us to infer from such overlapping that the two species are not absolutely distinct with respect to the form of the leaves. This fact will become convincingly apparent upon reference to Plate XXII, in which

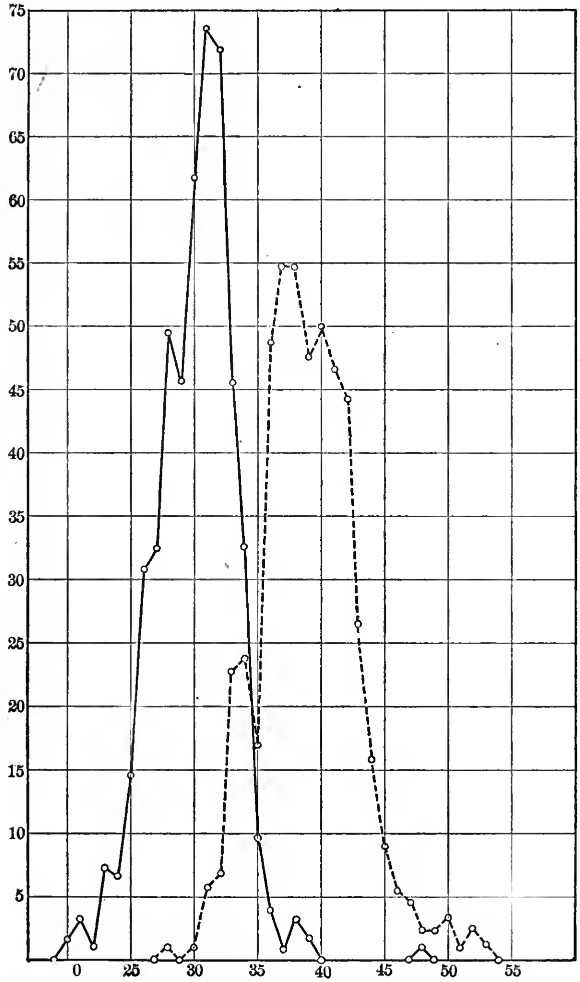


FIG. 8. Variation in ratio of width to length in the leaves of *Onagra rubrinervis* and *O. lamarckiana*, expressed in per cents. *O. rubrinervis:* Range, 20–48; M., 30.077 ± 0.084; σ, 3.098 ± 0.056; C. V., 10.30 ± 0.20 per cent. *O. lamarckiana:* Range, 28–53; M., 39.961 ± 0.123; σ, 3.811 ± 0.087; C. V., 9.53 ± 0.22 per cent.

are contrasted the leaves from the specimen of *O. lamarckiana* having the minimum mean ratio and those of the specimen of *O. rubrinervis* having the maximum mean ratio. According to this statistical measure, these two lots of leaves are the most nearly identical in form of any two plants, belonging to these two species, which were investigated. If to the difference of outlines as shown in the plate could be added the marked crinkling of the *lamarckiana* leaves, a character which disappears on pressing, the discontinuity would be even more obvious.

Interpretation of statistical results.—In reviewing the results of this study one feature stands out prominently, which appears to the writer to be of more fundamental significance than the mere determination of the differences in superficial characters of the several species under consideration. This feature will be apparent upon a comparison of the coefficients of variability throughout.

FIG. 9. Variation in the mean length of leaves in *Onagra rubrinervis* and *O. lamarckiana*. Curve for *O. rubrinervis* shaded with lines rising to the right. Range, *O. rubrinervis*, 86.28 to 107.15 mm.; *O. lamarckiana*, 88.42 to 112.82 mm.

The variability of the mutant is significantly higher than that of *Onagra lamarckiana* in four of the six characters considered. In the number of lateral branches, one of the remaining two characters, the excess in favor of *O. lamarckiana* is far within the probable error, and therefore has no significance. Only in regard to the leaf-length of *O. rubrinervis* is there a significantly higher variability in *O. lamarckiana* than in its mutant, and this is a character in which the mutant presents no material difference from its parent, the difference between the mean lengths of leaves in the two species being only 1.1 mm. in excess of the sum of the probable errors.

Probably related to the same causes which determine this greater variability of the mutants is the fact that there is a lower degree of correlation between the length and breadth of the leaves of *O. rubrinervis* than in *O. lamarckiana*. Correlation tables of these two characters are shown in figs. 12 and 13. The lesser correlation of the former is apparent to the eye in the more scattered distribution of the variates. The coefficients of correlation are as follows: *Onagra lamarckiana*, 0.7916 ± 0.0090; *Onagra rubrinervis*, 0.6604 ± 0.0119. This is simply another way of expressing the fact that the leaf-form of *O. rubrinervis* is more variable than that of its parent-species.

If increased variability and decreased correlation be, as here indicated, a general feature of those characters in which a mutant departs markedly from the parental condition, how is it to be interpreted? It is hinted by Weldon ('02) that these mutants are possibly the result of selection and isolation. No one can deny that there has been selection and isolation in their culture, but it may be questioned whether

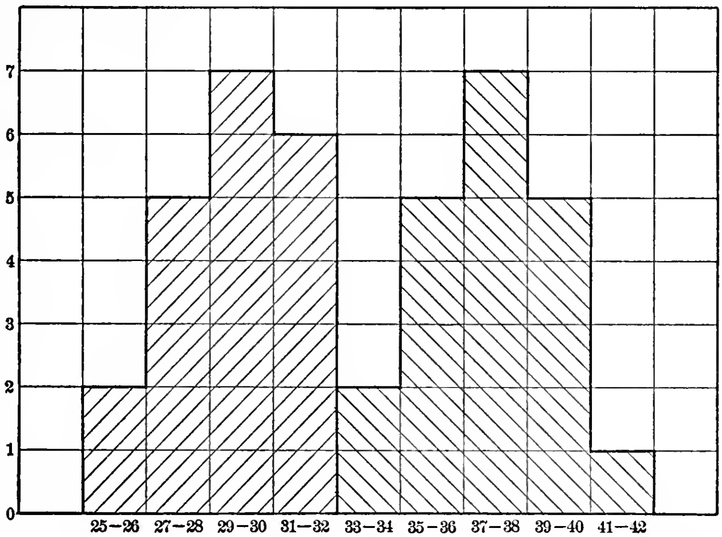


FIG. 10. Variation in the mean width of leaves of *Onagra rubrinervis* and *O. lamarckiana*. Curve for *O. rubrinervis* shaded with lines rising to the right. Range: *O. rubrinervis*, 25.93 to 32.53 mm.; *O. lamarckiana*, 33.74 to 41.64 mm.

these processes have been carried on to such an extent as to explain the peculiar behavior of the mutants as compared with that of an extreme variate. This question will not be satisfactorily answered until a newly arisen mutant shall be subjected to various conditions of cross and self fertilization, and the results are studied statistically. It seems fair to assume that there has been a more discriminating selection in the case of the several mutants than in *O. lamarckiana*. It is therefore something of a surprise, if Weldon's suggestion be true, to find the latter less variable in nearly every character studied. This surprise is due to what may be a false assumption, namely, that selection necessarily operates to lessen variability. Is it not conceivable that the selection of an extreme condition may result in increased variability even after several generations?

The supposed effects of self and cross fertilization can hardly be assumed as of any consequence in this connection, for both species have been self-fertilized during a number of generations. Just what effect this has had upon their variability is not known. De Vries does not think that cross-fertilization, even hybridization, has any appreciable influence on the frequency of origin of a given mutation in a mutating species. (De Vries, 1901, p. 211–212; 1903, p. 425–426.)

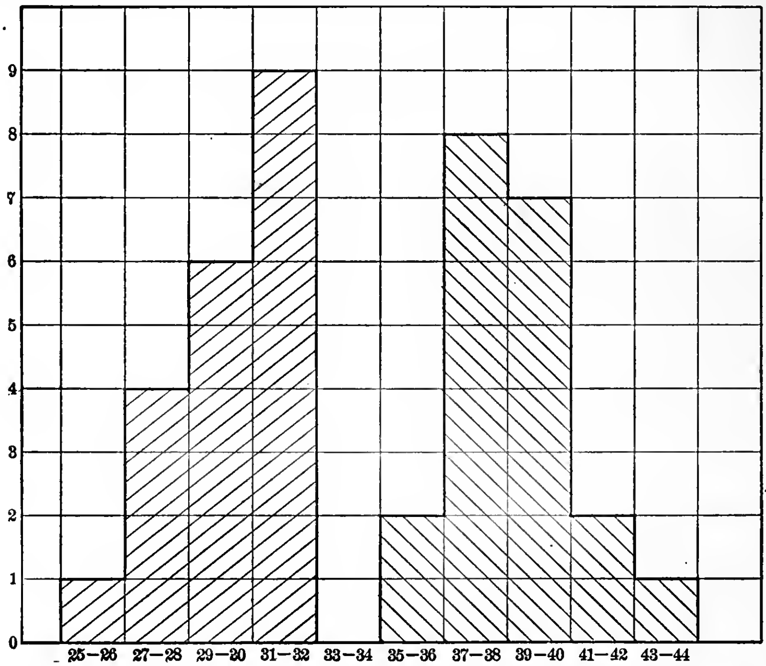


Fig. 11.—Variation in the mean ratio between width and length of leaves in *Onagra rubrinervis* and *O. lamarckiana*. Curve for *O. rubrinervis* shaded with lines rising to the right. Range: *O. rubrinervis*, 25.30 to 32.54 per cent.; *O. lamarckiana*, 34.62 to 44.41 per cent.

Weismann (1892) maintained in his earlier works that all hereditary variation is due to cross-fertilization, but more lately he has withdrawn from this extreme position, and now considers amphimixis "nicht als die eigentliche Wurzel der Variation selbst, denn diese kann unmöglich auf einen blossen Austausch der Ide, sie muss vielmehr auf einer Veränderung der Ide beruhen." He even looks upon cross-fertilization as a process by which the range of variation is lessened, and the variable forms which he thinks may arise at each "Neuanpassung," are condensed into a species and rendered constant. (Weismann, 1902, 2:235.)

Darwin performed a large number of experiments to test the effect of self and cross fertilization, but his object was to determine the advantages or disadvantages as measured by height, productivity, etc., rather than the effect on variability. The number of specimens used by him in each species studied was hardly sufficient to allow conclusions of value regarding variability, but he infers that variations are primarily

		X_2	−9	−8	−7	−6	−5	−4	−3	−2	−1	0	1	2	3	4	5	6	7	8	9	
			50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	
			55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	145	
X_1																						
−12	17					1																1
−11	18			1																		1
−10	19																					0
−9	20			1		1	3	1														6
−8	21		1					1			1											3
−7	22				1	2																3
−6	23						2	2	7	2		1										14
−5	24						1	2	6	2	1	2			1							15
−4	25						3	2	6	6	3	5	2			1						28
−3	26							3	5	6	11	3		1	2	1	1	1				34
−2	27							2	15	11	7	9	6	3	3				1			57
−1	28							3	4	10	8	16	5	9	1	2						58
0	29							1	2	11	19	10	3	6	5	1						58
1	30								1	13	12	10	16	10	8	1	2		1		1	75
2	31				1					2	11	18	21	6	3	1	1	1	1			66
3	32									1	8	17	20	8	7	3	3	1				68
4	33										1	9	9	7	6	3	2					37
5	34											1	6	15	5	7	1	2				37
6	35										2	3	4	13	5	2	1					30
7	36											1		1	3							5
8	37										1	1		1	2	1	2					8
9	38														2		1	2				5
10	39														2	1	1					4
11	40																1					1
			1	2	2	4	9	17	46	64	85	106	92	80	55	24	16	7	3	0	1	614

FIG. 12. Correlation table of length and width of leaf in *Onagra rubrinervis*. Width of leaf subject, length relative; $\rho = 0.6604 \pm 0.0119$.

due to differences of environmental conditions, and that cross-fertilization tends to produce uniformity when these variations are slight, and to increase the diversity when the variations are considerable. These questions need thorough reinvestigation, and their discussion is futile until such investigation is made. (Darwin, 1876, p. 452.)

If the *Onagra* mutants are not the result of selection and isolation, acting within the field of applicability of known laws of variation and heredity, but are really, as they have been called by certain German writers, "correlation-breakers," may not the increased variability and decreased correlation be explained by the newness of the species, which may be assumed to want that perfect adjustment to their surroundings which an older species has acquired through the cumulative effects of long-continued adaptive reactions, aided by natural selection—*i. e.*, by the elimination of the unadapted? This

		X_2	−9	−8	−7	−6	−5	−4	−3	−2	−1	0	1	2	3	4	5	6	7	8	9		
			45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135		
			50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140		
X_1																							
−13	24		1					1															2
−12	25				1																		1
−11	26			1	1																		2
−10	27					1	1		1														3
−9	28					1	1		1		1												4
−8	29						1	2	3	2	1												9
−7	30						1	2	2	2	3												10
−6	31							1			2	2											5
−5	32								2	2	4		2										10
−4	33						1	1	6	3	4	4	3										22
−3	34							1	1	5	8	3	3	1									22
−2	35							1	2	4	9	6	1	4	3	1		1					32
−1	36						1	1	1	2	5	10	4	5	1		1						31
0	37							1		3	11	9	11	8	5	3	1						52
1	38							1		4	3	11	10	16	3	1							49
2	39										3	7	7	8	4	1	1						31
3	40										6	4	9	6	12	3	4						44
4	41											1	8	10	5	5	1	4	1				35
5	42											2	7	9	5	3	2	1			1		30
6	43									1			1	8	4	2	2				1		19
7	44													3		6		2		1			12
8	45													1	1	1	1	2					6
9	46															1							1
10	47																				1		1
11	48																2				1		3
12	49													1					1				2
13	50												1										1
			1	1	2	2	6	12	19	28	60	59	67	80	43	27	15	10	2	1	4		439

FIG. 13. Correlation table of length and width of leaf in *Onagra lamarckiana*. Width of leaf subject, length relative; $\rho = 0.7916 \pm 0.0090$.

question also can be answered only by experimentation and observation continued through a series of years.

It appears highly desirable that the statistical study of *O. lamarckiana* and its mutants should be continued during a series of years, and that similar studies should be made of other mutating and mutant species. The exact status of the mutants with regard to their variability and capacity for self-maintenance may be most conclusively determined by the use of the methods entailed in such work.

GENERAL SUMMARY.

A brief *résumé* of the more salient features of the foregoing paper will serve to emphasize the contributions made to the subject during the course of the experimental work described.

A continuance of the effort to trace the nativity of *O. lamarckiana* has resulted in the discovery of records and specimens that appear fairly conclusive that it is a true and independent species native to America, although the matter is not decided with the finality afforded by living specimens observed in the field. That this species has remained unchanged during a period of a hundred and sixteen years is established beyond doubt, and renders the matter of its nativity of comparatively little importance as to the standing of the mutants derived from it. Perhaps no plant is known in which the purity of the strain has been so critically examined as Lamarck's evening-primrose. Some of the mutants are derivatives, most of which have become separated from the parent-form by the acquisition of new characters, while others are of a retrogressive character. Many of the new unit-characters displayed are not known in any of the other members of the natural group, and thus may not be regarded as degressive acquisitions, or as due to the retraction of a retrogressive step taken in the previous history of the parent-species.

The material used as *O. biennis* in the investigation described in Die Mutationstheorie proves to be a large-flowered species, which has probably been known to many workers as *O. biennis grandiflora.* The uniformly unilateral character of the cross between this species and *O. lamarckiana* (*O. lamarckiana* × *O. biennis grandiflora*) which was an unitypic hybrid very similar to the pollen-parent, a result which led De Vries to the conclusion that *O. lamarckiana* was a direct derivative of the latter, probably by mutation. A re-examination of the evidence, however, recalls that the cross with *muricata* was similarly unilateral to the latter when used as a pollen-parent, and it is evident that too much weight must not be given to the conclusion in question until confirmatory evidence is obtained.

A consideration of the groupings of characters leads to the conclusion that *O. grandiflora* Ait., *O. lamarckiana* Ser., and *O. argillicola* MacKenzie are much more closely related to one another by anatomical characters and physiological traits than to *biennis* or any other member of the genus. Furthermore, the ranges of the three species mentioned appear to be more or less identical, or overlapping.

O. grandiflora Ait. had been seen by but few botanists in a living condition in America, and its place in the American flora had become a matter of much doubt, but field expeditions guided by descriptions from Bartram's travels in 1776 resulted in a rediscovery of the species in a spot not far from the original locality. This found, the confusion which had arisen as to the separation of this species and *O. lamarckiana* is cleared up.

The cultures of the evening-primroses made in the New York Botanical Garden show that two or more elementary species are grouped under some of the specific names as ordinarily accepted. The failure to recognize these elements has resulted in the prevalent opinions as to the wide range of fluctuating variability exhibited by these plants. This is especially true of *O. biennis*, which has enjoyed a reputation for variation not justifiable by systematic and orderly observations made on plants grown under various conditions. One of the forms, apparently typical of the true *O. biennis* now under cultivation, is in a mutative condition, but description of the derivatives is reserved until they have completed a cycle of development.

O. cruciata as it exists at the present time in the cultures in the New York Botanical Garden, and in the Botanical Garden of Amsterdam is composed of three elementary species, which are fairly distinct and without intergrading forms. A careful analysis of the occurrence of the group leads to the inevitable conclusion that one of the forms is in a mutating condition.

It is evident that in the investigations of native species for possible mutating forms, the first and most important task to be completed is that of the resolution of the forms selected into their elementary constituents. Otherwise the seed obtained from plants belonging to separate strains might well give an appearance of variability not justifiable by the facts. Mutations, therefore, may be taken as properly authenticated only when appearing in guarded pedigree-cultures from seeds produced by a known individual, which should be preserved for comparison. Discussions of mutants secured under other conditions may serve an important purpose in offering clues which will be useful in the selection of research material, but can have no direct or actual value as a contribution to the subject.

The evening-primroses of eastern North America, from which probably all of the forms cultivated in Europe are derived, may be divided into two groups—a group including *O. biennis, muricata, oakesiana*, and *cruciata,* in which the flowers are comparatively small, and in which self-pollination is possible and frequent. The second group, including species native to a region farther south, comprises *O. argillicola, O. grandiflora*, and *O. lamarckiana*, in which the flowers are large and the stamens are much shorter than the pistil, a condition which with some accessory structures favors cross-pollination.

The hybrid *O. lamarckiana* × *O. cruciata* consisted of a single type in which the characters of the pollen-parent were largely dominant, although none of them were transmitted unchanged. A singular union of characters was shown in the relative lengths of the stamens and pistils, a feature favoring cross and self fertilization. Some of the flowers bore stamens shorter than the pistils, while in others these organs were of equal length. Many of the modifications of the predominating characters were dependent upon and were modified by the alterations in the general stature of the plant. This hybrid corresponds quite closely with the descriptions of *O. cruciata varia*, a supposed hybrid of *O. cruciata* and *O. muricata* given by De Vries.

The hybrid of *O. lamarckiana* × *O. biennis* was of a pleiotypic character, being composed of four well-differentiated types with no intergrading forms. This result differs widely from that obtained by De Vries in hybrids with *O. biennis grandiflora* and *O. muricata* as the pollen-parent. In both of the last-named instances the result of the cross was a unitypic hybrid closely unilateral to the pollen-parent. In *O. lamarckiana* × *O. biennis* some characters of both parents were transmitted to all of the four types of the hybrid, but the greater number of the active characters were those of the pollen-parent.

A remarkable predisposition or weakness to the attack of a fungal parasite was exhibited by one of the types. The habit of inequality of growth of the laminae resulting in crinkling, characteristic of *lamarckiana,* was transmitted to all individuals of the four types of the hybrid. The symmetrical form of the terminal rosettes of *lamarckiana* was transmitted unchanged to two of the types. No other characters of the pistil-parent were inherited in their entirety, although a number of qualities, approximating those of *lamarckiana* sufficiently to be termed "dominant" by some authors, were seen. Three of the types were goneoclinic to the pollen-parent, while the fourth (No. 2.24) may be fairly taken as furnishing an example of an intermediate form, so far as such estimations may be taken to be of value. The zigzag stem, No. 2.27, is an example of the dominancy of a feature usually latent in the pistil-parent, but exhibited by one of its mutants, *rubrinervis*. The capacity for self-fertilization was dominant in three of the types, but in the fourth a variability between cross and self fertilization was indicated by the varying relative lengths of the stamens and pistils. It is to be noted in this connection that *O. brevistylis,* one of the mutants of *O. lamarckiana,* has a pistil shorter than its stamens, and is therefore adapted to self-fertilization, although no actual physiological predisposition in the matter is found.

The recurrence of known mutants of *O. lamarckiana* was observed. *O. rubrinervis* appeared among the hybrid progeny of *O. lamarckiana* × *O. biennis,* in which imperfect castration had been accomplished and the parental strain appeared in the cultures. It appears therefore that the mutant may be considered as a derivative of the one parent purely, although the possibility is not excluded that it might have come as a hybrid strain, as has been observed by De Vries in several crosses. Better authenticated mutants were seen to arise from seeds obtained from purely fertilized plants of *O. lamarckiana* grown in the botanical garden at Amsterdam in 1901; also from seeds of the same species gathered in the New York Botanical Garden in 1903 after similar precautions had been observed. *O. albida*, *scintillans*, *gigas*, *oblonga*, *subovata*, and *O. elliptica* were found among the mutants, offering evidence of the indubitable occurrence of the mutants in purely fertilized seeds, and also that *O. lamarckiana* has not reached the end of its mutative period. Furthermore, seven forms not definitely assignable to any of the known mutants of this parent were found, showing that the range of the mutability of the species had been extended by unknown causes, but which were included in an environment of cultural conditions extremely favorable to rapid and vigorous growth and development. It seems safe to assume, therefore, that mutation is induced, or at least increased, by favorable, not adverse conditions, though the duration of the experiments has not been sufficient to permit an analysis of this phase of the subject.

O. gigas, the species most recently tested in the mutation-cultures in New York, was seen to agree in stature and habit with the individuals grown in the original locality at Amsterdam. Only about half of the individuals could be brought into bloom during the first season, although it was extended to ten months by special methods of culture—a fact in accord with the behavior of the plant in De Vries's cultures. The constancy of the species also extends to its variability as to the forms of the leaves, an attribute also previously recognized.

The results of the statistical studies show that some of the unit-characters of the mutants have a much greater variability than the corresponding features of the parent-form, and the greater amplitude of the fluctuations is coupled with a decreased correlation.

Thus the coefficient of variability of the height of the shoot of *nanella* is 31.84 ± 3.16 per cent, while that of *lamarckiana* is 5.37 ± 0.44 per cent. The coefficient of variability for the number of branches of *rubrinervis* is 15.0 ± 1.7 per cent, and for the total length of the branches is 43.7 ± 5.1 per cent, and for the ratio between width and length of the leaves is 10.30 ± 0.20 per cent; for the number of branches of *lamarckiana* 15.7 ± 1.7 per cent, for the total length of the branches 20.2 ± 2.2 per cent, and for the ratio between the width and length of the leaves 9.53 ± 0.22 per cent.

The great variability of the mutants does not, however, seem to result in any diminution of the gap that separates them from the parent form, and no movement in this direction has been observed in the long period which has elapsed since the new species came into existence. Thus the heights of *O. nanella* group themselves about the mean value of 22.81 ± 1.02 cm., with a range from 7 to 35 cm., while those of *O. lamarckiana* group themselves about the mean of 88.68 ± 0.55 cm., with a range from 77 to 96 cm. The number of branches per individual of *lamarckiana* ranged from 11 to 25, while that of *rubrinervis* was 34 to 62. The actual discontinuity is somewhat more fully expressed, however, by a comparison of the numerous features which elude measurements to be seen in Plate XXII, in which leaves from the specimens of *lamarckiana* and *rubrinervis* which approached each other most nearly are shown. The actual discontinuity between the retrograde variety, *O. nanella,* and its parent in the leading feature of height of stem is even more marked than the gap between the various unit-characters of *rubrinervis* and *lamarckiana*.

Recurring again to the amplitude of the fluctuations in the mutants, it is to be said that it is doubtless much greater in the leaf-forms of the retrograde variety, *O. nanella*, than in any which have been measured, if the entire mass of foliage is taken into account, since in a certain mid-stage in the rosette it is practically impossible to distinguish it from the parent, although fully distinct as to form and size of the leaves in the very young and very old rosettes. The very range of variation may be in itself a character of the mutants, in which case no reason could be given for its existence, any more than reasons could be given for the existence of any other unit-character. Similar difficulties might be encountered in seeking an explanation of the comparative amplitude of variation of any group of related forms.

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