MUTATIONS OF *OENOTHERA SUAVEOLENS* DESF.

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Besides *Oenothera Lamarckiana* there are quite a number of other species of the Onagra group, which exhibit analogous phenomena of mutability more or less frequently. The condition of *Oe. Lamarckiana* is thereby shown not to be an isolated one, as was formerly believed. All attempts to explain the mutations in this group by means of qualities observed in or assumed for this main species have now to be abandoned, unless they hold good for the explanation of the whole range of new facts. Such is especially the case for the views of those authors, who, by means of numerous unproven auxiliary hypotheses, try to compress the large group of the phenomena of mutation into the narrow limits of Mendelian segregation.

Considered from a broad point of view some mutations are parallel ones, recurring in two or more different species, whereas others are special for one type only. Of course, the parallel mutations claim a prominent place in our theoretical considerations. Among them the *gigas* type is generally described as a progressive change, on account of the doubling of the number of its chromosomes. It has sprung from *Oe. Lamarckiana* first, it arose of late in the cultures of BARTLETT among *Oe. stenomeres* and *Oe. Reynoldsii* and a very beautiful *Oe. grandiflora* mut. *gigas* with 28 chromosomes was observed in 1915 in my garden. Moreover *Oe. biennis* is known to mutate in the same direction, giving *Oe. biennis* mut. *semi-gigas*.[1] No wild species of Onagra with 28 chromosomes is known, and no serious attempt to explain this character on the ground of Mendelian splitting has as yet been made. The claim that the doubling of chromosomes observed in numerous other genera may have occurred in nature after the same sudden manner as in the experiments of BARTLETT and myself, cannot be dismissed.

Other parallel mutations are of a retrogressive nature and due to the

[1] The literature on parallel mutations has been reviewed in my article on the endemic plants of Ceylon and the mutating Oenotheras (DE VRIES 1916 a).

loss or latency of some character, which is active in the parent species. The dwarfs of *Oe. Lamarckiana, Oe. biennis* and *Oe. Reynoldsii* give the best known instances. It seems fully evident that their origin must be the same as that of numerous dwarfish varieties of garden plants. Any explanation must include all of them. The *sulfurea* mutations are evidently due to the disappearance of one of the factors of the bright yellow color of the evening primroses. They appear at once, just as the numerous color varieties of our garden plants have occurred in horticulture. It is of no use to give a separate explanation for them.

Some mutations, parallel as well as special ones, are of a taxonomic nature, repeating characters which are specific in other genera. I shall have to describe in this article an apetalous form of *Oe. suaveolens* and this condition is a specific mark for *Fuchsia procumbens, F. macrantha* and in other instances. Its explanation should be the same in both cases.

This analogy between specific and varietal marks in nature as well as in horticulture on one hand and some of the experimental mutations on the other hand constitutes the link between the theory and the experimental researches. The common aim of all critics in this field is to prove that this analogy does not exist, and that the phenomena observed in our experiments are essentially different from the origin of species and varieties in nature. Therefore it is desirable to broaden the experimental field and to study the mutability in other species, as STOMPS, BARTLETT, GATES, KLEBAHN and others have already done.

It is from this point of view that I have studied the mutability of *Oe. suaveolens* Desf. This form, which is manifestly different from *Oe. grandiflora* Ait., is widely distributed throughout France, where it occurs most profusely in the western departments and in the vicinity of Paris (DE VRIES 1914). I received seeds from the forest of Fontainebleau through the kindness of Prof. L. BLARINGHEM in 1912 and started my race from one of these. In the following year I visited the same spot in his company and assured myself of the purity of the station. At other places in the same forest, *Oe. suaveolens* grows together with *Oe. biennis* and the seeds from these stations contained some hybrids. For my experiments I have only used the plants grown from the pure station near Samois. Later, in 1914, I sowed some seeds, collected by M. EUGÈNE SIMON in the neighborhood of Royan, on the western coast of France near Bordeaux; they produced exactly the same form. The plants from the seeds of Prof. BLARINGHEM proved to be a uniform lot. Two of them were artificially self-fertilized in bags, and yielded two races, which were kept separate in the lapse of the generations and constituted so-called pure lines. They produced essentially the same mutants. As soon as this fact was ascertained one of them was abandoned and thus reduced to the rank of a control experiment. The other pure race yielded the results to be described here.

The original station of my *Oe. suaveolens* is an old orchard along the road from Melun to Fontainebleau situated near the cemetery of Samois (DE VRIES 1914, p. 156). The seeds for my cultures were saved there by Prof. L. BLARINGHEM in 1912. When I visited the place with him in October 1913 we found two or three hundred specimens still flowering and with ripe seeds. They all belonged to the same form; especially no *biennis* and no hybrids were observed, as is so often the case in the open fields of the same neighborhood. The seeds of 1912 yielded only a small culture in my garden in 1913, embracing 22 plants, of which 7 flowered. They were pure *Oe. suaveolens* without mutants and without visible differences. This was the more striking, since seeds from other stations yielded some aberrant individuals, as will be seen later on. I chose one of the most vigorous plants for starting my race, pollinated its flowers myself in small bags and saved the seeds separately. A second plant was dealt with after the same manner in order to have a control, as has already been said. I cultivated three succeeding generations from the main plant in 1914, 1915 and 1916, following always the same principles.[2]

In 1914 the seeds of the initial plant of my race yielded only one mutant, an *Oe. jaculatrix,* among 51 specimens. Besides this one, four typical individuals were self-fertilized and yielded the seeds for the larger cultures of 1915 in which almost all my mutants arose. In this race one-half of the seeds are empty, as in *Oe. Lamarckiana.* This character, however, does not seem to have any influence on the mutability, nor on the result of the crosses (DE VRIES 1916, p. 239). For all the cultures mentioned in this article the seeds have been soaked in water under a pressure of eight atmospheres in order to secure complete germination.

The fourth generation of the pure line, in 1916, was once more a small one with only 109 specimens, of which 59 flowered. It contained four mutants, viz., 3 *lutescens* and one *jaculatrix*. Second generations have been grown for all the types of the mutants, with the exception of *apetala,* which arose only in 1916 and began to flower in September only, too late for successful artificial fertilization.

The mutations, observed in 1914, 1915 and 1916, belonged to the following types (DE VRIES 1916 a, p. 7):

[2] These have been used in all my cultures of Oenothera since 1895, and endowed later on by JOHANNSEN with the appropriate though poetical name of pure lines.

(a) Taxonomic changes: *Oe. suaveolens* mut. *apetala.*

(b) Parallel mutations: *Oe. suaveolens* mut. *lata,* mut. *sulfurea* and mut. *lutescens.* The parallelism is mainly with *Oe. Lamarckiana* in the first case (fig. 1), with *Oe. biennis* in the second, and in the third with *Oe. grandiflora.*

(c) Narrow-leaved types: *Oe.* mut. *fastigiata* and *Oe.* mut. *jaculatrix* (figs. 2 and 3).

Other narrow-leaved types have been grown from seeds of different origin and will be mentioned later on. Narrow-leaved mutations are common in *Oe. Lamarckiana* and have been observed in some other species. Analogous changes constitute, as is well known, a main difficulty in the cultures of *Oe. Lamarckiana* mut. *gigas.*

These new mutations differ from the parent species by one or two striking marks, and show, besides these, some secondary characters, exactly as in the case of the derivatives of *Oe. Lamarckiana* and other species. Their main characteristics are:

(1) *Oe. suaveolens* mut. *apetala.* Flowers without petals, leaves narrow, stature low. But this is a half-race, producing also flowers with one or more petals.

(2) *Oe. suaveolens* mut. *lata.* Stature, flowers and fruits of *Oe. Lamarckiana* mut. *lata,* but smaller. Some flowers with a small supply of pollen, others without fertile pollen grains. An inconstant race, splitting into *lata* and typical *suaveolens* (fig. 1). Number of chromosomes 15.

(3) *Oe. suaveolens* mut. *sulfurea.* Flowers sulfur.

(4) *Oe. suaveolens* mut. *lutescens.* Foliage pale, especially in springtime.

(5) *Oe. suaveolens* mut. *fastigiata.* Side branches and flowers erect; foliage narrow in youth (fig. 2).

(6) *Oe. suaveolens* mut. *jaculatrix.* Foliage very narrow throughout the whole life of the plants (fig. 3).

The four last-named types are constant and uniform from seed, excepting their mutability, which is essentially the same as that of the parent species. To this latter, however, they do not return.

I will now describe these mutants separately and give their origin their offspring and the results of some crosses made with them.

(1) *Oenothera suaveolens* mut. *apetala*

In visiting the different stations of the forest of Fontainebleau in 1913 I observed a specimen with two or three flowers without petals. They were its only open flowers, and no trace of a corolla could be found. It bore some ripe capsules, but from the seeds of these the anomaly has not been repeated, although more than one hundred offspring have flowered and have been observed daily during the two or three months of their blooming period.

In 1916 an apetalous mutant arose among the offspring of one of the self-fertilized individuals of mut. *jaculatrix* of the previous year. It was distinguished by somewhat broader leaves through the whole summer and began to flower in September. Soon afterwards it flowered on twenty or more side branches, giving a profusion of flowers, among which almost daily some were without petals. The majority of the flowers, however, had 1-4 petals, and showed all intermediates between hardly broadened stamens and the normal, oval form of the petals of *Oe. jaculatrix*. On specimens with more than one petal these differences could sometimes be seen in the same flower. Flowers with a normal corolla were rare; they repeated the type of the parent. The apetalous flowers often open only sideways, the sepals remaining united at their tips and covering the self-fertilized stigma.

On Sept. 20 I counted the petals of all the flowers of that day and in the buds for the next day. I found

Petals	Flowers
0	6
1	5
2	11
3	14
4	17
Total	53

There were thus 11 percent of apetalous flowers. This proportion varies, however, on different days. This behavior is the same as in my half races among other genera, as, e.g., in *Trifolium pratense quinquefolium,* which may be rich in leaves with 4-5 leaflets, without ever losing those with 3.

Since I have not as yet cultivated any offspring, the opinion that this individual belonged to a half race is founded only on its own characters. The leaves were narrow, e.g., 1.5 cm broad by a length of 8 cm; the fruits were smaller than in the species, reaching only half their length (20 cm against 40, by a width of 4 mm). Foliage of a dark green. Stature low, the same as in *Oe.* mut. *jaculatrix.*

(2) *Oe. suaveolens* mut. *lata*

Two mutants *lata* (fig. 1) have arisen in 1915 in the third generation of my pure race, from the seeds of two of the four self-fertilized speci-

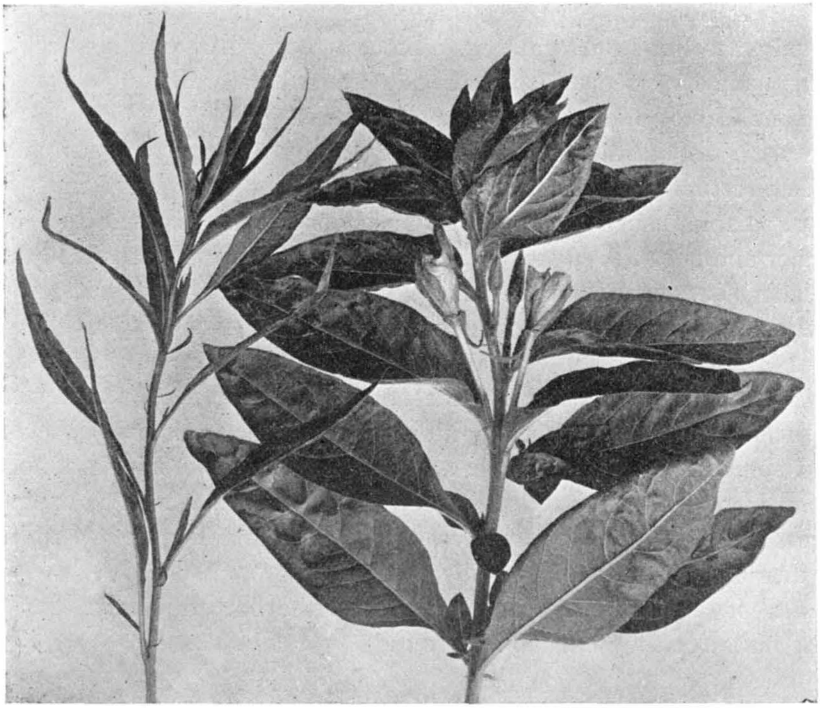

FIGURE 1.—*Oenothera suaveolens* mut. *lata* (broad-leaved) and mut. *jaculatrix*, July 17, 1915. Side branches of mutants of 1915.

mens of the previous year. The cultures embraced 150 seedlings each, giving a percentage of almost 1 percent *lata* (0.7 percent). The two mutants were exactly the same in outward appearance and in hereditary behavior. One of them was weak and did not yield any fertile pollen; the other was very vigorous and richly branched, without pollen during the first two weeks of its flowering, but producing afterwards a sufficient supply for artificial self-fertilization. The female flowers were fecundated with the pollen of one of the typical *suaveolens* individuals of the race and thus I got three sets of seed. From these I had the second generation in 1916; it consisted partly of *lata*, repeating the characters of the parent, partly of pure *suaveolens* and partly of mutants. Among these, the *lutescens* were frequent, the *jaculatrix* rare and no others were observed. I counted the cultures in the beginning of May, when the differences were sharp. They amounted to 54 individuals from the self-fertilized seed and 69 and 70 from the two crossed lots. The percentage composition of the three sets was as follows:

	Vigorous individual		Weak individual	Mean
	Self-fertilized	× *suaveolens*	× *suaveolens*	
lata	30	25	17	24
suaveolens	44	50	55	50
lutescens	26	22	25	25
jaculatrix	0	3	2	1

All the aberrant individuals and some of the type of the species were planted out and controlled until the period of flowering was almost over.

It is interesting to compare these figures with those given in my book on the *Mutation Theory* for the analogous splitting of *Oe. Lamarckiana* mut. *lata*. Here the mean percentage of *lata* is 22 percent, deduced from above 50 cultures. Thus we see that the proportion is as narrowly the same in both types of *lata* as could be expected, and this fact constitutes a strong argument for their exact parallelism, and for the assumption that they are due to the same internal change of the hereditary material. Moreover, we may deduce from our table that the pollen of *Oe. suaveolens* mut. *lata*, if present, has in this respect the same qualities as that of *Oe. suaveolens* and that the mutation changed only the maternal side.

There is still another analogy. *Oe. Lamarckiana* mut. *lata* is more mutable than *Oe. Lamarckiana* itself, producing especially a larger number of the pale and weak form *Oe. albida* (2 percent, DE VRIES 1913, p. 314). In the same way *Oe. suaveolens* mut. *lata* produces far more mut. *lutescens* than *Oe. suaveolens* itself usually does (about 1-2 percent). But here the difference is much larger. Moreover the chromosomes have been counted by my assistant, Mr. C. VAN OVEREEM, in the roots of the young plants of the second generation. The number was fifteen, exactly as in *Oe. Lamarckiana* mut. *lata*.

Already in May, about ten weeks after the sowing, when the seedlings are still small but ready for planting out, the distinguishing marks are clear. The leaves of *lata* are smaller and broader and have a rounded tip and smaller petioles. In June the plants make their stems, which are much lower than those of *suaveolens* of the same age. The foliage becomes less broad, but the tips of the leaves are always more or less rounded. The margin is usually turned upward. All of my plants flowered as annuals, but this is also the case with the parent species.

In August and September the *lata* reached only a height of 60-80 cm, whereas the *suaveolens* reached 1.5 meters and more. They were densely branched and of a dark green. The flowers differed in size on different individuals, the petals measuring ordinarily 2.0-2.5 cm in both directions. The lobes of the stigma were thick and sometimes partly concrescent with the style. In 1916 the largest number of the flowers had some good pollen, but far less than *Oe. suaveolens* itself. The fruits were small, less than half the size of the species, and hairy, with the same form as those of *Oe. Lamarckiana* mut. *lata.*

(3) *Oe. suaveolens* mut. *sulfurea*

The flowers are of a pale yellow, exactly as in *Oe. biennis sulfurea.* Otherwise all the characters are the same as in the species. On one of the stations near Fontainebleau on the border of the forest and at a large distance from that which yielded my race, I observed in 1913 about a dozen of specimens with such pale flowers. One of them had ripe capsules and their seeds yielded in 1914 a culture of 120 flowering plants, of which 53 were *sulfurea* whereas the remaining 67 had the same bright yellow color as the species itself. From this fact we may conclude that the *sulfurea* character was repeated after self-fertilization but was recessive to the bright yellow of the surrounding individuals. Since this behavior is analogous to that of *Oe. biennis sulfurea,* I have repeated the experiment with my own mutant.

This arose in 1915 in the second generation of my pure race from seeds of 1913, in a culture of 1011 flowering specimens from the seeds of the four self-fertilized individuals of 1914. The proportion is seen to be 0.1 percent, whereas *Oe. biennis sulfurea* was produced in my cultures in about 0.3 percent (DE VRIES 1915, p. 189). I fertilized some flowers with their own pollen in bags and brought their pollen partly on castrated flowers of a typical specimen of my race, but had no opportunity for making the reciprocal cross. But since the plant flowered among over one thousand normal specimens, I could be confident that its previous flowers which had been visited by bees would be partly self-fertilized and partly crossed with these, and so I saved their seeds.

The self-fertilized seeds yielded 25 plants, the flowers of which were all of the same pale yellow as in the parent. The cross *Oe. suaveolens* × *suaveolens* mut. *sulfurea* yielded 52 flowering plants, all of which had the pale color of the mutant. There were two mutants *fastigiata* and one mutant *lutescens,* which, however, did not flower. The seeds from the open-pollinated flowers yielded 54 flowering individuals. Among these 46 were *suaveolens* mut. *sulfurea* like the parent, 6 were *suaveolens* with the bright flowers of the species and two were hybrids of the type of *suaveolens* × *Lamarckiana,* and with bright yellow flowers. Evidently the first group was due to self-fertilization, the second to vicinism or to the fecundation by neighbors, and the third to *Lamarckiana* pollen brought by insects from a distance. They strengthen the conclusion that the cross *Oe. suaveolens* mut. *sulfurea* × *Oe. suaveolens* must give the flower color of the latter species.

Thus we have, in regard to the color of the petals:

Oe. suaveolens × *Oe. suaveolens* mut. *sulfurea* = *sulfurea;*
Oe. suaveolens mut. *sulfurea* × *Oe. suaveolens* = *suaveolens.*

All other marks are the same in both parents. The behavior is exactly the same as in the analogous crosses of *Oe. biennis* mut. *sulfurea* (DE VRIES 1913, p. 298). The hybrids are goneoclinic toward the pollen parent, or, as it is called, patroclinic. The parallelism of the two mutants is obviously not limited to the external marks, but holds good also for the hereditary qualities. It is only the pollen, that decides as to the color.

(4) *Oe. suaveolens* mut. *lutescens*

This derivative is easily recognized in early youth by means of the pale, yellowish green color of its foliage. Moreover the leaves are broader and shorter than in the parent species. During the summer time the difference in the color gradually decreases, but that in the form increases. The stature is low, the branches spread more widely, but in weak specimens the stem often remains unbranched. The stems are soft, their wood does not develop sufficiently and this causes many of the weaker specimens to die off before the flowering period or in its beginning. The petals are as long as in the species but much narrower, of an ovate shape. The fruits are thin and small, with few fertile seeds.

In the spring of 1915 I sowed sufficiently large quantities of seed of the four self-fertilized specimens of my race, to determine coefficients of mutation. The seedlings were counted in April, shortly before being planted out. I found:

Parent No.	Seedlings	*lutescens*	Percent
1	700	5	0.7
2	280	7	2.5
3	245	4	1.6
4	175	9	5.1
Totals	1400	25	1.8

Moreover I made the same determination for two seed-bearers of the control experiment, mentioned above, and found among 210 and 420 seedlings 6 and 7 *lutescens,* giving percentages of 2.9 and 1.7. Leaving out the extremes, we may therefore assume the coefficient of mutation to be about 1-3 percent, which is a high figure, compared with those of *Oe. Lamarckiana* and other mutating species.

In 1916 I sowed some seeds of the third generation of my race and found among 120 seedlings 3 *lutescens,* or 2.5 percent. Thus the mutability was seen to be the same in two succeeding generations.

In 1915 I planted out 17 specimens of *lutescens,* rejecting the weaker ones. I succeeded, however, in self-fertilizing only two of them and got the next year 2 and 53 seedlings, all of which repeated the characters of their parent. I also fecundated a third plant with the pollen of the most vigorous individual, but got only 8 seedlings, all of them *lutescens.* Although small, these figures show that this mutant form is constant in its progeny.

The question arose whether this constancy is due to the hereditary qualities of both the male and female gametes, or only to one of them as in the case of our *sulfurea.* For this reason I crossed the *lutescens* with the species, in both directions. I found:

	Seedlings	Pale green	Dark green
Oe. lutescens × *suaveolens*	17	17	0
Oe. suaveolens × *lutescens*	66	4	62

The plants were cultivated until they flowered, but some of them were lost from the reason already given, being too weak. If we assume the four pale green individuals of the second cross to be due to mutated egg cells of the female parent, the experiment shows that the hereditary qualities of the offspring were, for this character, decided by the mother and not by the father. In other words the visible qualities of *lutescens* were handed down through the egg cells.

(5) *Oe. suaveolens* mut. *fastigiata* (fig. 2)

In early youth it is hardly possible to distinguish the two narrow-leaved mutants from one another. In both of them the radical leaves are almost linear with a long, sharp-pointed tip. Even at the time of planting out, in the midst of April, I could not separate the two forms, although some specimens had already somewhat broader leaves. The individuals with the narrowest leaves are very weak from this cause and some of them do not survive the transplanting. For this reason I have preferred to determine the coefficient of mutation jointly for both

FIGURE 2.—*Oenothera suaveolens* mut. *fastigiata,* Aug. 13, 1915, showing the erect position of the flowers. Cf. fig. 4. Mutant of 1915.

of them, and found in the experiments described above for the production of *Oe.* mut. *lutescens* 5, 12, 2, 2, together 21, narrow-leaved mutants among the 1400 plants mentioned. This makes a percentage of 1.5. In the two control experiments I counted 5 and 6 of these mutants, among 630 seedlings, giving 1.6 percent. I planted out 30 specimens, lost three and counted in August, at the time of flowering, 8 *fastigiata* and 19 *jaculatrix*. If we may assume these small experiments as sufficiently reliable, we may conclude that there is a coefficient of mutation of about 0.5 percent for *fastigiata* and of about 1 percent for *jaculatrix*.

Besides these two mutants other narrow-leaved forms of *Oe. suaveolens* occur from time to time. One of them I got through the kindness of Mr. ARMANDO CORTEZAO from Coimbra in Portugal. From these seeds I had a uniform culture in 1914, in which 15 specimens flowered. The leaves were almost as broad as those of the species but more smooth and thin; the whole stature lower. Two other types occurred among seeds sent by Prof. BLARINGHEM from Fontainebleau, but from another station than that which yielded my race. Their leaves were half as broad as those of the species, measuring, e.g., 15 × 2.5 cm as compared with 15 × 5 cm. One of them had large and the other small flowers. It seems that the width of the leaves is as variable in this species as it is in *Oe. Lamarckiana*.

At the time of protruding its stem, *Oe. fastigiata* makes broader leaves, and soon they become as broad as those of the species, but remain shorter. The foliage is denser but of a lighter green and smooth and even at this time the plants cannot be mistaken for *Oe. suaveolens*. Afterwards the branches are erect, running almost parallel to the main stem, whereas in the species they stand out under an angle of 40° or more. The flowers are also erect, and pressed against the stem, making the spikes narrow instead of loose. The fruits are smaller and thicker, measuring, e.g., 25 × 7 mm and not turned outward. The whole plant remains much lower than the species, reaching often less than one meter in height.

I succeeded in saving self-fertilized seeds of 7 specimens of *Oe.* mut. *fastigiata*, but they yielded only a small progeny. Among this, no single specimen recurred to the type of *Oe. suaveolens*, but on the other hand the more common mutations of this species were repeated, and this by almost every parent. All in all I counted 262 seedlings, of which 141 were *fastigiata*, 34 *jaculatrix* and 87 *lutescens*, giving percentages of 54, 13 and 33. Almost all of these plants flowered in August and

September 1916, making a bright show of the three new types. It is very interesting that this mutant should produce the two others in such high proportions, but the same condition prevails among the offspring of *Oe.* mut. *jaculatrix.* Thus we see that *Oe.* mut. *fastigiata* and *Oe.* mut. *jaculatrix* are very mutable derivatives, whereas *Oe.* mut. *lutescens* is almost immutable.

In 1915 I crossed three specimens of my mutant with the species and made one reciprocal cross. The harvest was only a small one, but the results were very clear. I counted the progeny in June and July at the time when the characters were most sharp and found:

	suaveolens	*fastigiata*	*jaculatrix*	*lutescens*	Total
Oe. fastigiata × *suaveolens*	0	11	8	18	37
Oe. fastigiata × *suaveolens*	0	3	3	0	6
Oe. fastigiata × *suaveolens*	0	26	25	14	65
Total	0	40	36	32	108
Oe. suaveolens × *fastigiata*	64	0	1	2	67

The characters of *Oe.* mut. *fastigiata* were handed down through the egg cells and not through the pollen, exactly as in the case of *Oe.* mut. *lutescens.* Moreover the high degree of mutability of *Oe.* mut. *fastigiata* was inherited in the same way, showing a curious correlation between the visible and the invisible characters.

A very conspicuous mark of *Oe.* mut. *fastigiata* is seen in the rosettes of the radical leaves. These are bent downward and pressed with their tips against the soil, whereas in *Oe. suaveolens* and in *Oe.* mut. *jaculatrix* they are straight and erect. This makes the rosettes of *Oe.* mut. *fastigiata* very dense, but those of the two other forms loose.

(6) *Oe. suaveolens* mut. *jaculatrix* (fig. 3)

Throughout the whole evolution the leaves of this form are almost linear, but with a long and sharp tip. They are dark green and in vigorous specimens sufficient for the nourishment of the plant; in weak ones, however, often deficient in this respect. The stature is always very low, seldom exceeding half a meter at the time of flowering. The flowers are small, the petals narrow, leaving gaps between them. Their size is 15 × 20 mm against 30 × 30 mm in the species. The fruits are short and thick and pressed against the axis; they yielded ordinarily only a small supply of seeds. I succeeded in self-fertilizing only three

FIGURE 3.—*Oenothera suaveolens* mut. *jaculatrix,* Aug. 13, 1915. Flowering side branch of second generation.

specimens in 1915; they gave 3, 7 and 6, together 16 offspring, of which 7 were *jaculatrix*, 3 *fastigiata* and 6 *lutescens*. No pure *suaveolens* was seen among them. This indicates constancy of the type combined with a high degree of mutability, just as we have seen in *Oe.* mut. *fastigiata.*

I have not succeeded in making fertile crosses of the mutant with the species.

From the mutant of 1914 I had a second generation of two identical specimens in 1915, but they yielded no fertile seeds after self-fertilization.

CROSSES OF *OE. SUAVEOLENS* WITH ITS NEAREST ALLIES

With the exception of *Oe. Lamarckiana* and *Oe. grandiflora,* the species of Onagra, when crossed with one another, give, as a rule, uniform and constant hybrids. For this reason I have made some crosses of *Oe. suaveolens,* in order to ascertain whether this species would behave in the same manner. The result was, that more or less clearly intermediate hybrids were obtained, which gave a uniform progeny in the second generation, as far as investigated.

I shall limit myself here to the crosses with *Oe. biennis* L., *Oe. syrticola* Bartl., which is the *Oe. muricata* L. of my book on "Gruppenweise Artbildung" and *Oe. biennis Chicago,* a form described in that book, very different in all respects from the *Oe. biennis* of LINNAEUS.

The following crosses were studied:

Cross	Year of crossing	Type of hybrids	Number of specimens	
			F_1	F_2
Oe. biennis × *suaveolens*	1914	*conica*	60	70
Oe. suaveolens × *biennis*	1914, 1915	*biennis*	7+59	80
Oe. syrticola × *suaveolens*	1913	intermediate	80+28+70	64
Oe. suaveolens × *syrticola*	1914	*gracilis*	(70)—1	—
Oe. biennis Chicago × *suaveolens*	1914	intermediate	80	70
Oe. suaveolens × *biennis Chicago*	1913	intermediate	60	—

Besides these I studied two double reciprocal crosses, viz.:

	Cross	Type	Individuals
Oe. (suav. × *bi.)* × *(bi.* × *suav.)*	1915	*suaveolens*	70
Oe. (bi. × *suav.)* × *(suav.* × *bi.)*	1915	*biennis*	80

As already indicated the main result was that these hybrids were uniform and constant in their progeny. No *lutescens* and no other deviating forms occurred among them with the exception of some specimens of *Oe. lutescens* in *Oe. suaveolens* × *biennis,* to be described below.

Oe. biennis L. × *suaveolens*

This hybrid has been described elaborately by GAGNEPAIN (1900) from cultures derived from wild seeds. I made the cross in 1914 between two individuals of my cultures. From the seeds I raised 60 specimens, almost all of which have flowered. They were a uniform lot and grew to a height of about two meters. They strongly resembled the hybrids with other species, in which *Oe. biennis* was the female parent and showed, like these, the type known as *conica*, having weak stems with few branches, a pale green foliage, large flower buds, etc. The leaves were narrow with their margins folded upward, the flowers large with petals of 3 cm and with the stigma surrounded by the anthers, insuring self-fertilization in the buds. They were clearly intermediate between *Oe. suaveolens* and the *conica* type of the hybrids of *biennis* and could easily be recognized as hybrids of these two types.

In 1916 I cultivated a second generation of 70 flowering plants, and compared them through all the time of their development. There was no trace of splitting; all the specimens were alike, resembling those of the previous year.

Oe. suaveolens × *biennis*

On account of the heterogamy of *Oe. biennis* this cross cannot be expected to yield the same hybrids as the reciprocal one. From crosses of other species, in which the pollen of *Oe. biennis* was used, we must expect a prepotency of its influence, and such has been the result of my experiments. I made the cross in 1914, but since I got too small a progeny from it, repeated it in 1915. The first cross gave only 7 offspring, of which 6 were very vigorous and strongly resembled the pollen parent, and one a *lutescens*, which flowered like the *Oe. suaveolens* mut. *lutescens* described above. Of the 6 other hybrids one remained a rosette and 5 flowered in August and September. The cross of 1915 gave 59 offspring, three of which were *lutescens* and flowered. Among the remaining individuals only 18 made a stem and 38 remained throughout the summer in the condition of rosettes.

It is evident that the specimens of *lutescens* in these cultures must be considered as due to egg cells of *Oe. suaveolens* which had mutated in this direction, and thus they constituted hybrids between *Oe.* mut. *lutescens* and *Oe. biennis*. Since I had 4 of them among 66 specimens, their percentage was 6 percent, a relatively high figure, but about the same as in the cross between *Oe. suaveolens* and *Oe.* mut. *lutescens* (4 *lutescens* among 62), as described above. The seeds of these *lutescens* yielded in 1916 a uniform progeny of 37 annual plants, among which 14 flowered in August.

From the seeds of the main type of the hybrids of 1915 I had in 1916 a culture of 80 specimens, which were uniform throughout their whole life, and exactly resembled their parent. There were 70 rosettes and 10 annuals, of which 7 flowered.

The resemblance with *biennis* was so strong as to make a description of the differences very difficult. The radical leaves were, however, narrower and longer, reminding of the marks of the other parent, but had the red mid-veins of *Oe. biennis*. At the time of flowering there were only small differences in the density of the spike and the size and structure of the flowers.

Oe. syrticola × *suaveolens*

I made two crosses in 1913, sowed the seeds of one pair of parents in 1914 and of another in 1915. All the seedlings became annual and more than half of them were left to flower in August and September. They were a uniform lot, showing the bluish green foliage of other hybrids of *Oe. syrticola* and resembling this parent in many points. A high stature with strong stems and almost linear leaves and small flowers reminded of the female parent. But the foliage and especially the spikes were more loose, the leaves broader, the petals larger, etc., showing clearly the influence of the pollen parent. In almost all respects the hybrids were more or less intermediate.

I repeated the cross in 1915 and had in 1916 a first generation of 70 plants, half of which flowered. They were as uniform as the previous lots, and of the same type.

From the cross of 1913 I sowed a second generation (seeds of 1915) in 1916 and got 64 flowering plants. Here a splitting occurred which, however, did not reproduce one of the parental types, but that of the mutant *lutescens*. There were 24, or 37 percent, of these deviating specimens. They were almost exactly like *Oe. suaveolens* mut. *lutescens*. The remaining plants repeated the former generation in all their visible marks. It is evident that this occurrence of specimens of *lutescens* must be ascribed to the mutability of *Oe. suaveolens*, but a detailed explanation would need further experiments.

Oe. suaveolens × *syrticola*

Like the crosses of the pollen of *Oe. syrticola* with other species, the seedlings of this cross were for the greatest part yellow and weak. Among 70 seedlings 58 died from this cause before they could make their first leaf. Of the 12 others, the cotyledons of which had a greenish yellow color, but were still too weak, only one has survived. It had the long and narrow leaves of the type described as *gracilis* for other hybrids of *Oe. syrticola;* the radical ones measured, e.g., 20 × 3 cm. It has not flowered.

Oe. biennis Chicago × *Oe. suaveolens*

The cross of 1914 yielded in the next year 80 offspring, all of which became annual and reached a height of nearly one meter. Half of them were left to flower. They were a uniform group, combining the characters of both parents. The main traits were those of *Oe. biennis Chicago,* but the height was less, the leaves narrower and the spikes less densely covered by the bracts. The flowers were of an intermediate size, having almost the size of those of *Oe. biennis Chicago,* and the internodes of the spikes were also much smaller than in the female parent. They were observed till the end of August.

The seeds of a self-fertilized specimen of 1915 were sown in 1916, the progeny embraced 70 flowering individuals which were uniform and exactly like the previous generation. No trace of dimorphy could be discovered.

Oe. suaveolens × *Oe. biennis Chicago*

Cross of 1913, of which 60 offspring were cultivated in 1914. One half was left to flower and reached a height of 2½ meters at the end of August. They were uniform, resembling the pollen parent, but with white mid-veins in their leaves and relatively large flowers. Length of petals 3 cm. The marks of *Oe. suaveolens* did not come out strongly in the hybrid, but a comparison with *Oe. biennis* × *biennis Chicago* and *Oe. syrticola* × *biennis Chicago* showed the differences in the influence of the female parent clearly. Especially the flower buds resembled those of *Oe. suaveolens.* No second generation has been studied.

Oe. (suaveolens × *biennis)* × *Oe. (biennis* × *suaveolens)*

The cross was made in 1915 between two of the hybrids described above, and a specimen of the *biennis* type of the first group was chosen as female parent. From the rules for the double reciprocal hybrids of *Oe. biennis,* it was to be expected that most of the characters of this species would disappear, viz., all those which are different in their female from their male gametes. Only those marks, which are the same for both sexes, could be repeated in the double reciprocal hybrid.

I cultivated a group of 70 specimens, almost all of which flowered. They were intermediate between the pollen parent *(Oe. biennis* × *suaveolens)* and the pure species *Oe. suaveolens,* showing the disappearance of nearly all the marks of the *biennis* type. In July, when they flowered, the resemblance with *Oe. suaveolens* increased; the plants were almost as high and as richly branched as these, with their large flowers. The petals were 2.5-3 cm long and broad enough to cover one another along their margins.

Oe. (biennis × suaveolens) × Oe. (suaveolens × biennis)

Cross in 1915; 80 specimens were grown in 1916, of which 16 were *lutescens,* showing that the corresponding mutability of *Oe. suaveolens* passed unweakened through the double cross. The *lutescens* flowered in August but of the remaining only 10 have flowered, whereas the others stayed in the condition of rosettes of radical leaves throughout the whole summer. They resembled exactly *Oe. biennis,* and so did the ten flowering plants in all their marks.

From these facts we may conclude that *Oe. suaveolens* is a *heterogamic* species in the same sense as *Oe. biennis,* though perhaps somewhat less completely so.

The appearance of *lutescens* in the described crosses seems to point to some kind of mass mutation in the sense proposed by BARTLETT (1915), since the figures are always relatively high. But it is complicated by the fact, mentioned above, that in the crosses between *lutescens* and *suaveolens* the marks of *lutescens* are handed down through the egg cells and not through the pollen, at least to the first generation of hybrids. Moreover the production of *lutescens* is not a regular, but rather a rare phenomenon. This is shown by the following review of the experiments:

Appearance of Oe. lutescens in crosses of Oe. suaveolens with other species.

Cross	Percentage of *lutescens* in 1st generation	Percentage of *lutescens* in 2nd generation
A. Pollen of *suaveolens*		
biennis × suaveolens	0	0
biennis Chicago × suaveolens	0	0
syrticola × suaveolens	0	37
(suaveolens × biennis) × (biennis × suaveolens)	0	....[1]
B. Egg cells of *suaveolens*		
suaveolens × biennis	6	0[2]
suaveolens × syrticola	0	....
suaveolens × biennis Chicago	0	....
(biennis × suaveolens) × (suaveolens × biennis)	20	....

[1] . . . indicates that the generation has not been cultivated.

[2] No *lutescens* from the *biennis* specimens; the *lutescens* of the first generation were constant from seed.

If it were allowed to apply the ideas of Bartlett (1900) concerning mass mutation to our case, we might assume a stray initial mutation of a sexual cell of *Oe. suaveolens* into *lutescens* and its copulation with a normal gamete. This would give a half-mutant, which after self-fertilization might split into three types. If then we assume the presence of two lethal factors, one linked to the normal and the other to the mutated gametes, this would explain the presence of one-half of empty grains among the seeds, the absence of the two expected constant types and the repeated splitting of the third type.

CROSSES OF *OE. SUAVEOLENS* WITH *OE. LAMARCKIANA*

From all the results of our experiments as well as from the systematical descriptions, we may conclude that *Oe. suaveolens* and *Oe. biennis* are near allies, resembling one another in numerous and prominent characters. From this consideration we might further infer the probability, that *Oe. suaveolens* would behave in the same way in its crosses with *Oe. Lamarckiana* and split this species into the hybrid types *laeta* and *velutina*, if *Oe. suaveolens* is the female parent, but yield uniform hybrids if its pollen is made use of in the cross. On the other hand, the discussion of the possibility of a mass mutation, just given, would lead to the expectation of the appearance of mutants of the type *lutescens*, even as in the case of *Oe. suaveolens* × *biennis* described above. As a matter of fact this mutability occurred in both the reciprocal crosses, as will be shown below. In the crosses with other species the normal gametes would yield the intermediate hybrids, whereas the *lutescens* gametes should give *lutescens* hybrids. But why these should occur so rarely and fail in so many of our experiments, remains to be investigated. In crosses with *Oe. Lamarckiana* four types of hybrids would thus have to be expected, of which two might be externally identical as in the case of *Oe. grandiflora* × *Oe. Lamarckiana*. This would explain the occurrence of *laeta*, *velutina* and *lutescens* in the proportion of 2 : 1 : 1. A large degree of likeness in the behavior of *Oe. suaveolens* to that of *Oe. Lamarckiana* and *Oe. grandiflora* would thus be revealed. But since the aim of my experiments was essentially the study of the mutability of *Oe. suaveolens* and not that of its hybrids, I have postponed these questions to a later opportunity.

Oe. Lamarckiana × *suaveolens*

I made this cross in 1914 and cultivated 59 offspring in 1915, all of which became annual. When they reached a height of half a meter in

July and proved uniform with the exception of the *lutescens,* I threw away one half of them and left the others to flower in August and September. I counted 46 normal specimens and 13 *lutescens,* giving a percentage of 22 for the latter. The *lutescens* resembled the hybrids of the same name, described above, and the typical specimens were hardly to be distinguished from the *laeta* of the reciprocal cross. I self-fertilized two specimens of the main type and one of the other.

From the seeds of the typical ones I had 64 and 66 offspring, almost all of which flowered in August 1916. They were uniform and repeated the characters of their parents. There was, however, a large degree of fluctuating variability in the foliage and the petals also showed differences in size, ranging from 2-5 cm in length. Besides these I found, in the beginning of July, 5 and 3 weak specimens of *lutescens,* giving a percentage of 6 percent, which is much smaller than in the previous generation.

The seeds of the *lutescens* of 1915 yielded a uniform progeny of 70 specimens, which were intermediate between typical *Oe. suaveolens* mut. *lutescens* and *Oe. Lamarckiana,* having somewhat narrower leaves than the former but large flower buds of a yellowish green. There was much fluctuating variability among them or perhaps a splitting of minor marks, which I have not studied.

Setting these aside, the main result of our experiment is that the hybrids showed only two types: (1) a typical intermediate one, and (2) that of one of the mutants of *Oe. suaveolens.* In *Oe. Lamarckiana* × *biennis* no such mutants appear, and the progeny of the cross is uniform and constant in the next generation.

Oe. suaveolens × *Lamarckiana*

The cross of 1914 yielded 61 offspring, which clearly constituted three types. Two of them resembled those of the reciprocal cross, and the third was evidently a *velutina,* having the typical marks of *Oe. (biennis* × *Lamarckiana) velutina* combined with those of *Oe. suaveolens.* There were 58 percent of typical specimens or *laeta,* 21 percent *lutescens* and 21 percent *velutina,* pointing to a proportion of 2 : 1 : 1. I repeated the cross in 1915 and cultivated from it 66 hybrids in 1916. In August I found among them 81 percent *laeta,* 9 percent *lutescens* and 10 percent *velutina.*

In 1915 I self-fertilized three specimens of *laeta,* one of *lutescens* and one of *velutina,* in order to test their constancy. I had 70 plants of each of the four former lots and 32 of the *velutina.* These cultures proved to be uniform and like their parents in so far as no trace of a repetition of the splitting of the first generation was seen among them. On the other hand the *laeta* are far from being a wholly uniform group, showing many secondary types, in the characters of size and form of the leaves, hairiness, density of spike, color of the stems, size of the flowers and so on. But these I have not subjected to any study, although I observed the same phenomena in corresponding crosses of some derivatives of *Oe. Lamarckiana.* Probably they will afterwards yield the material for an analysis of the characters of *Oe. suaveolens.* Among the *laeta* the production of *lutescens* was repeated but there were only $1 + 0 + 3 = 4$ of this type among $3 \times 70 = 210$ plants.

The progeny of the *lutescens* were uniform, almost yellow in their first youth but becoming more green in the course of the summer. They made their stems without first producing rosettes of radical leaves, just as the *Oe.* mut. *lutescens* usually does, and had the broad foliage and yellowish flower buds characteristic of this type. The offspring of the *velutina* of 1915 constituted a uniform type with almost linear leaves, conical flower buds and a striking hairiness of all the organs, repeating thereby the characters of the seed-bearer, and resembling almost exactly the *velutina* of the crosses *Oe. biennis* × *Lamarckiana* and *Oe. syrticola* × *Lamarckiana.* In the midst of August I had 24 large flowering specimens and 8 weak rosettes with very long and narrow radical leaves. I compared them with the *velutina,* which I cultivated at the same time from seeds of my second cross, and found them identical. Moreover I got the same types from the corresponding cross of *Oe. suaveolens* × *Oe. Lamarckiana* mut. *nanella,* to be described elsewhere. See fig. 4.

In the flowering specimens the petals were 4 cm long, the stigma elevated above the anthers, the flower buds thick (1 cm), the fruits more or less conical but thin, 3 cm long. All organs were covered with the gray hairs, which are so characteristic of the *velutina* type in general. Leaves narrow, e.g., 4×13 cm. The plants reached a height of about 2 meters and were richly branched.

Apart from the appearance of specimens of mut. *lutescens* and the variability in minor marks, we may conclude that *Oe. suaveolens* behaves like *Oe. biennis* in its crosses with *Oe. Lamarckiana.*

Oe. Lamarckiana mut. *lata* × *Oe. suaveolens*

The conclusion just reached may be strengthened by a study of this cross. In its crosses with *Oe. Lamarckiana* this *lata* produces about 25 percent, but in those with *Oe. biennis* about 50 percent of specimens

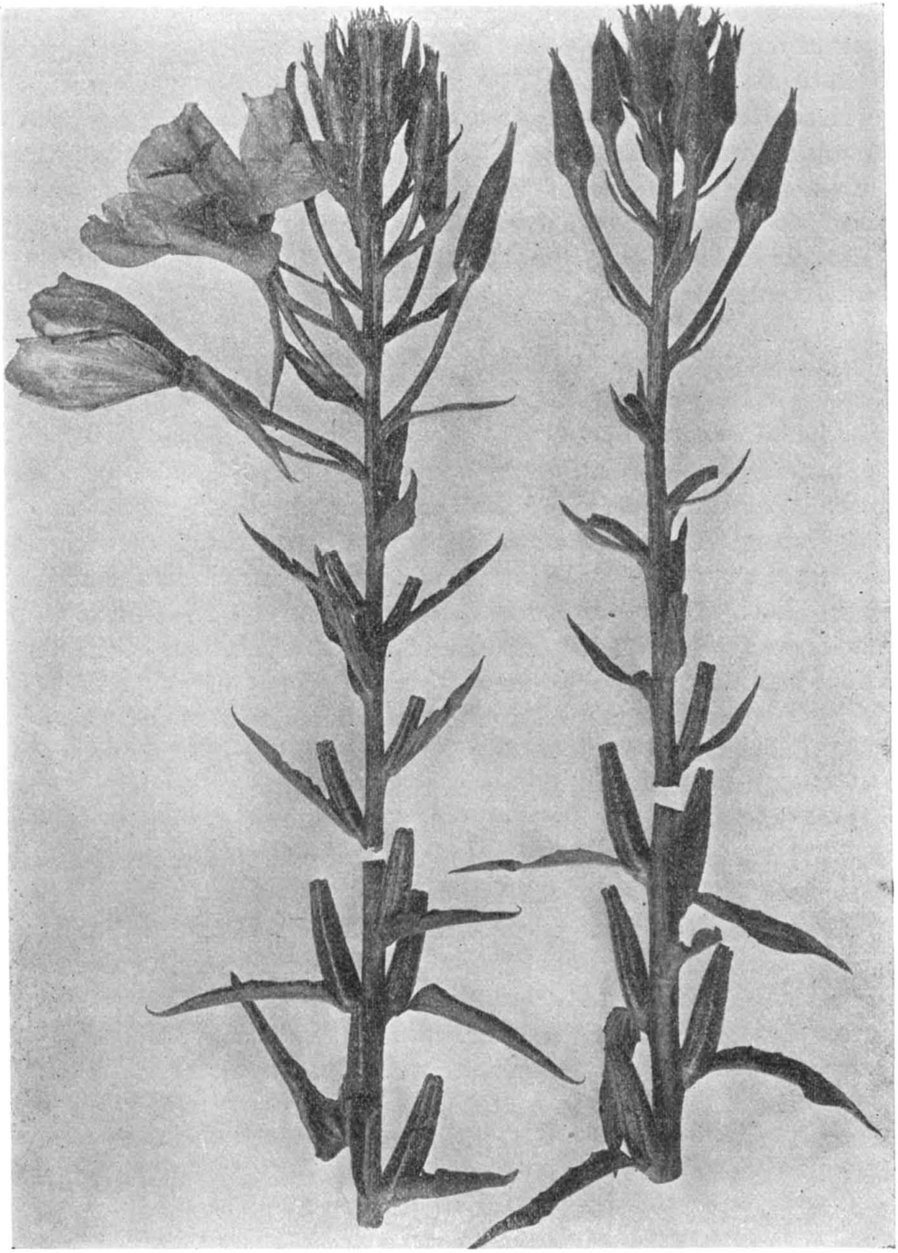

FIGURE 4.—*Oenothera suaveolens* × *Oe. Lamarckiana nanella*, Aug. 14, 1915. Twin hybrids of the first generation after crossing. To the left a flowering spike of *laeta*, to the right a spike of *velutina*, deprived of its flowers. Bases of spikes with almost ripe fruits below the tops.

of the *lata* type (DE VRIES 1913, p. 251). I fertilized two specimens of a culture of *Oe. Lamarckiana* mut. *lata* in the midst of July 1913 and repeated the cross at the end of August on the same spikes, using the pollen of the same specimens of *Oe. suaveolens.*

The four cultures consisted in 1914 of the same two types, of which one was an intermediate between *lata* and *suaveolens,* showing the characters of the first very clearly, whereas the other was the same as the hybrid between *Oe. Lamarckiana* and *Oe. suaveolens.* I sowed the seeds of the four lots in February and counted the young plants in June, when the differences were clear and sharp. I found:

	Specimens	% *lata*
No. 1, base of spike	109	46
No. 1, top of spike	113	46
No. 2, base of spike	118	41
No. 3, top of spike	114	40

I cultivated some *lata* and some *suaveolens*-like individuals until September. The latter maintained their resemblance to *Oe. Lamarckiana* × *suaveolens* in all respects, as was to be expected, whereas the first developed the characters of the mutant *Oe. suaveolens* mut. *lata,* described above. Their stature was low, exceeding one meter only in September, their leaves were broad and dark green, with rounded tops, being intermediate between the leaves of the two parent forms. The stigmata were thick and unequally developed in the same manner as is so characteristic of *Oe. Lamarckiana* mut. *lata* but in a lesser degree, and in some instances with the same broadening of the upper part of the style. The anthers were mostly dry, without fertile pollen, but in many flowers I could find a sufficient supply of this powder, almost as in the mutant.

No *lutescens* appeared in these cultures.

The figures given show no difference between the base and the top of the spike, but a clear, though small one between the two sets of parents. This indicates a dependency on the individual vigor of the plants. Leaving aside these minor points, the main result indicates a complete analogy with the cross between *Oe. Lamarckiana* mut. *lata* and *Oe. biennis.*

Summarizing the figures of these experiments, we get the following table:

Crosses between Oe. suaveolens and Oe. Lamarckiana.

A. First generation

Cross	Year	Number of plants	Percent *lutescens*
Oe. Lamarckiana × *suaveolens*	1914	59	22
Oe. suaveolens × *Lamarckiana*	1914	61	21
Oe. suaveolens × *Lamarckiana*	1915	66	9
Oe. mut. *lata* × *suaveolens*	1913	454	0

B. Second generation

	Number of plants	Percent *lutescens*
Oe. (Lamarckiana × suaveolens) typica	130	6
Oe. (suaveolens × Lamarckiana) *laeta* (58%)	210	2
Oe. (suaveolens × Lamarckiana) *velutina* (21%)	70	0
Oe. (suaveolens × Lamarckiana) *lutescens* (21%)	70	uniform
Oe. (Lamarckiana × suaveolens) lutescens	70	uniform

The splitting into three types in the cross *Oe. suaveolens* × *Lamarckiana* is obviously analogous to that of the first generation of *Oe. Lamarckiana* × *Oe. grandiflora* and points to a mass mutation as discussed above.

SUMMARY

1. *Oenothera suaveolens* Desf. has produced in my cultures, since 1912, half a dozen of different mutants, some of which are the same as those observed in allied species. The coefficients of these changes were 1-3 percent or lower. These phenomena happen in the same manner as in the other mutating species of Onagra and evidently depend upon the same internal and external causes.

2. The mutations, parallel to those of related species, were called *lata, sulfurea* and *lutescens*. The first occurs also in *Oe. Lamarckiana,* the second in *Oe. biennis* and the third in *Oe. grandiflora.* Their coefficients of mutation were 0.7, 0.1 and 1-3 percent.

3. Among the special mutations one is of a taxonomic nature, viz., *Oe. suaveolens* mut. *apetala,* with flowers without petals. This character is specific in some species of the allied genus Fuchsia. The mutant, however, had the characteristics of a half-race, having also flowers with four petals besides all the intermediates.

4. Two narrow-leaved types occurred: *Oe.* mut. *fastigiata* with erect branches, and *Oe.* mut. *jaculatrix* with almost linear leaves. Their coefficients of mutation were 0.5 and 1 percent.

5. The mutant *lata* is an inconstant type, splitting into about 25 percent *lata* and 50 percent *suaveolens,* and producing besides these as high as 25 percent *lutescens.* It repeats almost all the special characters of *Oe. Lamarckiana* mut. *lata.*

6. *Oe.* mut. *sulfurea* and mut. *lutescens* are constant types, but their characters are visibly inherited in the first generation through the gametes of one sex only.

7. *Oe.* mut. *fastigiata* and mut. *jaculatrix* are also constant, in so far

as they do not return to *Oe. suaveolens,* but their progeny is very rich in mutants of the alternating narrow-leaved type and of mut. *lutescens.*

8. Crosses of *Oe. suaveolens* with allied species (*Oe. biennis, Oe. syrticola* and *Oe. biennis Chicago*) give intermediate and constant hybrids, which are often different for the reciprocal combinations. Double reciprocal crosses between this species and *Oe. biennis* resemble the peripheral parent in the formula, with a more or less complete exclusion of the central one. They run parallel in this respect to the double reciprocals between *Oe. biennis* and *Oe. syrticola.*

9. Crosses with *Oe. Lamarckiana* for which *Oe. suaveolens* yields the pollen, give a uniform and constant progeny of an intermediate type. excepting the occurrence of mutants of the type of *lutescens.* The same hybrids result from the cross with *Oe. Lamarckiana nanella* and *Oe. Lamarckiana lata,* but in the latter case 40-46 percent specimens with the type of *lata* arose. In these cases the behavior of *Oe. suaveolens* is the same as that of *Oe. biennis.*

10. The fecundation of *Oe. suaveolens* by *Oe. Lamarckiana* yields the twin hybrids *laeta* and *velutina,* besides mutants of the *lutescens* type. The *laeta* and *velutina* each repeat their own type in the next generation.

11. From all these crosses we may infer that many prominent hereditary qualities are the same or almost the same for *Oe. suaveolens* and *Oe. biennis.* But in respect to the production of mutants they are, as we have seen, largely different, the main difference being the production of *Oe. lutescens* in percentage figures which indicate a secondary or mass mutation. It seems probable that this latter is connected with the presence of about one-half of empty grains among the seeds.

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