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THE DISTRIBUTION OF THE FLORA IN THE ALPINE ZONE.[1]

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[WITH TWO TEXT-FIGS.]

THE botanising hitherto done in the Alps gives us but very imperfect information on the local distribution of the alpine flora. Attention has been specially directed to rare plants, whose least localities are recorded, while the common species are often neglected. But from the standpoint of the factors which regulate distribution the common species are the most important. The rare species of the alpine flora, those which appear only in a few isolated stations, sometimes only in a single one, are usually either species with a very sporadic general distribution, or they are endemic species, or finally they may be "glacial relicts." All these categories are of great interest from the standpoint of the history of floras; their presence in the stations which they now occupy is explained not only by the ecological conditions they find in these stations, but also by historical causes, and especially by the conditions of post-glacial immigration.

[1] This article is translated from the French original (which appeared in the *Revue générale des Sciences*, 15th December, 1907, pp. 961—967) and published in THE NEW PHYTOLOGIST (by kind permission of M. Olivier, the editor of the *Revue générale*) at Professor Jaccard's request. The Editor acceded to this request the more readily, inasmuch as the statistical method employed by Professor Jaccard appears worthy of being tested over a wider range of vegetation. With suitable development, these and similar statistical methods promise to form an important means of connecting the study of floristic distribution with that of the determination and distribution of units of vegetation.—EDITOR, NEW PHYT.

Is the same true of the common species which form the basis of the vegetation of the Alps?

In order to reply to this question I have considered, in an alpine district of fair size, various natural sub-divisions, presenting, besides numerous resemblances in their ecological conditions (*i.e.* conditions dependent on soil and climate), a few characteristic differences; and I have sought to determine, by comparison, the influence of these resemblances and differences on the composition of the flora.

I.

My researches have been chiefly carried out on three districts about fifty kilometres distant from one another. These are:—(1) The upper basin of the Sallanche and of the Trient, (2) the *massif* of the Wildhorn, (3) the upper basin of the Dranses.

From the topographical point of view these three districts present great analogies: all three contain high summits covered with snow and ice: all three, except the northern slope of the Wildhorn, open to the valley of the Rhone: finally, owing to their proximity, the meteorological conditions appear very similar.

From the petrological standpoint, on the other hand, they are sharply dissimilar. The *massif* of the Wildhorn is essentially calcareous; the basin of the Trient includes both gneiss and limestone; while the basin of the Dranses presents the most various substrata, including the Casana schists, carboniferous schists, Antigorio gneiss, primitive rocks of the Mont Blanc series, calciferous triassic schists, etc.

Each of the three separate districts is sub-divided into parallel valleys, forming as many comparable sub-districts.

In making a complete list of all the species of plants met with in the alpine and niveal zones of each of these three districts, the following approximate numbers were obtained:—

1.	Wildhorn (W) -	350 species.
2.	Trient (T) -	470 „
3.	Dranses (D) -	600 „
4.	The three together -	660 „

Of the 600 species of the basin of the Dranses, about 60 have not yet been met with in the other two districts: again of the 470 species of the Trient basin, about 60 are absent from D and W: finally about 30 species noted in W are absent from T and D.

In each case at least half the species noted in one of the three districts, and absent from the two others, are common sub-alpine or woodland species, whose presence in one of the three districts to the exclusion of the two others is explained by the particular topographical configuration and by the greater or less continuity of the districts with the adjoining sub-alpine and lower zones.

About thirty are fairly common species in the Valaisian Alps, but are sometimes absent from considerable stretches of country, though it is impossible to explain such absence in one or another of the three districts by any special ecological conditions.

Finally, of the 660 species of the three districts, scarcely 40 are really *rare*, or are strictly localised either in the Alps composed of crystalline rocks (Pennine Alps and the *massif* of Mont Blanc), or in the calcareous Alps (western portion of the Bernese chain).

It seems then that the great majority of species (more than nine-tenths) might be met with in all three districts. But, as the annexed table shows, this is far from being the case.

Total numbers of species occurring in pairs of districts.

Trient and Dranses together	645
Wildhorn and Trient ,,	525
Wildhorn and Dranses ,,	647

Species common to two districts.		Percentage common to two districts.
Trient and Dranses	390	60
Wildhorn and Trient	295	56
Wildhorn and Dranses	327	50

Each of the districts W, T and D thus possesses, besides the rare species mentioned above, a considerable number of species which are absent from *one* of the other two.

The ratio of the number of species common to two districts (T and D for example) to the total number of species collected in the two districts together (T + D), *i.e.*, their *coefficient of community*,[1] varies in the three cases given in the table between 50 and 60 per cent.

Thus in spite of their proximity and the similarity of their ecological conditions, the florulæ of our three districts possess very different compositions, and the comparative study of these

[1] $\dfrac{\text{Number of species common to the two districts}}{\text{Total number of species in the two districts}} \times 100$

florulæ shows that a great number of common species with a distribution through the entire chain of the Central Alps are actually absent over considerable stretches of country, while the conditions apparently capable of assuring their existence are everywhere realised.

We are thus led to ask whether the commonest species possess, like the rare species, a discontinuous distribution within the area of their occurrence.

In order to try and find a solution of this problem, a comparison was made, not of all the species of the districts W, T and D, but only of those constituting a single type of formation. For this purpose the alpine meadow above 1900 metres was chosen, and localities of equal area were selected, as closely similar as possible in respect of declivity, humidity and the general state of development of the flora.

The following is a list of these localities, with exposure, nature of substratum, and number of species collected in each case. The areas, averaging 3 to 4 hectares (say 7 to 10 acres each), the slope (20—30°) and altitude (between 1900 and 2400 metres), differ very slightly in the different cases.

	Locality.	Substratum.	Exposure.	Number of Species
1.	Plan la chaud, Val Ferret - -	Calciferous Triassic schists - -	West	101
2.	La Peulaz, Val Ferret - -	,, ,,	East	107
3.	South slope of Col Ferret - -	Lower Jurassic (with quartzites) - -	South-West	106
4.	Alpes des Tsesse-taz, Combe de La, Entremont - -	Dolomite - -	East	99
5.	Alpages des Vingt-Huit, Bagnes -	Calciferous Triassic schists and Casana schists - - -	West	140
6.	Barberine, Trient	Lower Jurassic limestone - -	South-West	114
7.	Luisin, Emaney -	Gneiss - - -	West	173
8.	Gagnerie, Salanfe	Upper Jurassic limestone - -	West	147
9.	Iffigen, Wildhorn	Cretaceous & nummulitic limestone	South-East	147
10.	Küh-Dungel, Wildhorn - - -	,, ,,	North-East	150

From the standpoint of floristic richness these ten localities may be divided into two groups, five possessing about 100 to 114 species, the other five about 140 to 173.

But it is easy to satisfy oneself that the coefficients of community of different pairs do not depend on the number of species. The pairs of localities belonging to the first group (1—4, 6) possess in round numbers the following coefficients;—

1 and 2 ...	35%	2 and 3 ...	36%	3 and 4 ...	39%
1 and 3 ...	40	2 and 4 ...	26	3 and 6 ...	27
1 and 4 ...	40	2 and 6 ...	30	4 and 6 ...	27
1 and 6 ...	21				

Average 32·1%

The coefficients of the pairs of the second group are:—

5 and 7 ...	30%	7 and 8 ...	26%	8 and 9 ...	31%
5 and 8 ...	38	7 and 9 ...	27	8 and 10 ...	38
5 and 9 ...	36	7 and 10 ...	34	9 and 10 ...	42
5 and 10 ...	22				

Average 32·4%

If the whole ten localities are taken in pairs the mean coefficient of the 45 pairs so obtained is also about 32% (actually 31·5%).

The lowest coefficient is 21% (between 1 with 101 species and 7 with 103): the highest coefficients 39%, between 4 (99 species) and 9 (147 species): 40% between 1 (101 species) and 4 (99 species); and 42% between 9 (147 species) and 10 (150 species).

But if the values of the coefficients of community do not depend on the floristic richness of the localities compared, they must have a relation with ecological characters of localities, though it is often impossible to observe any strict proportion between the degree of ecological resemblance or dissimilarity and the value of the coefficients.

II.

As a result of the comparison in pairs of our ten localities we have found that on the average a third of the species growing in two localities taken together are common to the two.

In face of the relative constancy of this coefficient of community we might suppose the existence of a group of ubiquitous species which are found in every locality and constitute a sort of permanent nucleus of community. *But this is not the case.* Of 370 species collected in our ten localities taken together, 108, or almost a third, have only been noted in a single locality, and 73, or about a fifth, in only two localities. There are only 10% of the total number common to four localities, 3 to 4% common to six localites, and 1 to 2% common to eight localities. Three species only, *Gentiana excisa*, *Homogyne alpina* and *Nigritella angustifolia*, or less than 1%. have been collected in each of the ten localities. And meanwhile, what naturalist does not carry away from the Alps the impression that the *majority* of the species of the alpine meadows and swards are found everywhere ? Close observation, supplemented by careful statistical analysis, is necessary to convince us of the infinitely various floristic composition of the alpine meadow, and that different stations, in spite of physiognomic uniformity, are in reality covered by very different plant associations. The fact is that besides the obvious ecological variations, such as those of the degree of humidity, of slope, of exposure, and of the chemical nature of the soil—variations which betray themselves in the plant covering by a comparatively small number of *formations* (meadows, swards, rocks, screes, bogs, etc.)—there exist many slighter variations of habitat, more difficult to appreciate, which, in a station apparently uniform, create an infinite diversity. The substratum especially, even the most homogenous from the geological standpoint, may present in its chemical composition, in its structure, in its compactness, and in the thermal and hygroscopic properties which depend upon these characters, numerous differences which have their effect on floristic composition.

In this respect nothing is more instructive than the flora of the summits of the southern Jura, of which the uppermost zone, formed entirely of Kimmeridgian and Sequanian limestones, with some outcrops of Argovian, possesses a remarkable petrographical uniformity. All the summits are of about the same altitude, between 1671 and 1723 metres: they are all situated on the southern ridge of the Jura and present the greatest similarity in regard to topographical conditions, especially in the direction, force and frequency of the winds. Everywhere we have the same turf-covered ridges, the same escarpments of white limetone, the same dryness, accentuated by the same winds. And everywhere, apart from some scattered Alpine and Mediterranean types, there is a depressing floristic uniformity.

Yet in spite of this extraordinary apparent uniformity, any two localities of approximately a hectare (say 2 acres), and each separated by from two to ten kilometres, possess in common only 40 to 50% of the species collected on the two together.

The results obtained by comparing adjacent areas, each one square metre in extent, from one and the same meadow, are even more surprising. In a sub-alpine meadow at an altitude of 1,200 metres in the valley of the Ormonts (Alpes Vaudoises), where the species of 52 different square metres, each showing an average of 25 to 30 species, were enumerated, the proportion of species common to two adjacent square metres generally varied between 60 and 75%. Thus on two square metres, A and B, peopled by 38 species, only 25, or 66% were common to A and B.

The dominant conclusion which emerges from the facts given above, is *the infinite diversity of the alpine flora, and of the associations which constitute it*, a diversity so great that probably no two square metres of vegetation in the whole chain of the Alps, possess exactly the same floristic composition.

This diversity, which seems at first to escape all rule, really presents elements of regularity, which we have now to establish.

III.

Among the species which make up a plant covering, some are frequent, others less so, others again are very infrequent. These different degrees of frequency may be expressed by the four terms, *rare*, *somewhat rare*, *somewhat common* and *common*. These terms, as they are generally applied in the floras, are partly subjective, according to the degree to which the country to which they are applied has been explored, and to the judgment of the individual botanist who uses them.

It is however possible to give such terms a purely objective value. If an area be divided into four equal and comparable portions, those species found in only one may be called rare, those found in two, somewhat rare, those found in three, somewhat common, and those found in all four, common. Using this principle, all degrees of frequency that may be desired can be determined by increasing the number of divisions of the given area.

This method has been carried out for the 370 species collected on the 10 alpine meadows mentioned above, and for the 240 species noted on 12 localities of the pastures on the highest zone of the southern Jura.

For the former we obtain the following degrees of frequency expressed in percentages :—

Species noted in	1	locality	...	29%
,, ,,	2	,,	...	20
,, ,,	3	,,	...	12
,, ,,	4	,,	...	9
,, ,,	5	,,	...	8
,, ,,	6	,,	...	5
,, ,,	7	,,	...	6
,, ,,	8	,,	...	5
,, ,,	9	,,	...	4·5
,, ,,	10	,,	...	0·9

Fig. 1 shows the character of the curve corresponding to these figures (dotted line B). If the ten localities are grouped according to four degrees of frequency the following figures given below are obtained, and these give, in the graph, an almost straight line (B″) in which the irregularities of B disappear. The line B′ corresponds to five degrees of frequency.

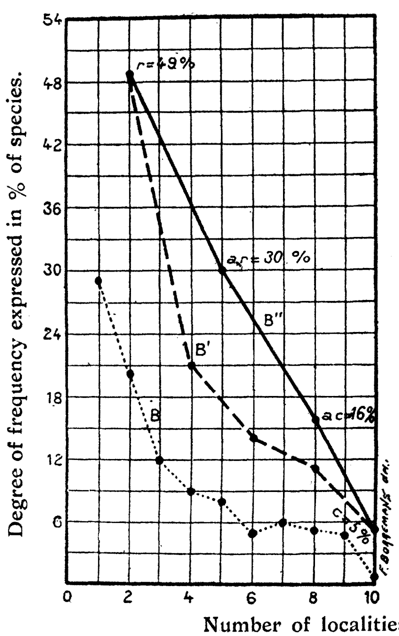
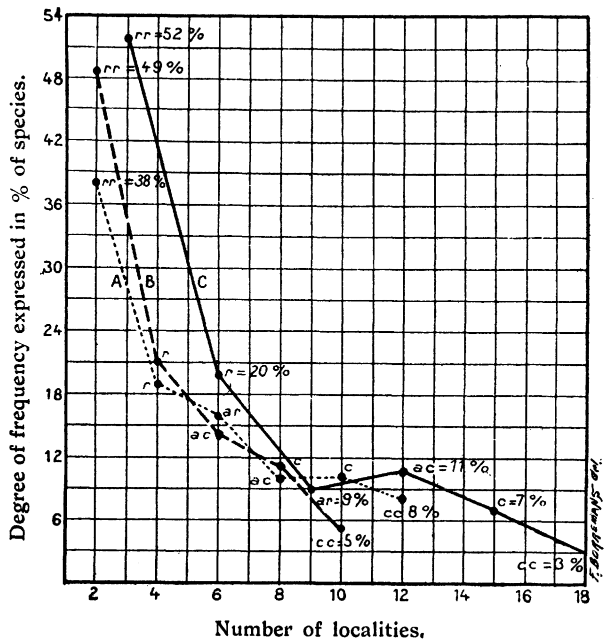


Fig. 1. Graph showing degree of frequency of 370 species of alpine meadow. B, B′ and B″ curves, corresponding with 10, 5 and 4 degrees of frequency.

Species noted in	1 and 2 localities	(rare)	49%
,, ,,	3, 4 and 5 ,,	(somewhat rare)	29
,, ,,	6, 7 and 8 ,,	(somewhat common)	16
,, ,,	9 and 10 ,,	(common) ...	5·4

Fig. 2 shows clearly that quite generally in the alpine zone the number of rare species is much the greatest and that of common species the least.



Fig, 2. Graph showing relative proportion of species which are very rare (*rr*), rare (*r*), somewhat rare (*ar*), somewhat common (*ac*), common (*c*) and very common (*cc*).

A, in 240 species of the southern Jura.

B, in 370 species of the region W.T.D.

C, in 178 species of the Graian Alps (upper alpine zone).

It is impossible not to be struck by the resemblance between these graphs and the curves representing organic variation (Galtonian curves, binomial curves). This resemblance would doubtless be still more marked if the number of species and localities considered were greater, and it may be supposed that in that case the curve expressing the different degrees of frequency of the associated species would correspond with a Galtonian "half-curve." While awaiting its verification on a larger scale, the relation revealed derives special validity from the fact that it appears even in the distribution of a small number of species.

For the 92 species of the Ormonts meadow already mentioned the following figures are obtained: rare species, 60%: somewhat rare and somewhat common, 23%: common, 10%.

These figures confirm what has been said above, and enable us to conclude quite generally :—

(1). That in alpine grassland *rare species are the most numerous* (*numerous* not *frequent*) and common species the least numerous.

(2). That the *observed decrease in number in passing from the rare to the common species takes place according to a mathematical law of the same order as that which expresses the different degrees of frequency of organic variations.*

It is almost superfluous to remark that though the number of rare species exceeds that of the common ones, this is not true of the *individuals*, and that it is *the individuals belonging to the common species which are most numerous.*

The data necessary to determine the relative proportion of individuals according to the degree of frequency of the species to which they belong, in other words *individual frequency* in relation to *specific frequency*, are still lacking. But it can be seen that the curve of individual frequency will be contrary in direction to that of specific frequency.

To sum up, if we consider the commonest species of a given station as being the best adapted to the ecological conditions of that station, as being, so to say, the mean floristic expression, or that which realises the greatest number of individuals, we see that around this mean type of maximum individual frequency the others are distributed in decreasing numbers according to their decreasing degree of adaptation.

The local distribution of species on each limited portion of alpine grassland results then not only from the combination—essentially variable from point to point—of ecological factors capable of favouring or hindering the extension of competing species, but also from a factor of mathematical regularity, showing itself by the constant relation existing between the different degrees of frequency of species and of associated individuals. And, as we shall see, this factor of regularity is not the only one.

IV.

In determining for the districts of the Dranses, Wildhorn and Trient, or for wider or more restricted areas, the ratio of the number of genera to the number of species which enter into the composition of their flora, it may be shown that this ratio—which may be called the *generic coefficient*—varies within fairly wide limits. This is clear from the following table ;—

	Number of Species.	Number of Genera.	Generic eoefficient per cent.
Flora of Switzerland[1]	2453	659	27
„ Valais	1850	592	31
„ the region W.T.D.	661	221	33
„ upper basin of the Trient ...	470	211	45
„ 10 areas of alpine grassland ...	370	210	57
„ 12 areas of Jura grassland ...	240	141	60
„ 9 localities in Ormonts grassland	92	73	79
„ 1 area of Jura grassland ...	106	90	85

It has been demonstrated elsewhere[2] from a considerable number of examples that, generally, *the generic coefficient varies inversely with the variety of ecological conditions in the areas compared.* This is shown very clearly in the table given below, in which a a series is given in order of decreasing ecological diversity. The factors which have the most influence on the value of the generic coefficient are, as has been shown in one of the memoirs already mentioned, especially the extent, the topographical and petrographical complexity, the degree of isolation, and finally the latitude and altitude. In this place only the figures relating to altitude will be cited, since this factor is particularly seen in the composition of the alpine flora. The following figures, taken from data collected by Oswald Heer in his *Die nivale Flora der Schweiz*, are most convincing in this respect. They show that in the eight belts of 500′ each established by Heer in the niveal zone of the Swiss Alps, above an altitude of 8000 (2600 metres),[3] the generic coefficient constantly increases as we pass to higher levels.

Belts (increasing altitude).		Number of Species.		Number of Genera.		Generic coefficient per 100 Species.
I.	...	338	...	139	...	41·4
II.	...	227	...	111	...	49
III.	...	153	...	78	...	51
IV.	...	122	...	68	...	55·7
V.	...	47	...	29	...	62
VI.	...	22	...	16	...	73
VII. VIII. }		22	...	17	...	77·3

[1] The new Flora of Switzerland by Schinz and Keller indicates 2459 species and 660 genera: the generic coefficient is scarcely altered.

[2] Particularly in two of the memoirs whose titles are cited at the end of the article.

[3] 8530 English feet.

For the corresponding zones of the Graian Alps the generic coefficient is 53% between 2600 and 3200 metres, 69% between 3200 and 3500 metres.

We therefore conclude, generally, that *in the alpine zone the value of the generic coefficient increases with altitude*, or, in other words, that with increasing altitude the number of genera decreases less rapidly than the number of species.

This phenomenon, far from being the result of any specific influence of altitude, is in reality only a special case of the general law already stated relating the generic coefficient with the diversity of ecological conditions. It may in fact be established that in the degree that a station, such as alpine grassland for instance, becomes uniform, it becomes poor in species more rapidly than in genera. When the ecological uniformity is at its maximum the associated species almost all belong to different genera. But in the upper alpine zone, the increase of altitude, owing to its influence on the distribution of light, of heat, and of humidity, becomes a cause of ecological uniformity, and this is translated into terms of vegetation by the physiognomic uniformity of the vegetation of the heights. Only the species which have a close adaptation to such a habitat succeed in maintaining themselves. Among species of the same genus, only those persist which possess the most complete adaptation, to the exclusion of others, and so much so that most of the genera are represented only by a single species.

Thus we are led to conclude that the genus is not a more or less arbitrary taxonomic unit, but a biological entity whose value appears in the distribution of plant species in a state of intensive competition.

V.

This conclusion applies equally, though in a less absolute fashion, to the great sub-divisions, classes or orders of plants. It proves true in every case for the great sub-divisions Dialypetalæ and Gamopetalæ, whose generic coefficients show parallel variations, and are usually almost identical with the generic coefficient of the whole flora.

This appears in the following table:—

	Generic Coefficients of		
	The area W.T.D. 661 species.	Jura meadow: 12 localities, 240 species.	Ormonts meadow: 9 localities, 92 species.
Dialypetalæ ...	33% ...	63% ...	76%
Gamopetalæ ...	33·6 ...	63 ...	74
Total Flora ...	33·4 ...	61 ...	79

In the first area containing 661 species, the agreement of the coefficients is surprising: in the second and third it is still very remarkable; and the fact that it manifests itself in such small numbers of species (240 and even 92) leads us to consider it as a fundamental law of distribution.

An examination of the floras of extensive areas (*e.g.*, Switzerland, France, Germany) shows that this agreement is quite general:—

	Generic Coefficients of		
	Germany 2500 sp.	Switzerland 2450 sp.	France 4250 sp.
Dialypetalæ ...	28·3% ...	26·2% ...	19%
Gamopetalæ ...	28 ...	26 ...	19
Total Flora ...	28 ...	26·4 ...	19·7

The agreement which occurs, in areas whose extent and floristic richness are very different, between the generic coefficients of Dialypetalæ and Gamopetalæ and of the whole flora, seems to indicate that *the plants of these two classes have a sensibly equivalent power of adaptation, since in the competition which takes place among them for the conquest of ground, their different genera present a similar specific diversity.*

This being so, is it not legitimate to hold that in the struggle which takes place between them, individuals are not only the representatives of such and such a species more or less well adapted, but also the champions of higher biological groups, of genera, orders and classes, to which they secure a definite proportion in the entire distribution?

VI.

To sum up, analysis permits us to consider the distribution of plants in the alpine zone as a resultant of the combined action of three orders of factors: (1) *ecological factors* (nature of soil and climate); (2) *biological factors*, expressed by the degree of adaptation of species to their station, and better still by the *power of adaptation*, which is very unequal in different species; (3) *sociological factors* created by the competition which occurs between associated species.

The action of the first two factors has, as a consequence, in any station, the elimination of a certain number of species (eliminative selection). The third factor determines the local distribution of the species which are not eliminated (distributive selection).

This last kind of selection being at once numerical and taxonomic, we may distinguish: (1) A *numerical selection*, determining the *number* of individuals, and of associated species; (2) A *specific selection*, determining the nature of associated species, *i.e.* their distribution among the genera, families, and classes to which they belong.

Note.—In order to avoid undue length a consideration of the other great sub-divisions of the plant kingdom is not entered upon here. Those readers who may be interested in such questions are referred to various memoirs in which they are discussed in detail; among others:—

1. "Distribution florale dans une portion des Alpes et du Jura."
2. "Distribution de la flore alpine dans le bassin des Dranses, etc." *Bulletin de la Soc. vaud. Sciences naturelles*, Vol. XXXVI Lausanne, 1901.
3. "Lois de distribution florale dans la zone alpine." *Ibid*, Vol. XXXVII, 1902.
4. "Gesetze der Pflanzenverteilung." *Flora*, 1902.
5. "Nouvelles recherches sur la distribution florale." *Bull. Soc. vaud. sc. nat.*, 1908.
6. "Apropos du coefficient générique." *Ibid*, Procès-verbaux, Dec. 1908.

AN ONAGRACEOUS STEM WITHOUT INTERNODES.

By Reginald R. Gates, M.A., Ph.D.

[Plates II and III].

For several years I have been making analytical cultures of Œnotheras from the sandy coast of Lancashire. These North American forms are known to have been naturalized in this locality for at least a century,[1] where they have long been growing in large numbers. Bailey[2] and MacDougal[3] were the first to show that these forms contain what are now known as *O. Lamarckiana* Ser., together with certain forms corresponding to some of the mutants of De Vries' cultures, such as *O. lata* and *O. rubrinervis*. In subsequent cultures of a more detailed character I have found

[1] See Sowerby's English Botany, Vol. 22, pl. 1534, 1806.

[2] Bailey, Charles. "De Lamarck's Evening Primrose (*Œnothera Lamarckiana*) on the sandhills of St. Anne's-on-the-Sea, North Lancashire." Address to Manchester Field Club, January, 1907.

[3] MacDougal, Vail and Shull. "Mutations, variations and relationships of the Œnotheras." Carnegie Inst. Pub. No. 81, 1907.