THE DISPERSION OF BRITISH PLANTS.

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I.—Introduction.

Last session I had the honour of reading, before your Society, a paper on "the World-distribution of British plants." An attempt was therein made to arrange the members of our flora into certain groups, according to the area which they occupy outside of Britain, the larger groups being further subdivided into sections. The paper concluded with lists of species, in which a figure was attached to each group or section, indicating its extent of area or "degree of distribution." The lowest figure, 1, indicated the most limited area noticed—that of plants which are found only in Europe, in the countries bordering the Atlantic. From this the figures increased, as the areas became more extensive, until 12 represented the dispersion of the most widely ranging species, viz., those which occur not only in all three continents of the Northern hemisphere, but in more than one of the Southern continents as well. To each species was thus assigned a figure representing its degree of dispersion; and by averaging these figures we can ascertain the mean *specific* area of any order or class, or of any number of plants possessing in common some distinguishing feature. In the present paper I propose, by means of averages thus obtained, and carried for greater exactness to two places of decimals, to examine into sundry questions respecting the

dispersion of plants, many of which have already been treated of by different authors, and especially by Professor Alph. De Candolle in his *Geographie Botanique*.

In questions of this nature, the results obtained from the examination of the flora of only a single country cannot be regarded as by themselves conclusive: they require to be confirmed by similar investigations over a wider field. Still they have some value so far as they go; and the restriction of the field of observation may in some respects even possess advantages of its own. When the flora under examination is one that has been so well studied as that of Britain, all the species that compose it can be taken into account; for, being generally well known to botanists, they are the more readily recognised when met with elsewhere, and greater confidence can be felt that they are correctly identified. But when we seek to bring into view the plants of the whole world, not only do we find many species doubtful or imperfectly known, whose real geographical area is consequently quite uncertain, but we are also confronted with a large number of absolutely spurious species. It is unfortunately but too common for a plant, when met with in a fresh country, to receive a fresh name, and to be regarded as a distinct species; and as it is clearly undesirable to include all these reputed species, we are forced to make a selection. A doubt then at once arises whether the result arrived at may not be in some degree affected by the selection. If the basis of investigation must of necessity be a partial one, our first ground may as well be the whole of a well-known flora, as a more or less arbitrary selection of species.

II.—Dispersion with regard to latitude.

Wide range of Northern plants.—On considering the comparative area of plants, one of the first facts which cannot fail to attract attention is that Northern plants range

more widely East and West than those of more Southern latitudes. This is at once apparent from the lists we have under notice; for of Arctic plants therein enumerated 77 per cent. belong to the "Universal" division, *i.e.* are found in all three continents of the Northern hemisphere; of Northern plants 76 per cent. are Universal; of Temperate plants only 42 per cent; and of Southern plants the insignificant proportion of 6 per cent. Two of the causes which have been assigned for this appear evident, viz.:—1st. That the actual extent of ground which a plant has to cover to reach from one quarter of the globe to another is much less at a high than at a low latitude; and 2nd. That about the Arctic circle there is almost continuous land, as Asia is separated from America only by Behring's Straits. In the greater expanse of sea which now lies between Europe and America, the intermediate stations of the Faroes, Iceland, and Greenland serve as stepping stones; and the greatest interval between them, that between the Faroes and Iceland, does not exceed 230 miles. Under a favourable climate, and with a sufficient length of time, the spread of a species over land is easy; the chance of seeds being carried across sea, whether by winds, currents, or birds, increases as the distance to be traversed diminishes; and in Northern seas it is considered that icebergs serve as means of conveyance. It is obvious, therefore, that Northern species possess special facilities for migration between the Old and New Worlds, even under existing conditions; and possibly, at a tolerably recent geological period, conditions may have been still more favourable, as Europe and America may have approached nearer to each other than at present.

The effect of these influences can be perceived also among Temperate plants, many of which, although excluded by their occurrence at a lower elevation further South from being classed as Arctic plants, nevertheless stretch Northwards into Arctic regions, and can even now be aided by the superior

means of transit which there exist. How far they have done so may be inferred from the fact that of our Temperate plants, out of 279 ranging over the three continents, 194, or 70 per cent., have been recorded from within the Arctic circle ;* but out of 384 with a more limited range, 103, or only 27 per cent. Of the 443 plants included in the "Universal Division," 332, or 75 per cent., are at present found in the Arctic regions ;† and Mr. Darwin has further pointed out that in the Pliocene age, during the period of increased temperature which prevailed before the Glacial period, species at present confined to the more Southern latitudes were probably driven far to the North, and would, if they then existed, have had the opportunity of crossing by the bridge now rendered impassable to them by cold, and open only to plants which still stretch to the extreme North; while, on the other hand, during the Glacial period itself, Northern species would migrate into Southern regions, in the mountains of which many of them still survive as Alpine plants.

If we accept this theory of a glacial migration, it follows that (to use the words of Dr. Hooker) "the existing Scandi-"navian flora is of *great antiquity ;*" and we thus have in their superior age a third cause of the wide diffusion of Northern plants, to which especially must be assigned their range from North to South.

Viewed with regard to their zones, our *native*‡ plants give the following average degree of dispersion :—

* Of the 85 species not yet recorded from actually within the Arctic circle, 31 have been found in Lapland, Iceland, or Greenland, and thus they closely approach it.

† Stress must be laid upon this point, as by Professor A. Gray's "Statistics of the Flora of the Northern States," out of 230 species common to them and to Europe, only 28 per cent. have been detected within the Arctic circle upon the American continent.

‡ Plants known, or even suspected, to be only naturalised in Britain have been excluded from all the comparisons in this paper, excepting in that one relative to weeds of cultivation.

Species.		Average.	Species.	Average.
69	Arctic	9·09		
124	Northern	8·82	490	8·84
297	Temperate, penetrating within the Arctic circle	8·79		
366	Temperate, not found within the Arctic circle	6·45	661	5·63
295	Southern	4·62		
Total 1151	.....	7·00		

III.—Dispersion as affected by Station.

Aquatic plants.—From the circumstance that a plant can, under favourable conditions, spread rapidly over land, it might be supposed that terrestrial plants would be the widest rangers; but this is just the reverse of the fact. Their number is so great, and the struggle for existence between them so fierce, that, if climatic or other conditions are in the least degree adverse, their progress is at once checked; and we consequently find that among terrestrial plants very few favoured and dominant species have attained a range over the whole world, and some of these only as weeds of cultivation, whose dispersion has principally been effected by human agency. It has long been noticed that, on the contrary, aquatic plants, in common with other fresh-water productions, are as a rule widely dispersed, and although their number is only moderate, a considerable proportion are cosmopolitan.

Besides the truly aquatic plants, whose leaves are altogether submerged or floating, there are many which may be regarded as semi-aquatic or palustral, as they grow on the edges of ponds and streams, in marshes, bogs, and wet places generally, and have their roots often below water. Such are found to have a higher degree of dispersion than plants usually met with in drier situations; the average areas of our British species are as follows:—

Species.		Average.
49	Aquatic	8·94
268	Semi-aquatic or palustral	7·93
834	Terrestrial	6·59

The tendency is most marked in those plants which belong to orders wholly or principally composed of aquatic or palustral species. Thus, of the 49 aquatic plants—

36	Nymphæaceæ, Haloragaceæ, Hydrocharideæ, Potomaceæ, Lemnaceæ and Marsileaceæ, average	9·11
13	belonging to other orders.....	8·46

and of the palustrals—

101	Droseraceæ, Pinguiculaceæ, Alismaceæ, Typhaceæ, Juncaceæ and Cyperaceæ, average	8·16
167	belonging to other orders.....	7·79

At first sight it seems that fresh-water plants, equally with land plants, would find the sea a barrier to their transit from continent to continent; and that, in addition, they would have in the land itself a serious obstacle to their passage from one river-basin or detached piece of water to another, but the spread of the American water-weed (Elodea canadensis) in Britain affords a recent and well-known instance of how readily the latter obstruction can be overcome. Mr. Darwin considers that the power of ranging widely, possessed by fresh-water productions in general, may arise from their having become fitted for short and frequent migrations from pond to pond, or from stream to stream, and thus simultaneously acquired the capacity for longer journeys. He also suggests that, as they are generally low in the scale of nature, and we have reason to believe that such beings change more slowly than higher organisms, they have had *a longer time* for their migration. In the case of plants, however, he seems to regard the extensive range as due not so much to any quality inherent in the plants themselves, as to a mere accident of their

station; for he attributes it mainly to "the wide dispersion "of their seeds by animals, more especially by fresh-water "birds, which have large powers of flight, and naturally "travel from one to another, and often distant, piece of water." He points out two ways in which dispersion by birds may be effected: by wading birds, when suddenly flushed, carrying away adherent to their feet some of the viscid mud in which they have been standing, which he shows by experiment is sometimes very highly charged with seeds; and by fishes swallowing seeds, and being afterwards themselves devoured by birds, in which case the seeds would probably be subsequently disgorged by the birds in the shape of pellets.

It must be borne in mind that the seeds of aquatic and palustral plants, being naturally adapted for a long continuance in water or wet mud, would be less likely than the seeds of land-plants to lose their vitality when carried by rivers to the sea; and might also have a greater chance of preserving their power of germination when transported further by ocean currents. It would be desirable to test by experiment whether the seeds, or rather the fruits, of such plants as Potamogeton and Ceratophyllum, or even as Alisma and Carex, will not withstand maceration in sea-water for a longer period than the seeds of land-plants.

Maritime Plants.—Professor De Candolle selects the whole of the two orders Plumbaginaceæ and Salsolaceæ as representatives of maritime or salt-loving plants; and finding that their mean specific area, calculated and expressed according to his method, is 10·3 against 4·5 that of flowering plants generally, he concludes that maritime plants, like aquatics, have a range more extended than the average. Of the eleven individual species which he names as instances of particularly wide distribution, six appear in our lists; yet, so far as the British flora is concerned, the degree of dispersion of salt-loving species, including those belonging to other orders as

well as to the two named by Professor De Candolle, is less than that of other plants.

Species.		Average.
111	Maritime	6·32
1040	Non-maritime	7·07

This discrepancy, and other similar ones that will be met with hereafter, no doubt partly arise from the limited scope of the present inquiry, confined as it is to British species alone, and from the entirely different methods by which the mean specific areas are ascertained and expressed; but I believe they are chiefly occasioned by the present calculations being based upon individual species, considered each separately, and Professor De Candolle's upon entire orders. In the present case, the two orders selected as representing maritime plants contain many species that are not maritime; and *vice versâ* many maritime species are found amongst other orders. The two representative orders happen also to be treated of in the later volumes of the "Prodromus," in which the geographical distribution is very fully given; while in the earlier volumes, containing many important orders reckoned as non-maritime, a much more limited area is frequently assigned to species than they have since been found to possess.

Calcareous Plants.—Those plants that evince in Britain a preference for chalk or limestone soils have a lower degree of dispersion than our other plants.

Species.		Average.
81	Calcareous	5·43
1070	Non-calcareous	7·12

The species classed as calcareous comprise, however, no aquatic or palustral plants; and as we have seen that such are the widest rangers, a more correct comparison is, perhaps, one confined to terrestrial plants. It is as follows:—

Species.		Average.
81	Calcareous	5·43
753	Other terrestrials.....	6·71

On the other hand, calcareous plants include an undue proportion of Orchids, an order that has only a limited specific range. Omitting these again, the comparison is :—

Species.		Average.
67	Calcareous	5·60
735	Other terrestrials.....	6·70

Sand Plants.—It is more difficult than in the case of calcareous plants to separate as a distinct group species that are partial to a clayey or a sandy soil. Clay plants, indeed, I find it impossible to distinguish satisfactorily, but I have taken out those plants to which our floras generally ascribe a preference for sand. They include some species that have been ranked above as maritime plants, such as Carex arenaria, Phleum arenarium, and Elymus arenarius, and give the following result :—

Species.		Average.
85	Sand-loving plants	5·81
1066	Other plants	7·09

or omitting aquatics and palustrals—

73	Sand-loving plants	5·52
761	Other terrestrials.....	6·69

Sylvestral plants.—The species to which such a station as "woods, copses, and hedges" is usually assigned may be divided into two lists. 1st, The trees of which the woods themselves consist: they will more fitly be noticed when we come to treat of dispersion in relation to habit. 2nd, The smaller shrubs and herbs which rejoice in the shade and shelter of the trees. Their average dispersion is :—

Species.		Average.
158	Sylvestrals	6·39
993	Other plants	7·09

In their case, however, the limitation of area appears to arise principally from there being no aquatics and hardly any palustrals amongst them: while, as there are no woods in the extreme North or at very high elevations, no Arctic plants can be sylvestral. Omitting aquatics and palustrals the average of "other plants" is reduced to 6·64; and further omitting Arctic plants it is reduced to 6·36.

Heath plants.—Species that are usually found on dry heaths, moors, and commons have also a rather limited degree of dispersion, the comparison between them and other terrestrials being as follows:—

Species.		Average.
35	Heath plants	6·31
799	Other terrestrials.....	6·60

Weeds of cultivation.—The greater number (70 out of 91) of the "weeds" now found in Britain are only naturalised here; and for the purposes of the following comparison these colonists have been included with our natives The weeds have been entered in the lists according to the area in which each is believed to be indigenous, except in a few cases in which it is quite impossible to decide where the weed is indigenous and where it has been introduced by man. The average of these, which may be termed their *natural* areas, is less than that of terrestrials generally.

Species.		Average.
91	Weeds of cultivation	6·10
743	Other terrestrials...	6·65

If, however, we regard, as Professor De Candolle has done, not the natural areas, but those to which the weeds have been carried by human agency, we have the average at once greatly raised. They have migrated widely with man: the greater number of those now found with us have been introduced into N. America; many are naturalised at the Cape, and in

Australia; and some in different parts of S. America. Their degree of dispersion, as introduced plants, is thus swelled to 8·78; considerably exceeding that of palustrals; and almost equalling that attained by aquatics.

Parasites.—The conditions necessary for the spread of parasitic plants are more complex; as some are not only affected by soil and climate, but also dependent on the existence of those species from which they draw their nourishment. It might therefore be expected that their mean specific area would be small; and such is the case with the few complete parasites that are found in Britain, belonging to the Loranthaceæ, Cuscuteæ, and Orobanchaceæ.*

Species.		Average.
9	Parasites	5·33
1142	Other plants	7·01

The Rhinantheæ, Monotropa, Thesium, and Epipogium, which are considered to be at any rate partly parasitic, have on the other hand, taken together, a rather high degree of dispersion; so that, including these, the average of

21	Parasites and semi-parasites rises to	6·52
1020	Other plants	6·77

From the above it would appear that plants which are confined to, or have a decided preference for, any *special* station, have as a rule a limited range; the main and very marked exceptions being aquatics and palustrals.

IV.—Dispersion in relation to habit and duration.

Trees and Shrubs.—According to Professor De Candolle's figures trees and shrubs have a much less extended range than herbaceous plants. In this instance his system of

* This does not agree with Professor De Candolle's figures, which give Orobanchaceæ and Cuscuteæ a higher, and Monotropaceæ a lower, than average specific area.

representative orders is in one respect exact, for many orders consist entirely or nearly so of ligneous species: but most of those upon which he has based his calculations are tropical or sub-tropical; and the Amentiferæ are excluded, to which belong so large a proportion of the trees and shrubs of temperate regions, and the mean area of which he remarks would increase the average of ligneous plants. Of our native trees only about a fifth (5 out of 24) belong to his representative orders; of our shrubs less than half (31 out of 75); and thus it happens that although the following comparison shows that our ligneous plants have a low degree of dispersion, the contrast is not so marked as in Professor De Candolle's figures.

Species.		Average.
24	Trees	6·13
75	Shrubs.....	6·47
99	Ligneous plants	6·38
1052	Herbaceous plants	7·06

None of our trees are "Arctic" or aquatic, nor have we any trees amongst our Cryptogams. Omitting such from amongst herbaceous plants also, the comparison is:—

24	Trees	6·13
881	Herbaceous plants	6·65

Some of our shrubs are Arctic, but none appear amongst aquatics or Cryptogams: omitting the two latter, we find—

75	Shrubs...	6·47
942	Herbaceous plants	6·80

Of our trees, only three are indigenous in America; but their average degree of dispersion is brought up by the compensating circumstance that only a small proportion is confined to Europe alone: in other words, our trees range

rather more widely than herbaceous plants over land, rather less so over sea. Reduced for the sake of comparison to percentages, the proportions are,—trees 12½ per cent., herbs 41 per cent., indigenous on both sides of the Atlantic; trees 8 per cent., herbs 20 per cent., found in Europe alone. In connection with, and perhaps partly accounting for, the small number of our trees that reach America, I may remark that, although the observations of Professor Heer and others prove that during the Miocene age trees flourished as far north as Spitzbergen and Arctic Greenland, few can withstand the rigour of the climate which now prevails about the Arctic Circle, or can take advantage at the present time of the bridge of almost continuous land above described as existing there. The percentages recorded from within the Arctic Circle are,—trees 7 per cent., herbs 41 per cent.

Creeping Rhizomes or Stolons.—Farmers know by experience how much more difficult it is to exterminate those weeds that have creeping rootstocks, or trailing and rooting stems or stolons. It is very hard to kill such a plant; and this extreme tenacity of life would be of material advantage in the struggle for existence; and if the species had existed long enough might enable it to attain a wide range. The British species thus benefited number

342	With an average of.....	8·10
809	Other plants average	6·53

A large proportion of our aquatics (about ⅔rds) have creeping rootstocks or stems, but this does not materially affect the above results. Omitting aquatics, the figures stand thus—

308	With creeping rootstocks, &c. ...	8·07
794	Without do. do. ...	6·45

Annuals, Biennials, and Perennials.—The average areas of our herbs, divided according to their duration, disagree entirely with Professor De Candolle's figures based upon the

plants of the whole world, by which Monocarpic plants appear more widely diffused than perennials, which of the former annuals have a more extended range than biennials. British herbs give the following result.

Species.		Average.
175	Annuals	6·35
31	Annuals or Biennials	6·13
23	Biennials	5·44
229	Total Monocarps.....	6·23
296	Perennials	7·31
27	Doubtful duration	6·70

In a synopsis of the flora of Spitzbergen, Malmgren remarks that the plants of that high northern locality are all perennials; and attributes it to the effect of occasional inclement seasons, which prevent the production of ripe seeds during the short summer, and thus prove fatal to species that have only annual roots, while the permanent stocks of perennials survive. It thus happens that, with the single exception of Gentiana nivalis, all species that I have classed as "Arctic" are perennial, and their wide range increases the perennials' average. Omitting Arctic plants the perennial degree of dispersion is reduced to 7·14, but even then exceeds that of Monocarps.

Of the representative orders selected by Professor De Candolle as being largely composed of annual species the principal is that of Gramineæ, which indeed contains $\frac{3}{5}$ths of the whole. In this respect our British grasses are different, the great majority of them (76 out of 94) being perennials.

V.—Dispersion according to character of the flower.

Structure.—Those differences in the structure of the flower which are considered most important for purposes of classification, and according to which the great classes of Exogens

and Endogens are broken up into divisions, are not accompanied in either class by any material differences in dispersion; but on comparing one class with another we find that Endogens give a higher average than Exogens, while the flowerless Cryptogams exceed both. The wide range of Cryptogams is perhaps attributable to their great antiquity, for the vegetation that flourished during the Coal era was almost entirely cryptogamic. Our sixty-one Cryptogams average 9·51, while our Phanerogams compare as follows :—

Species.		Average.
172	Thalamifloræ	6·98
205	Calycifloræ..... ...	6·52
306	Monopetalæ	6·41
92	Apetalæ	6·84
775	Total Exogens	6·62
129	Petaloideæ.....	7·23
186	Glumaceæ	7·55
315	Total Endogens.....	7·45

If, instead of dividing Endogens according to the whorled or imbricated arrangement of their floral envelopes, we regard rather their herbaceous or scarious condition, and thus include the Juncaceæ and Eriocaulon with the true Glumaceæ, the comparison stands :—

		Average.
103	Petalloid Endogens	6·81
212	Glumaceous do.	7·77

The average of petalloid Endogens is raised considerably by the aquatic orders Potomaceæ and Lemnaceæ; and somewhat by the palustral order Alismaceæ. Omitting aquatics and palustrals, the average of petalloid Endogens sinks to 5·41 against 6·80, that of other terrestrial Phanerogams.

Inferior ovary.—Professor De Candolle remarks that not a

single order having an inferior ovary has a wide range. This is not exactly the case amongst British plants, as our Onagrariaceæ have a high degree of dispersion, 8·62 : indeed, amongst the 27 orders of Phanerogams in our flora containing 10 or more native species, they are surpassed by no order of Exogens ; and only by the aquatic Potomaceæ amongst Endogens. Our figures, however, corroborate the main fact, that plants with an inferior ovary are on the average less widely dispersed than other Phanerogams.

Species.		Average.
268	with ovary inferior.....	6·17
822	other Phanerogams	7·08

It is difficult to see in what way inferior ovaries can be any special disadvantage.

Conspicuous flowers.—Mr. Darwin has shown how important a part is played by insects in the fertilization of flowers ; and how great a benefit is the cross-fertilization effected by their means. He considers that all plants with conspicuously-coloured flowers, powerful odours, or honeyed secretions, are fertilized by insects ; " and he concludes that " before honey-feeding insects existed, the vegetation of our " globe could not have been ornamented with bright-coloured " flowers, but consisted of such flowers as pines, oaks, " grasses, nettles, &c."* If this conclusion be correct, plants with inconspicuously-coloured flowers have probably attained a greater *age* as species, and, having thus had a longer time for their migration, we may expect to find that they have also a high degree of dispersion, which will be most conspicuous in orders that are entirely composed of such plants. On dividing our British plants, to ascertain whether this is the case, I find not only that it is so, but also that plants with *white* flowers are more widely dispersed than those with

* The quotation is from Dr. Hooker's address to the British Association.

coloured, a result which I was not expecting. Further analysis shows that plants with flowers sometimes white and sometimes coloured, such as the Wood Anemone, many of our Violets, Thistles, and Campanulas, are intermediate in this respect, having a more limited range than those whose flowers are always white; and on the other hand a more extended range than those with flowers always coloured. The averages compare as follows:—

Species.		Average.
316	of whole orders having inconspicuous flowers	7·71
64	other plants with inconspicuous flowers	7·19
380	Total with inconspicuously-coloured flowers	7·62
179	with flowers always white	7·04
176	with flowers variable in colour	6·66
355	with flowers always coloured	6·05

Averages taken out separately for yellow, red or pink, blue or purple, and parti-coloured flowers do not differ much from each other, or from the average of coloured flowers taken all together.

Although the wide range of green, and to a smaller extent of white-flowered plants, has been named in connection with the presumed greater age of the species, I by no means wish to contend that it is entirely, or even mainly, caused thereby. Other influences have probably contributed, such, for instance, as that of *latitude*. It is notorious that the flowers of tropical or sub-tropical countries are more brilliantly coloured and showy than those of temperate and Northern regions; and we have seen that, physical conditions being specially favourable for the migration of the latter from one quarter of the globe to another, they have attained a high degree of dispersion, by which the average of inconspicuously-coloured flowers may be appreciably raised. Amongst British Phanerogams

of those classed in our lists as "Southern," 58 per cent. have flowers always or sometimes coloured; of "Temperate" plants 47 per cent.; of "Northern" 43 per cent.; and of "Arctic" only 31 per cent. If, however, a comparison be made for each zone separately, the degree of dispersion of plants with inconspicuously-coloured flowers is still found to exceed that of white-flowered (except in the Northern zone), and yet more that of coloured-flowered. To the extent shown by the means of the four zones in the following table, this result may be regarded as the effect of other influences than that of latitude.

Zone.	Flowers.					
	Inconspicuous.		White.		Variable and Coloured.	
	Species.	Average.	Species.	Average.	Species.	Average.
Arctic	30	9·33	15	8·80	20	8·75
Northern	37	9·06	27	9·59	48	7·92
Temperate	238	7·90	91	7·46	296	6·92
Southern	75	5·40	46	4·11	167	4·29
Mean of 4 zones.	..	7·92	..	7·49	..	6·97

Again, it has been supposed that some plants are not only fertilized by means of insects, but may require for the purpose to be visited by particular species of insects. Such plants would thus be as dependent for their propagation on the co-existence of these particular insects as some parasitic plants are for their nourishment on the existence of particular victim-plants; and their power of extending would be limited accordingly by the range of the insects, irrespective altogether of their younger age as species.

Amongst aquatic plants a majority (32 out of 47) have inconspicuous flowers; but this can hardly be deemed a cross influence, for the wide range of fresh-water productions has been attributed partly to their having attained a greater age

as species; and the preponderance amongst them of inconspicuously-flowered species would be merely an evidence of this.

Unisexual flowers.—So many monœcious and diœcious plants have inconspicuously-coloured flowers, that the comparison between them and plants having at any rate some flowers perfect, resembles in great measure the last. It is as follows:—

Species.		Average.
152	with only unisexual flowers ...	7·63
1204	other Phanerogams	6·73

VI.—Dispersion according to the nature of the Fruit.

Fleshy fruits.—It has been considered that plants bearing succulent fruits have a greater chance of dispersion by means of birds; for, although grain when eaten by birds is killed by the process of digestion, seeds swallowed in a berry or other succulent fruit not unfrequently pass through uninjured, and retain their powers of germination. Professor De Candolle cites as an instance a practice of feeding turkeys upon hawthorn berries, for the purpose of subsequently sowing their seeds, which are found to grow better when thus treated than when sown in their natural condition. Amongst our British species, however, the average of fleshy-fruited plants is very little above that of dry-fruited. They compare as follows:—

Species.		Average.
71	With succulent fruit.....	6·92
1019	„ dry fruit	6·86

If we exclude from among succulent fruit those containing large seeds, not likely to be swallowed by birds, their average is somewhat raised.

Dehiscence.—In dry fruits the character which appears most likely to affect dispersion is their dehiscence or indehiscence. In cases where the seed vessel bursts, the naked seeds seem to be more exposed to vicissitudes; when enclosed in indehiscent carpels they are more likely to float, and, having the advantage of an additional protection, would presumably withstand for a longer period the action of sea-water. Indeed, Mr. Darwin's experiments on this point showed that seeds preserve their vitality in sea-water longer when enclosed in seed vessels than when naked. Our lists give the following results:—

Species.		Average.
584	With indehiscent fruit	6·93
434	,, dehiscent fruit	6·76

showing less difference than might be expected. This may arise from the fact that dehiscent fruits have generally more *numerous* seeds, an advantage that may compensate in great measure for the disadvantage of the seeds being exposed naked.

Special adaptation for dispersion.—The fruits and seeds of certain plants are to all appearance specially adapted for dispersion, being furnished with appendages which enable them to float in the air, and thus be easily wafted about by the wind; or to cling to the coats of animals: and in either case the chance is increased of their being conveyed to a distance. These appendages consist (1) of a coma or pencil of hairs attached to the *seeds;* (2) of a feathery pappus or awn, or (3) of hooked bristles or tubercles, bent or spiral awns, or some other grappling organ, borne by the *fruit* itself. Our native species thus furnished compare as follows:—

Species.		Average.
32	With seeds having a coma	7·28
94	,, fruits furnished with pappus, &c.....	6·39
34	,, ,, ,, grappling organs..	6·74
930	Not specially adapted	6·90

These results agree with those obtained by Professor De Candolle, whose calculations also show that whereas a coma attached to the *seed* is accompanied by a wide range, feathery appendages borne by the fruit are not. As regards plants furnished with the latter, several circumstances might be suggested as possibly exerting a counteracting influence—such as that they contain no aquatic species, but, on the contrary, an undue proportion have an inferior ovary, and nearly all bear coloured flowers and exalbuminous seeds; but on comparing Compositæ by themselves, in which all the conditions referred to are similar, we find—

Species.		Average.
81	Furnished with feathery pappus	5·98
2	With grappling organs	9·50
14	Without pappus	6·36

VII.—Dispersion according to character of the Seed.

Size and number.—Professor De Candolle has shown that Palmaceæ, Sapotaceæ, and some other smaller orders, nearly all tropical, and mostly arborescent in habit, producing fleshy fruits with *large* seeds, have a more limited range than certain other orders which have ordinarily *small* and *numerous* seeds, and many of which grow in the temperate zone; the average of the latter being the same as that of Phanerogams generally. From this, and from the fact that Cryptograms, whose spores are excessively minute and numerous, have an extended average range, it has been generally accepted that small and numerous seeds favour a wide range. So far as regards *size* this is not apparent amongst our native plants, perhaps from the variation in the size of their seeds not being sufficiently great. Orchidaceæ and Orobanchaceæ, orders whose seeds are very small, have only a low degree of dispersion; and our native species belonging to the representative

orders, selected by Professor De Candolle as having small seeds, give an average almost identical with that of other Phanerogams. Thus:—

Species.		Average.
314	Belonging to the small-seeded orders ...	6·81
776	Other Phanerogams	6·88

I have made several attempts to institute a more exact comparison on this point, but the change in the size of the seeds is so gradual that I have found myself quite unable to draw the line between large and small-seeded plants.

As regards *number*, however, it is not difficult to separate species having solitary seeds from those with more than one seed in each cell, and the result is rather adverse to the generally-received belief.

Species.		Average.
623	With seeds solitary in each cell	6·93
464	,, two or more seeds in each	6·74

It is possible that the production of numerous seeds is, indeed, even amongst British plants, favourable to dispersion; but that this advantage is neutralized by the fact that when a plant produces numerous seeds its fruit is nearly always dehiscent, while solitary-seeded species have as generally indehiscent fruit; and the additional protection which this affords to their seeds may fully compensate for their paucity in number.

Testa.—Differences in the seed deserve our special attention, for it is in this shape that a plant is most likely to be carried from one part of the world to another; and if any peculiarity of the seed enable it better to withstand the various vicissitudes to which it must be exposed during transit, or to establish itself, and maintain a footing in the struggle for existence when it has reached a new country, the effect may be traceable in the specific area. We have already seen that a coma or down attached to the seed is accompanied by a high

degree of dispersion ; and the nature of the testa, or outer coat of the seed, may next be suggested as likely to exert an influence. It might be anticipated that a thick, hard, leathery or crustaceous testa would resist for a long time the action of sea-water, and by enabling the seed it encloses to retain its vitality for a lengthened period when carried by oceanic currents, favour its dispersion to a distance.* Such, however, hardly appears to be the case. In Mr. Darwin's experiments on the action of sea-water, seeds endued with a thick testa, *e. g.*, of Leguminosæ and Hibiscus, were amongst the earliest to lose their powers of germination ; and the following comparison shows that our plants whose seeds have such a testa reach a lower degree of dispersion than plants whose seeds have a membranous testa on the one hand, or a soft cellulose or mucilaginous testa on the other. Omitting species in which the nature of the testa is doubtful, we have—

Species.				Average.
665	With testa	thin or membranous	.....	7·03
47	,,	,, soft cellulose, &c.	.....	7·64
192	,,	,, thick, leathery, or crustaceous		6·05

It may be remarked that seeds with a membranous testa are most frequently enclosed in an indehiscent fruit, to the pericarp of which the seed is, indeed, in many cases adherent. The apparent deficiency of the testa might be thus more than compensated for ; but I was surprised to find that the specific area does not appear to be affected by this. Some orders, as, for example, Primulaceæ and Juncaceæ, have seeds with a thin testa, but contained in a dehiscent capsule : of these our native species number 124, and their average degree of dispersion is 7·04.

Albumen.—In the determination of natural orders, a

* Dr. Hooker, in his paper on the flora of the Galapagos Islands, expresses an opinion that the "indurated seed-coats of some" (plants) "probably aid "them in resisting for some time the effects of salt-water."

character of the seed to which great importance is usually attached is the presence or absence of albumen. If the function of albumen be to supply nourishment to the embryo during germination, its possession may enable a seed to retain its vitality longer, and maintain its existence more sturdily when it reaches a new country, than a seed in which no such store of nourishment is provided, and thus favour the dispersion of the species. Whether this be the case or not, we at any rate find that our plants with exalbuminous seeds have a lower degree of dispersion than those with albuminous; and that among the latter, differences in the nature of the albumen are accompanied by variations in the average range—plants in which the albumen is farinaceous exceeding in this respect those in which it is fleshy, dense, or horny:—

Species.				Average.
303	With albumen	floury or mealy.		7·37
347	,,	,,	fleshy or horny...	6·80
439	,,	,,	absent or very scanty ...	6·55

This is the more remarkable, as the majority of our aquatics have seeds destitute of albumen. Omitting aquatics, the figures stand:—

Species.				Average.
299	With albumen	mealy or floury.....		7·35
333	,,	,,	fleshy or horny.....	6·66
411	,,	,,	absent or very scanty ...	6·41

This accords with the experiments of Mr. Darwin on the resistance of seeds to sea-water, in so far as the two orders which he found were soonest killed, Leguminosæ and Malvaceæ have no albumen; while of the five orders which retained their vitality longest, Chenopodiaceæ, Polygonaceæ, and Gramineœ have a floury, Solanaceæ a fleshy, and Umbelliferæ a dense albumen. In Compositœ and Cruciferœ, however, orders destitute of albumen, the majority of species experimented on survived fairly well; and Dr. Hooker's observations

on the Galapagos flora led him to believe that an exalbuminous embyro the most readily survives a sea transit; while of the albuminous-seeded plants presumed to be there introduced, "the majority have that substance dense and carnose, some "farinaceous, but two or three only." Other authors, so far as I am aware, have not discussed this point. Professor De Candolle has not alluded to it; but his figures respecting the dispersion of natural orders (*Geographie Botanique*, vol. i, pp. 515 to 517) give, when analysed according to the albumen contained in the seeds, the following results, confirmatory of those above obtained from British plants:—

Albumen.	Orders.	Species.	Percentage found in more than 2 districts.
Farinaceous	23 ...	9·254 ...	7·9
Fleshy or dense	96 ...	20·790 ...	4·2
Absent or very scanty	62 ...	29·001 ...	3·6

VIII.—Dispersion according to classification.

Natural Orders.—In connection with the structure of the flower have been given above the average degrees of dispersion of the *Classes* into which Vascular plants are divided, and of their divisions. The following are the averages of the *Orders* most largely represented in our flora, namely, those having fifteen or more native species:—

	Species.	Avge.		Species.	Avge.
Ranunculaceæ ...	25	7·88	Boraginaceæ	18	5·89
Cruciferæ	39	7·59	Primulaceæ	16	6·88
Caryophyllaceæ ...	48	7·35	Chenopodiaceæ ...	18	6·33
Leguminosæ	55	5·36	Polygonaceæ	25	7·40
Rosaceæ	42	7·44	Amentiferæ	30	7·03
Saxifragaceæ	17	7 65	Orchidaceæ	36	5·97
Umbelliferæ.....	49	5·41	Liliaceæ	17	5·47
Rubiaceæ...	15	6·27	Potomaceæ	18	9·06
Compositæ	97	6·10	Juncaceæ	25	8·56
Ericaceæ	23	7·22	Cyperaceæ	92	8·07
Scrophulariaceæ ...	36	6·89	Gramineæ	94	7·16
Labiatæ	30	6.53	Filices	43	9·44

These larger orders, taken together, give an average of 7·04, against 6·84 that of smaller orders; or, omitting Cryptogams, 6·91 against 6·67. There are, however, some orders, such as Solanaceæ, which, although they are extensive abroad, have only a few British species. When viewed according to their total number of known species, and divided into four classes, viz., 1st, largest, those that contain 2000 species or more; 2nd, large, those with 1000 to 2000; 3rd, moderate, those with 500 to 1000; and 4th, small, with less than 500 orders, give the following comparison, excluding Cryptogams:—

Species.		Average.
426	Of the 8 largest orders.....	6·65
204	„ 7 large „	6·76
187	„ 11 moderate „	7·03
273	„ small „	7·13

Specific area would thus seem to be in inverse ratio to the size of the orders. In the case of *Large Genera*, however, a different result is obtained. Mr. Darwin, in support of his views of the nature of a "species," adduces the fact that large genera comprise a greater proportion of *dominant species* than small genera, the predominance of the species being shown by—1st, extensive geographical range; 2nd, general diffusion over the area which they occupy; 3rd, commonness, or being represented by an abundance of individuals; and 4th, variability, or a tendency to produce varieties differing from the typical form.

Our subsequent comparisons are in this connection, and show that a range more extensive than the average accompanies each of the other characteristics of predominance enumerated above.

Having regard to only our British species, and considering those to be large genera that have eight or more native representatives, we find that

Species.			Average.
362	belonging to	26 large genera	7·38
789	„	smaller „	6·82

But there are some genera, such as Astragalus and Lobelia, that have a large number of foreign species, although but poorly represented in Britain. Including foreign species, the large genera may be divided into two grades, the largest containing 200 or more species, and those coming next in size containing 100 to 200 species—when we have the following :—

Species.			Average.
148	belonging to	20 largest genera.....	7·42
269	„	44 large genera	7·04
734	„	smaller genera.....	6·90

General diffusion.—On this point I have followed Mr. Watson's census of counties in the " Compendium." Classed according to his figures therein given—

Species.			Average.
150	found in	90 or more counties	8·01
336	„	60 to 89 counties	7·24
665	„	fewer than 60 counties ..	6·65

The larger average thus attained by the plants most generally diffused in Britain is the more remarkable, inasmuch as Arctic plants are excluded from amongst them, being in this country necessarily confined to districts of high elevation. Omitting Arctic plants, the average of species found in less than sixty counties is reduced to 6·37.

Commonness.—Taking as a guide our best-known floras, I have averaged the plants that are therein described as " common," " abundant," or " plentiful." Commonness usually accompanies general diffusion, but not always, for some plants are thinly scattered over a great part of the country, yet cannot be regarded as common. Again, certain plants are quite common in some districts, yet do not extend to others. For instance, a plant may be common in the south

of England, but hardly found in Scotland; another may be plentiful in the Highlands, but almost unknown elsewhere; or plants may be common only in particular stations, as on sandy sea-shores or peat-mosses. Such may be termed "partially "common," and I have averaged these, also, separately:—

Species.		Average.
319	generally common.....	7·54
83	partially „	7·16
749	less plentiful or rare	6·75

Variability.—Regarding as variable all species of which more than one form is distinguished by Professor Syme in "English Botany;" and averaging separately those in which the variation of the forms is so great that they are ranked as "sub-species;" and those of which only "varieties" are recognised; we get the following result:—

Species.		Average.
92	divided into sub-species	7·76
205	„ varieties.....	7·64
854	not variable	6·76

These figures are not materially changed if amongst the variable species are included those which present distinct varieties abroad, although only one form is found in Britain.