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On the Causes which limit the Distribution of Plants in the North of Europe and analogous Regions. By M. ALPH. DECANDOLLE*.

THE fundamental problem of geographical botany is the investigation of the modes in which species are limited in geographical expansion, with the laws regulating them, and in the simplest case, namely on the surface of a continent considered independently of the mountains which may exist upon it. It is evident that the limitation of species involves their proportion in families in each country, and is connected with important physiological and agricultural questions. Geologists also, and natural philosophers, require to know how far the presence of the same species in two epochs or in two countries proves analogy of climate, and with what degree of precision the geographical distribution of a species proves an equality of external conditions of temperature. Most questions of this kind relate to northern or, more strictly speaking, to polar limits. In the present essay the author disregards the southern limits.

Opinions on the subject of polar limits have changed with the progress of physical geography. At first the limits of species were compared with mean annual temperatures, and singular anomalies were found. In 1815 and 1817 Humboldt caused a great and happy transformation of physical geography by his comparison of lines of mean annual temperatures (isothermal lines), mean temperatures in the three months of winter (isochimenal), and of summer (isothermal). He showed that the *averages* of the seasons were often more important than those of the year, and that in most cases two similar climates might be divided into very dissimilar fractions which neutralized each other in the *mean* of the year. Hence it appeared probable that the temperatures of the seasons or of the months would explain the habitats of species, or in other words, that each species would advance on a continent as far as a certain line of temperature, equal during one period of the year, at least where not arrested by too dry or too humid a climate, or some material obstacle,

* Abstract from the Ann. des Sc. Naturelles, 3 série, Botanique, vol. ix. p. 5, Jan. 1848.

such as the sea. M. DeCandolle formerly thought (and stated in his essay 'On the Geographical Distribution of Alimentary Plants,' Bibl. Univ. de Genève, April and May 1836), that the annual species should be pretty constantly limited by the isothermal lines, because their vegetation wholly or chiefly occurs during the three months of summer; and it appeared to him that herbaceous perennial and ligneous species would often be limited by the lines of equal temperature during several months of the fine season, or by the *minima* of winter in the case of plants particularly subject to injury by cold. This view has been more or less shared by botanists, who have zealously investigated thermometric averages. Disagreements have been attributed to errors of observation, to the uncertainty of the averages obtained, or to causes independent of the temperature, such as dryness or moisture. Several facts, and the ingenious researches of M. Boussingault on the heat required for cultivation in various countries, raised doubts in the author's mind, and he determined to seek the solution of the question by a direct method; the following is the path he has followed:—

He chose for his investigations twelve annual, twelve herbaceous perennial, and twelve ligneous species, selecting plants which have their limits in Europe, as Europe is the only region where the local floras are numerous or the conditions of temperature well known; and avoiding cultivated or easily confounded species, such as might have escaped the notice of the authors of the floras or had a troublesome synonymy. Their polar limits were settled by means of a great number of floras and catalogues, researches in herbaria, and by questions addressed to botanists residing in the less explored parts of Europe. The author then traced the limits of the species on the map, and next consulted the most complete *résumés* of the temperatures of months and seasons of the cities of Europe, such as those of Kämtz, Berghaus, Mahlmann and Dove, completing them by means of special researches.

The following are the results, at the first glance, of that comparison, founded upon very certain facts:—

1. In no case does the limit of a species coincide exactly with a line of equal temperature during *any* epoch of the year.
2. The limits of the annual species in the plains of Europe cross frequently. The limits of herbaceous perennial and ligneous species cross equally in different directions; the two are far from parallel when they do not cross.

This alone shows how much the lines of vegetation differ from the lines of equal temperature; for if we construct lines of equal temperature in a certain season, they will be pretty nearly parallel; if we then construct them for another season, they will

be nearly parallel with each other, but undoubtedly different from the preceding. Thus isochimenal lines will cross isothermal lines; but neither of the sets ever cross among themselves, at least in regions of plains.

A little reflection makes it evident that it is useless to pursue the comparison of lines of equal temperature and of the limits of plants, at all events in Europe and countries analogously situated. The vegetation of a plant commences at a different time of the year, according as the climate of the locality differs in the different seasons. Lines of equal temperature relate to fixed periods, while the vegetation of any particular species endures for variable periods in different parts of Europe, and any relation between the two is but accidental.

In order to arrive at the law of the limitation of species it was necessary to start from two principles, admitted by all agriculturists and botanists, but the combined effect of which had not previously been calculated.

It is well known that great heat during a short time will produce the same effect upon plants as a lower degree enduring for a longer period. The forcing or keeping back of plants is dependent on combinations of time and heat, and plants are thus made to flower or ripen at a particular epoch. M. Boussingault* has given these facts a more precise form, by showing, in the case of most of our cultivated annual plants, that if we count the number of days which the culture endures and multiply the number of days by the mean temperature, the product is similar for each crop in all countries and in every year. The heat thus acts proportionately to its force and duration. But M. Boussingault has not presented his calculation in such a general form, and with good reason; there is a second principle which modifies this, and is at least equally important in geographical botany.

This second principle is, that every species requires a certain *minimum* of heat for each of its physiological functions. Not only are temperatures below 0° (Centigrade) useless on account of the congelation of liquids, but 1°, 2°, 3°, &c. are useless to a great many species, and must not enter into the calculation of temperatures which exert influence over them. Thus wheat, cultivated in a temperature always below 4°, will live a long time, and the product of the number of days by the temperature will rise very high; but the stem will not enlarge and no flower will be formed. M. Ch. Martins† correctly says, "Each species of the vegetable kingdom is like a thermometer which has its peculiar zero." It would therefore be wrong to suppose that

* *Economie rurale*, vol. ii. p. 659.

† *Voyage botanique en Norwège*.

10° during ten days would produce the same effect on all plants as 5° during twenty days. In both cases the sum of the heat is 100° , but for plants which will not vegetate under 6° , for instance, the number 100 ought to be diminished by all the values between 5° and 6° , which would occur in one of the cases; while for those which will not vegetate under 10° , if such exist, the useful heat would be reduced to 0° . Therefore, if we wish to estimate the heat *useful* to a plant, we must only regard in the calculations the values above a certain temperature, varying with the species in question.

To determine the conditions which define the limits of a plant, it is necessary to know at what degree of temperature its vegetation begins and ends; and further, what sum of heat it requires within this time; this may differ in different countries. The author therefore determined, for certain cities of Europe, on what day the temperatures of 1° , 2° , 3° , 4° , up to 8° , begin and end in an annual average; and the sum of heat received between the beginning and end of each of those degrees of temperature in each place. These calculations show an agreement between the climate of those places, which does not exist in the monthly averages or in those of the entire years, and which explains the very different limits of the plants. A plant, for example, which begins to germinate or to develop at a mean temperature of $4\frac{1}{2}^{\circ}$, ceasing at the same, and requiring a sum of 3430° , may extend in the north-west to London and in the north-east to Odessa. The mean temperature of $4\frac{1}{2}^{\circ}$ begins in London on the 17th of February and ends on the 15th of December; at Odessa it begins on the 3rd of April and ceases on the 18th of November; and these two places, so differently situated, give sums of heat which differ very slightly, 3431° and 3423° . The shorter interval is compensated by the greater heat of the summer at Odessa, but this compensation does not occur in the same way in those periods in which the temperature falls below $4\frac{1}{2}^{\circ}$ or 3° , or rises above 5° or 6° . Odessa and London lie neither in the same isothermal nor isochimeneal lines; even the monthly averages are different. *Alyssum calycinum*, an annual plant*, goes as far as Arbroath ($56\frac{1}{4}^{\circ}$ N. lat.) in Scotland, to 54° N. lat. in Holstein†, in Russia to 56° and 55° N. lat. The line of this does not coincide with any line of equal temperature, but agrees with the hypothesis that this species requires a

* According to the Rev. G. E. Smith (Phytologist, ii. 282), this plant is probably at least occasionally biennial.—ED. B. G.

† In Fries's 'Summa Vegetabilium Scandinaviæ,' *Alyssum calycinum* is stated to extend all through Denmark to the south of Sweden; *Euonymus europæus* occurs in Norway. (Note by a reporter on this paper in the 'Flora,' Nov. 21, 1848.)

heat of from 2280° to 2300° in the time between the beginning and end of a mean temperature of 7° . Edinburgh under $56\frac{1}{2}^{\circ}$, the north of Denmark, the south of Sweden (57° to 58° N. lat.), the island of Aland (60°), Moscow and Pensa (52°), are the limits of *Euonymus europæus*, a ligneous species. The annual averages vary upon this line about 4° , the summer temperature about 3° or 4° , the winter about 12.7° , but over the entire line the sum of heat is 2480° during the period of the year when the mean temperature is above 6° . *Dianthus Carthusianorum*, an herbaceous perennial, is limited in the west by humidity, but from Königsberg to Kasan, where the temperature limits it, the plant requires at least 2450° between the days of the beginning and end of the mean of 5° .

When hypotheses of this kind are thus repeatedly verified in particular cases, and, moreover, depend on incontestable principles of physiology, they may be said to correspond to a law. The law may be thus expressed here: "*Every species which has its polar limit in Central or Northern Europe advances as far as it meets with a certain definite sum of heat, calculated between the days of the commencement and termination of a certain mean temperature.*"

The apparent exceptions to this rule are explained by two causes which restrain its application:—1. Excessive moisture, as in the north-west, or excessive dryness, as toward the north-east, depending upon the position in regard to the ocean. Pretty generally this kind of cause determines the eastern and western limits of a plant, the next law that in the north. 2. Extreme cold in winter, which operates on herbaceous perennials, and especially on ligneous species. The limit given by this extends from the north-west to the south-east, as the greatest cold is experienced in the interior of the continent. It is often difficult to determine whether the limit on the east is given by cold or dryness, when the law above expressed ceases to apply.

In endeavouring to comprehend the effect of temperature on species solely by thermometric averages or *minima* of winter cold, it was impossible to explain why many species were limited at those very parts of Europe where the averages differed least in long intervals; of which Scotland affords a striking example. A multitude of species have their limits near Edinburgh, so that the flora of the country beyond the Grampians has always been considered as an appendage of those of Lapland and the Shetland Isles, rather than of the British. The law above laid down explains these facts. On account of the very uniformity of the averages in Scotland, a long interval elapses between the days when the temperature, for example, of 4° and that of the average of 5° begin. If then two species are so constituted, that one

commences an active vegetation at 4° , the other at 5° , the first will profit for a long time by a temperature which is useless to the second, and their limits will be considerably removed from each other. This is not the case in the eastern climates, where the passage from 4° upward occurs so rapidly, that all the species begin to vegetate about the same time. Thus in the west the initial and final temperatures necessary to a species are the most important influences; in the east the total sum of heat.

The law is doubtless applicable to the limits of species in altitude. It is probable also that by means of it, the flowering and ripening of species in different localities and different years will be explained; but there will be great difficulty in the application, from the nature of the facts to be observed and the variability of the years.

At the conclusion of the essay the author adds a few words on the bearings of his researches on geological problems. The actual limits of the species he has examined in the British Islands are always explicable by meteorological causes, and the material obstacle of the sea does not seem to have the slightest influence upon them. He thinks it improbable, in regard to several species, that their seeds have been transported across the sea; and is inclined to conclude that the Channel has been formed since the existence of the species. This opinion has already been sustained by Mr. Wilson (?)*, who explains in an analogous manner certain botanical relations between the British Islands and distant countries, such as Spain, the Azores, Lapland, &c. The case is different in regard to the islands of the Mediterranean; several cases may be cited where the absence or presence of a species cannot be explained by meteorological reasons. Thus, according to the observations of M. de la Marmora, not very complete it is true, the south of Sardinia presents the same conditions as certain parts of Sicily as to rains and monthly temperatures, but several Sicilian species are wanting in Sardinia, and *vice versâ*. *Chamaerops humilis* grows in Sardinia and at Villefranche near Nice, but is wanting in Corsica, between the two. In general, in spite of certain evident analogies in the vegetation, the islands and peninsulas of the Mediterranean present numerous anomalies in the limits of species. It appears that this region must have been disturbed by many successive geological changes since the existence of the plants of our epoch, and that accidental transport of seeds has not been sufficient to bring back the limits into accordance with the climates.

* On the Connection between the Distribution of the Existing Fauna and Flora of the British Isles with Geological Changes; by Ed. Forbes. Mem. of the Geological Survey of Great Britain, &c., vol. i.