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THE TEMPERATURE INTERVAL IN THE GEOGRAPHICAL DISTRIBUTION OF MARINE ALGÆ[1]

The idea of geographical distribution came as a new and inspiring, although rather indefinite, concept to the German fathers of botany in the latter portion of the fifteenth and earlier portion of the sixteenth centuries. The attempt to explain geographical distribution according to the influence of environmental factors began, practically, with Alexander von Humboldt in 1805. Since his time, temperature has generally been regarded as the chief limiting factor in climatic distribution. In 1893, I called attention to the relationship existing between the position of the isotheres (mean maxima for the hottest month) of 10°. 15°, 20°, and 25° C. of the surface waters of the oceans and the limits of distribution of certain groups of kelps (Laminariaceæ). In 1894, and again in 1898, C. Hart Merriam proposed dividing the United States into certain "life-zones" or "crop-zones" according to the "summation-indices" of the temperature of the frostless season and showed the close relation of the boundary lines of these "zones," or belts as they may be more distinctly designated, to the isotheres (isotherms of mean maxima for the six hottest weeks of the season) of 18°, 22°, and 26° C. In 1913, Livingston and Livingston proposed a series of "efficiency indices" for use in plant distribution and climatology, presumably resting upon more of a physiological basis than the summations of temperature or statistical relations to various isotherms. The efficiency basis of their system is founded upon the application of the van't Hoff-Arrhenius principle as to the velocity of vital activities at different temperatures. In

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1915 and in 1917, I brought forward additional facts bearing on the relation of the 0°, 10°, 15°, 20°, and 25° C. isotheres and added arguments for the careful consideration of the relation also of the 0°, 10°, 15°, 20°, and 25° C. isocrymes, or lines of mean minima, *i. e.*, the mean temperature of the coldest month, of the surface waters of the oceans, to the demarcation, or division, points in the marine floras.

The various writers I have just cited take up the subject of the relation of temperature to distribution almost entirely from the distributional side. They show certain, at least, of the relations of the intensity- and duration-variables in their influence on those activities of the organisms which make for persistence in the particular localities where they are to be found permanently. The activities controlled are, undoubtedly, all the necessarily vital activities of the organism, but we may feel fairly certain that those subject to the special control of the limited temperature interval are those more or less immediately connected with reproduction. In general, it may be said with some confidence, that the reproductive activties are carried on at the maxima of the temperatures at which the plant is actively and most normally performing any of its strictly vital functions. The initial temperatures, *e. g.*, those of the germination of the seeds or spores, are undoubtedly lower, in most cases at least, as are also those of most rapid growth and those of the most active metabolism. All, however, have their optima which are the temperatures connected with successful and orderly development, within comparatively narrow limits and are to be considered apart from the temperatures possibly to be endured in states of rigor, but without immediate death. Most of the physiological experiments on the influence of temperature on plants emphasize their sensitiveness as regards intensity, but do not yield many data bearing on duration effects of slightly unfavorable temperatures such as are most desirable for assisting in the solution of the problems of geographical distribution. A notable and illuminating discussion between the two different points of view is shown in the controversy between A. J. Ewart (1896 and 1898) and W. and G. S. West (1898). Ewart argues from the point of view of an experimental worker in the laboratory, testing under controlled conditions, while the Wests bring forward from their long experience in the field, seemingly discordant facts.

Phenologists are acquainted with many facts that tend to show the close relations existing between certain intensities of temperature and flowering in certain plants, particularly in fruit trees of temperate regions. Certain exotic ornamentals may live on from year to year in certain localities and never blossom. Some such may blossom in an occasional warm season, but not produce seeds, while the same species, in some sheltered and warmer spot in the same general region may flower every season and even produce scanty or abundant seed. Some plants may blossom only where the sun strikes them, on the southern side, in the northern hemisphere. In a hedgerow, the spotwise blossoming is often very noticeable and can readily be traced to insolation. I have watched such a hedge of Laburnum in Berkeley, California, in which the spots receiving the most sun blossomed out a week or more earlier than the rest. I have observed rows of *Azalea californica* in the neighborhood of the Yosemite Valley, largely shaded by tall trees, blossom only in the spots where the sun penetrated to them. Many such instances might be evidenced, but the resultant inference is the same. Lloyd (1917) has recorded his observations on the "Critical flowering and fruiting temperatures for *Phytolacca decandra*." At Tucson, Arizona, this species produces flowers and seeds in abundance, but at Carmel, California, a locality of decidedly lower temperature maximum, it fails to do so, although, otherwise, it grows well and apparently normally. Plants grown in a small glass shelter at Carmel, however, produced an abundance of flowers, fruits and perfectly viable seeds. In one or two instances single branches of plants without the shelter, but in sheltered positions, also bore seeds. As a result of temperature readings under the different conditions, Lloyd came to the conclusion that raising the temperature not over 5° F. would be sufficient to produce normal flowering at Carmel. M. Moebius (1897) has treated of the matter of temperature in his "Beiträge zur Lehre der Fortpflanzung der Gewächse" and brings forward many authenticated cases of the effects of changes of temperature on the flowering and fruiting habits of plants. He calls attention to the fact that plants provided with effective methods of vegetative multiplication, such as the members of the Lemnaceæ, may occur in abundance in cooler regions, such as Central Europe, but seldom or never (Wolffia) fruit, while they bloom and fruit abundantly in warmer regions where they are equally common. The difference in temperature in these cases is partly of greater intensity, although presumably not considerably, partly also of duration of the higher intensity.

It seems to me that it is this narrow interval of temperature which separates the carrying through of reproductive processes from their inhibition, that is indicated by correspondingly narrow temperature interval between the isotheres and isocrymes which seem to delimit so accurately the different floras from one another. From the physiological point of view, there seems to be indication that the optima of effective reproduction which makes for persistence in distribution, lie within an interval of 5° C., an interval surprisingly narrow. The controlling influence of this narrow interval, however, so far as the persistence of the various species in any zone or zones is concerned, seems well substantiated by the various tabulations and critical examination into seemingly exceptional cases which I have made and published elsewhere. The overwhelming majority of the known marine algæ of the world are recorded from only one zone. A considerable number are said to occur in two zones, a very few in three zones and a very small percentage in four or five zones. It seems, therefore, fairly certain that the normal interval is one zone of 5° C. amplitude and that the invasion of other zones than the normal is due to the existence in the invaded zones of temperatures of the same intensity and duration found in the normal zone. This has been shown in a sufficient number of cases to indicate that it is to be looked for as a general rule.

There is another interval besides that mentioned above, which has more or less to do with the life, normal and invading, of any particular zone and that is the interval of amplitude of seasonal variation in temperature in each zone. There may be certain portions of the tropical zone in which there is little, if any, seasonal change of temperature. In certain portions of the oceans, free from currents of a strongly influencing nature, the isocrymes and isotheres 5° C. apart are very nearly superposed and it seems logical to assume that this seasonal interval is normal. The extreme interval in portions of zones thus affected is, therefore, 10° C. in amplitude, the interval between extreme mean maxima and mean minima estimated from monthly variations. This interval, viz., 10° C., may be assumed to be the interval of optimum temperatures for persistence and including all actively vital processes of the particular species normal to any zone. There are regions in some zones, however, where the mean seasonal variation alone amounts to 18° or 20° C. It is undoubtedly a fact that where the seasonal interval is large and particularly where it is much greater than 5° C., the species normal to the zone pass the colder portion of the season in a state of quiescence, or rigor, either in the vegetative or in the seed or spore stages of development. In the colder seasons of any region of a zone suffering a considerable seasonal interval, the invading species from a lower zone are to be found in vegetative and reproductive activity and pass into a condition of quiescence when the temperatures characteristic of the zone prevail, a sort of heat rigor. As a result of the extreme seasonal variation in temperature of the northeastern coast of North America, for example, *Ascophyllum nodosum,* one of the rockweeds or Fucaceæ, whose normal zone is the region of Greenland in the upper boreal zone and where it develops its vegetative body and fruits abundantly in summer and below the isothere of 10° C., extends south to the northeastern coast of New Jersey where it develops and fruits at the winter and spring temperature of 5° C., but is sterile and evidently quiescent at the summer temperature of 22° C. Since it is a perennial species, it is to be found in the southern portions of its range among the summer subtropical species of the Long Island Region and this is extremely misleading until the conditions of its existence south are understood. When these are made clear, it stands out as a conspicuous and convincing example of the narrow interval of temperature making for persistence.

Connected with these narrow intervals seeming to control persistence in certain groups of species of marine algæ and limit their distribution, there is associated the observed fact that the 10°, 15°, 20°, and 25° C. isotherms of the surface waters sharply mark off the life-zones from one another. This conclusion comes as a result of the critical study of the relations of these isotherms to certain well-known division points, or demarcation areas, between distinct floras. In a recent study of the relation of Cape Cod to the floræ of the New England coast, where I had at hand detailed information of greater abundance, variety and accuracy than it is generally possible to obtain about such matters, I found that the isothere of 20° C. certainly seemed to divide very sharply the northern species as to their distribution, from the southern. The details of this investigation will be published elsewhere, as it is unnecessary to go into them here, but I desire to mention one which will emphasize the point I am trying to make evident. At the entrance to Vineyard Sound, between Gay Head on Martha's Vineyard and Sow and Pigs off the southern end of the Elizabeth Islands, as Sumner and Davis (1913) have shown in various charts, the surface temperatures in summer are slightly above and the bottom temperatures are slightly below 20° C. and the southern species are found in the surface waters, while the northern species inhabit the depths. This, it must be remembered, is only one example of a considerable number which might be cited, to show how abruptly species stop or start in their distribution at one or another of these isotherms. The marine algæ extend slightly below 0° C. Thus far I have not been able to determine satisfactorily the conditions at the 5° C. isothere, but the 5° isocryme seems possibly a limiting line. There can be no question, as it seems to me, but that the isotherms, both isotheres and isocrymes, of 10°, 15°, 20°, and 25° C. definitely limit the extension of particular floras of marine algæ and that too, very sharply and exactly.

The explanation of the narrowness of the temperature interval seemingly, at least, of such paramount influence in controlling distribution, is by no means clear. If we lay stress on the interval of 5° C. which seems to control reproduction, we have no physiological basis at present apparent. If we consider the probability that the normal interval of each zone and its peculiar flora, is 10° C., then we may perhaps feel inclined to suggest that each marine algæ may persist up to the point where its initial vital activities, in accordance with the working of the van't Hoff-Arrhenius principle, may be doubled in velocity, but no more. In case this may be the proper explanation, the interval of 10° C. seems to be more exact and regular than it has been found to be even as determined for purely chemical reactions. Possibly the temperature intervals may have to do with the varying viscosities of the sea-water or its power to dissolve gases such as oxygen or carbon dioxide. On the other hand, it may have to do with the activities of some particular enzyme or group of enzymes which act effectively, as these are known to do, only within narrow limits of temperature. I feel, therefore, that I can do little more at the present time, than to lay emphasis on the narrowness of the interval and the seeming importance of the maximum and minimum isotherms very closely approximating 5° C. apart.

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