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Temperature Coefficients in Plant Geography

Temperature Coefficients in Plant Geography and Climatology. by B. E. Livingston; Grace J. Livingston

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here pointed out, of the residual soil moisture to the aerial environmental complex, becomes discoverable.

That we have in the water content of the soil at the time of permanent wilting, when determined under adequately defined conditions of evaporation, a function destined to be of great value to plant physiology and to scientific agriculture is beyond question. It is scarcely less certain, however, that the use of a living plant as an indicator of soil conditions must lead to very considerable error unless the experimentation be carried out with low evaporation rates, or accompanied by adequate determination and statement of the aerial conditions. In the wilting of the plant we are dealing not with a simple physical phenomenon but with a complex physiological problem, a change of condition in living protoplasm. The properties of the soil in which the plant is rooted constitute merely one of the group of environmental factors which collectively operate to bring about this change.

For details of the author's methods, and for his extremely valuable historical account of earlier work on the subject dealt with, the original paper should be consulted.

TEMPERATURE COEFFICIENTS IN PLANT GEOGRAPHY

Livingston, B. E., and Livingston, Grace J. "Temperature coefficients in plant geography and climatology." *Bot. Gazette*, **56**, 1913, pp. 349—375, 3 maps.

Although temperature has long been recognised as one of the most important of the conditions governing the distribution of plants and animals, little has been ascertained regarding the quantitative relations existing between the nature of plant and animal associations and the temperature conditions geographically concomitant therewith. The progress of descriptive ecology has shown that these associations have their geographical limits, and increased accuracy in description has developed hand in hand with the idea that the boundaries of associations represent the limits of certain complexes of environmental conditions. The descriptions of the climatic complexes characterising the vegetational or faunal dealt with in various recent papers on plant and animal ecology and geography have usually consisted in the mere quotation or compilation of various meteorological data. In order to correlate these data with physiological phenomena, in such a way as to throw light upon the effective climatic characteristics of the areas occupied by different associations, it will be necessary to devise methods, and frequently also instruments, by which the climatic conditions of any given area may be so integrated as to bring out their relations to the processes of growth and reproduction in organisms. At first, such methods will usually need to deal with single conditions or factors as they influence physiological phenomena, but biological science must eventually appreciate that single conditions, or any group of conditions comprising less than all the effective ones, cannot be considered as determining natural processes. Complexes of environmental factors must be analysed into simpler ones for purposes of study, but after the effectiveness of each has been experimentally ascertained—by maintaining all conditions other than the one in question constant and at a known and stated value or intensity—they must be recombined and their effects integrated before real knowledge is available.

The difficulty which ecological science has yet to surmount lies in the extreme complexity of the system of conditions which affect the success of organisms. The numerous factors of an environmental complex fall into categories of water, non-aqueous materials, heat, light, and mechanical conditions, to any one of which may belong the limiting condition that has prevented the occurrence of a given plant, for example, in a given area—mechanical conditions may have failed to bring the seed hither, moisture conditions or other conditions or material supply or removal may have annihilated the plant after it was really introduced, or annihilation may have followed from adverse temperature or light conditions, etc. The problem is further complicated by the obvious though seldom emphasised proposition that each separate or component condition of an environmental complex is a variable in at least two dimensions—intensity and duration. For instance, dried soil may cause the death of a seed, but this would probably not happen if the

soil were dry for only a day or a month, the condition of dry substratum must be maintained for a certain minimum period to be effective as a limiting condition. Some less well defined factors have to be considered in regard to a third variable dimension—quality; light for example may reach chlorophyll tissue in apparently sufficient intensity and during an apparently sufficient time period to produce a requisite amount of carbohydrate, but this may fail to happen because the radiant energy is of too short or too long wave-length, and thus quality here becomes as important as either intensity or duration. Finally, the difficulties of distributional as of other physiological problems are greatly increased by the fact that each organism is always in process of internal alteration, passing through various more or less well defined phases of development—thus a certain quality, intensity and duration of the light condition may be without sensible effect upon an unsoaked seed while the same dimensions of the same factor may be fatal to the same plant when in a more active developmental phase. Hence in studying external conditions it is useless to attempt to establish relations between these and organisms unless adequate consideration be given to internal conditions or developmental phases of the latter, and quantitative ecology must determine not only the environmental conditions to which the organisms are subjected and to what degree and for how long these conditions are present, but also during what developmental phases the conditions are effective.

Following these general considerations, the authors point out that the great desideratum for ecological and biogeographical studies, and for all other studies dealing with the conditioning or causation of life processes, is comparative measurements of these processes, or of groups of them, and corresponding measurements of the conditioning environmental factors; that special methods must be devised and applied for which there are at present no satisfactory facilities, measurements possible in present-day laboratories being applicable in some cases (especially with forms not influenced by light) but quite inadequate for making even a rational beginning in the quantitative study of environments in general; that in planning a campaign for such study any given environmental factor, as well as all the other effective ones, must be under control by the experimenter; but that until such facilities are available the way may be paved by carrying out such quantitative or semi-quantitative comparisons between vital activities and environmental conditions as are at present possible.

The present paper deals with an attempt to find a rational method for interpreting climatic temperature data for phytogeographic purposes, the matter being somewhat simplified in the case of plants since the temperature of the plant body follows very closely upon that of its surroundings, soil temperature and air temperature are roughly speaking closely related, and the heat condition of plants (as approximately measured by the temperature of the surrounding air) varies only in respect of intensity and duration. Geographically the study deals with the area of the United States.

The effectiveness of temperature conditions to promote plant growth in any locality has been measured by phenological observations involving direct summation of the daily mean temperatures, such summation extending through the period of any particular phase of plant development considered—for instance the period extending from the time of germination to that of flowering or of seed maturation. In these summations a certain minimum temperature (sometimes $0^{\circ}\text{C}.$, but more often a somewhat higher temperature) is assumed as a starting-point, and the amount added to the summation for each day as the season advances is the number of degrees (above the assumed minimum) which represents the mean temperature for that day. In using such temperature summations each station of observations is characterised each year by its summation index, and after a period of years these indices may be averaged to give a measure of the temperature factor in general for that particular place. In a somewhat similar way Merriam obtained summation indices of temperature for numerous stations in the United States and presented these as a chart showing climatic zones each with its own range of temperature summation indices; his temperature zones have come into fairly general use by American phytogeographers. Macdougall summed the temperatures above $0^{\circ}\text{C}.$ for the period occupied by certain developmental phases of certain plants, but instead of adopting as the terms of the summation the daily means or the means of daily maxima and minima his integration was made with a planimeter upon automatically traced thermograph records, the resulting indices of environmental heat conditions being expressed in terms of hour-centigrade-degree units.

Although such temperature summations as those of the phenologists and of Merriam have often appeared to give data consistent among themselves and forming on an empirical basis an apparently reliable criterion for the measurement of the intensity and duration aspects of the temperature factor, the authors consider that probably no fundamental principle regarding the influence of temperature on plant life may be derived from the relations thus brought out, and that the apparent value of such summations must rest upon some basic principle of physiology not indicated in the summations themselves. As regards temperature influence the most fundamental generalisation yet attained by physiology is the principle of temperature coefficients, which is primarily the application to vital phenomena of the chemical principle of van't Hoff and Arrhenius—that, within limits, the velocity of most chemical reactions doubles or somewhat more than doubles for each rise in temperature of 10°C . The results of various observers have shown that at any rate the elementary chemical processes involved in the relatively simple physiological processes investigated go on according to this principle, and that such processes possess temperature coefficients, within the ordinary limits of environmental temperatures, of an order of magnitude of from 2.0 to 2.5. When however many of these elementary or component processes are combined into a complex resultant, such as we have in growth for example, it is not immediately clear on *a priori* grounds that temperature coefficients of this same order of magnitude must obtain, but it should be remembered that the principle, even for simple chemical reactions, holds only between certain limits and that these limits cannot be expected to be the same for all processes, also that the full possible effect of a rise in temperature is frequently precluded by the failure of some other environmental condition to alter correspondingly. While there are a good many cases in which growth rates and other complex processes in plants and animals show temperature coefficients of about 2.0, in other cases this coefficient is probably operative though obscured by the limiting effect of some other environmental or internal condition.

Granting that the processes of growth and development show temperature coefficients, it is obvious that the study of environmental integrations should deal with these rather than with temperatures directly, and that if direct temperature summations furnish in some cases adequate criteria for evaluating the effectiveness of temperature conditions this must be true only within certain limits, also that the experimental study of temperature coefficients gives the only adequate means of locating these limits and establishing the direct summations on a rational basis. In their attempt to apply velocity coefficients to the study of effective temperature conditions as these characterise climatic and vegetational areas, the authors have assumed tentatively that the temperature coefficient of growth and development has a value of 2.0 for each rise of 10°C ., a value approximating those that have so far resulted from most physiological studies of temperature relations. This value seems likely to be too low for ranges of temperature commonly met with in nature, indeed its magnitude will probably be found to vary not only with different plant forms and with different stages of development of the same form but also with the values of the temperatures considered; the relation aimed at may be determined satisfactorily only by the use of a temperature coefficient which is itself a variable, changing in value with the progress of the organism through its life cycle and with the annual march of the seasons as well as with variations in the temperature itself.

Having thus tentatively established the intensity factor—the temperature coefficient to be taken as a measure of the effectiveness of temperature in advancing growth—a similar assumption must be made in the case of the duration factor. The time factor adopted by the authors is the average or normal length of the frostless season, the number of days which intervene between the last killing frost in spring and the first in autumn, as given by the observations of the U.S. Weather Bureau. The plan of their study is (1) to sum the normal daily mean temperatures of each station considered, for the period of the average frostless season; (2) to sum the temperature efficiencies corresponding respectively to the normal daily means and to the adopted coefficient for 10°C . of variation; (3) to plot both sets of temperature indices so obtained in the form of charts; and (4) to compare the form and location of the climatic areas or zones thus exhibited.

From the results obtained the authors arrive at the following conclusions. (1) The method of direct temperature summations has proved itself to give, in a broadly general way and for most of the area of the United States, nearly the same climatic zones as does the method of efficiency

summations; hence for practical purposes and for the present, the former method, till now based solely on phenological observations, seems thus to be placed in closer logical connection with the temperature coefficients of chemical, physical and physiological processes than has hitherto been the case. (2) The similarity between the results derived by these two methods of temperature integration is, however, only superficial and roughly approximate; the ratios of direct summation to efficiency summation range in magnitude, for the mean frostless season in the United States, from a minimum of 7.49 to a maximum of 10.44. (3) A rational and consistent climatic chart represents the geographical distribution of these ratio values; on such a chart the marginal regions of the country are frequently characterised by low ratios, and the two main mountain systems (Appalachian and Rocky Mountains) appear to control areas of high values. (4) There seems to be no doubt that the ratio here brought forward represents a climatic dimension or characteristic, which appears to be some sort of function of the daily normal temperatures upon which this whole study has been based and of the time distribution of the temperature data within the period of the mean frostless season.

A QUANTITATIVE STUDY OF WATER-CULTURE SOLUTIONS

Tottingham, W. E. "A quantitative chemical and physiological study of nutrient solutions for plant cultures." *Physiol. Researches*, **1**, 1914, pp. 133—245.

This paper on nutrient solutions will be of great use to all whose researches necessitate investigations into the nutritive solution of plants or the use of the water-culture method; and although not primarily an ecological paper it is one which has much bearing on some aspects of ecology.

The paper is divided into three parts. Part I consists of a concise and valuable *résumé* of the work that has been done up to now on water-culture. It is shown that the use of water-culture methods falls into three periods. (1) The early period, ending about 1860, established the idea of the soil minerals as a source of the nutrient material of plants. (2) The middle period, from 1860 to about 1900, established the value of water-culture for certain classes of problems and evolved also standard nutrient solutions for use in this method. Chief among the results obtained by the method in this period was the determination of the essential elements for plant nutrition. Other facts were also indicated, such as an optimum total salt concentration (0.3 % or lower if the solutions were changed frequently), although it was found that the relative amount of different salts could vary within rather wide limits without producing any apparent injurious effect. Selective absorption and excretion of certain salts were also indicated. (3) In the third and present period it is the selective absorption of ions rather than complete salts that is indicated, and so by this means the composition of the nutrient solution becomes altered. The importance of a physiological balance between the various elements in the nutritive solution has also been emphasised during recent years.

The author finishes this part of his paper by pointing out the great variations in relative amounts of different substances in the various standard nutrient solutions, and so concludes that it is justifiable to make "a thorough investigation of the relative values of different proportions of the salts employed in such culture media." The remainder of the paper constitutes the beginning of such a piece of work.

In Part II a chemical study is made of Knop's solution, as a result of which the most satisfactory method of making up a stock solution is described. It is desirable of course to make up a solution which is of as high a concentration as is consistent with stability. Tottingham suggests using two stock solutions, one of calcium nitrate alone, the other containing the other necessary salts. The latter solution is stable for about 14 days at a temperature of 23° C. in a concentration of 9 % or 10 % according as K_2HPO_4 or KH_2PO_4 is used as the source of