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Environmental Conditions and Wilting in Plants

The Relation of Environmental Conditions to the Phenomenon of Permanent Wilting in Plants. by J. S. Caldwell

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The working theory now formulated, however, is that the humus as a colloid holds all or practically all the water in a humous soil when other colloids such as clay are absent, so that even with relatively small humus contents the water-holding power of the non-colloid constituents may be neglected. Passing over the author's further discussion and omitting the many details, tables and formulae for which the original paper must be consulted, we give the following summary with which the author concludes his interesting contribution and indicates the lines upon which the thorough study of definite habitats—the only possible method if the coefficient of soil humidity is to be of service in ecology—can be prosecuted with advantage. (1) The mean value of this coefficient is the most important constant to be ascertained for every association whose distribution and existence are determined by soil moisture. (2) The coefficient for every such association will, however, prove to have a considerable variation from its mean value; given a sufficient number of estimations this variability would be best expressed by the “standard deviation,” but in practice it would be enough to ascertain the maximal and minimal values of a considerable number of estimations—these values mark the limits of the association and are probably determined by competition with other associations whose mean values are different. (3) There will also be a supramaximal and a subminimal value for any association or its component members, determined not by competition but by the physiological relations of the root systems with the soil water; when these values are reached and maintained the association can no longer continue to exist. (4) The subminimal value of the coefficient for any association will represent, and be the appropriate expression of, the *echard*. (5) The soil moisture index of an association will be fully determined by finding the five values—mean, maximal, minimal, supramaximal, and subminimal—of the coefficient of soil humidity. (6) These considerations only hold good at present in cases such as those considered by the author, where the humus practically holds all the soil water—that is, where there is no “free” water in the substratum, nor sufficient colloid clay to affect the balance.

ENVIRONMENTAL CONDITIONS AND WILTING IN PLANTS

Caldwell, J. S. “The relation of environmental conditions to the phenomenon of permanent wilting in plants.” *Physiological Researches*, **1**, 1913, 56 pages; price 75 cents.¹

The author of this interesting and valuable paper gives a useful historical summary of earlier work as a preface to his own observations. His main object was to discover (*a*) whether the water content of a given soil at the time when plants growing therein become permanently wilted remains a constant when wilting occurs under widely varying environmental conditions, and can therefore be determined with accuracy by calculation from the known physical constants of the soil, and (*b*) whether there is a definite and constant relation between the water content of the plant and that of the soil at the time of wilting, under such varying conditions.

The author summarises his chief results in the following 14 paragraphs.

(1) For large numbers of turgid individuals of the same age and species, the average water content of all the normal functioning leaves is approximately a constant under the midsummer conditions of southern Arizona. Departures of individual plants from the average normal foliar water content for the species were few and small in the five species studied.

¹ This new periodical, edited by B. E. Livingston, D. T. Macdougall, and H. M. Richards, will embrace contributions toward the advancement of a fundamental physiological knowledge of plants and animals. Each volume is to contain not less than 450 pages; each research is issued separately, preceded by an author's abstract, which is also reprinted in connexion with the full paper. Subscriptions are received either by the volume (5 dollars; abstracts alone, 50 cents per volume), or numbers can be purchased separately at prices to be announced in connexion with the respective preliminary abstracts; remittances should be made payable to “Physiological Researches,” Station N, Baltimore, Maryland, U.S.A.

(2) Plants beginning to lose turgor in the youngest leaves show an average foliar water content which is fairly constant for the species and which bears a definite ratio to the average normal water content for turgid individuals of that species.

(3) Temporary wilting of the younger foliage is of frequent occurrence and is conditional only upon a temporary, but more or less prolonged, maintenance of the rate of transpiration at a magnitude in excess of the rate of absorption for the same period; hence this form of wilting is related not merely to the moisture content of the soil, but also to aerial conditions, especially to the evaporating power of the air and to the intensity of solar isolation.

(4) The moisture content of the normal functioning leaves, taken collectively, at the time of *permanent* wilting, was found to be approximately constant for all individuals of the same species, at the same stage of development. This constant is unaffected by the external conditions under which wilting occurs; wiltings under all the conditions of the experiments yielded practically identical results.

(5) When wilting occurs in a shaded moist chamber having a nearly saturated atmosphere, the ratio of soil moisture content at permanent wilting, as found by actual determination, to that obtained by calculation from the physical constants of the soil, is approximately unity for all the soils used.

(6) For wiltings occurring under partial shelter or in the open, with relatively high evaporation rates, the ratio of observed to calculated soil moisture content at permanent wilting is always greater than unity.

(7) Under any given set of aerial conditions the observed soil moisture content at permanent wilting is approximately a constant for each of the soils used, and its value increases with increase in the rate of transpiration, being greater under conditions of high evaporation intensity and declining with decrease in the evaporating power of the air. For a series of plants grown in any one soil, and wilted under a number of different aerial conditions, all with relatively high evaporation rates, as many different soil moisture contents at permanent wilting are obtained as there are sets of conditions. Each of these is approximately a constant for all plants of that species undergoing wilting under identical conditions.

(8) The departure of the observed from the calculated soil moisture content at permanent wilting is greatest in soils having very low saturation capacities, and becomes steadily less as the water-holding power of the soil increases.

(9) Under the conditions of maximum evaporation prevailing at Tucson in the summer, the departure of observed from calculated soil moisture contents at permanent wilting is extremely marked for all soils; permanent wilting in the open occurs with a soil moisture content from 30 to 40 per cent. in excess of that present when the same or similar plants are wilted in a moist chamber.

(10) The progressive rise in the evaporating power of the air, as it occurs in the open during the progress of a single day, affects the moisture residue in the soil at permanent wilting as observed for plants wilting on that day; those plants attaining the permanently wilted condition at or near noon invariably show higher soil moisture percentages than do those wilting at an earlier hour.

(11) Transfer of plants from a location of lower to one of higher evaporation rate, or the reverse, just prior to the onset of permanent wilting, does not alter these general results; the soil moistures found are approximately similar to those obtained for plants grown and wilted under identical conditions in the same situation.

(12) Permanent wilting is a definite protoplasmic condition, brought about by reduction of the water content to such a point that loss of turgor has become established throughout the entire plant. When such a loss of turgor has been rapidly produced, as by high transpiration in the open at Tucson, the root hairs are found to be plasmolysed, but such root hairs promptly resume their normal appearance and functions when water is again applied to the soil. On the other hand, when loss of turgor has been very slowly attained, as is the case under conditions of high relative humidity and but slight air movement, there results a general death of the root hairs. This is shown by more pronounced plasmolysis than that occurring in the case just mentioned, by cessation of protoplasmic streaming, and by subsequent disintegration, even after abundant water has been supplied. Recovery of turgor in such plants, because of the great reduction of

functional absorbing surface, is a slow process requiring from 48 to 72 hours for its completion, whereas plants wilting in the open with high transpiration rates, recover about twice as rapidly after water has been supplied to the soil.

(13) The condition of permanent wilting may result from the operation of either one or both of two factors, (a) decrease in the soil moisture content and (b) loss of water from the plant by transpiration. The attainment of the permanently wilted condition indicates a certain degree of reduction of the amount of water contained within the organism. When this condition is reached under environmental conditions such as those of a moist chamber or an adequately controlled greenhouse,—with low evaporation rates and without great variation in the evaporating power of the air,—it also indicates a concomitant reduction of the amount of soil water to a definite limit. Marked increase in the evaporating power of the air accelerates the outgo of water without producing a proportionate increase in its rate of entrance from the soil. With every increase in transpiration rate above a certain limit, this rate becomes, therefore, more and more significant as a factor determining the extent to which the soil water may be exhausted by the plant before the advent of permanent wilting. Thus, permanent wilting under high rates of evaporation does not at all indicate that the available soil moisture has been exhausted. Instead, it merely indicates the reduction of the soil moisture content to a magnitude which corresponds to the residue of water left in the soil at the time when excess of transpiration over absorption has brought the entire plant into the permanently wilted condition. Repeated determinations, under widely varying conditions but with relatively high evaporation rates, show that the magnitude of this residue is directly related to the intensity of the evaporating power of the air.

(14) Except with relatively low rates of transpiration, any method which employs the permanent wilting of the plant as an indicator of soil properties must be accompanied by adequate characterisation of the aerial conditions under which the tests were carried out; otherwise the results cannot be available for comparison with those obtained under other aerial conditions.

General conclusion. Permanent wilting appears to be a condition of general plasmolysis, but not of death, in all the tissues of the plant, with accompanying cessation of certain of the protoplasmic activities. This condition is characterised by a water content of the functioning foliage which is nearly constant for any species. The reduction of the water content to this point is the resultant of the action of transpiration versus root absorption; if aerial conditions permit these two processes to go on at approximately equal and moderate rates until the water supply fails at its source, there remains in the soil a quantity definitely related to the physical constants of the soil—the “wilting coefficient” of Briggs and Shantz. If transpiration be long maintained at a rate considerably exceeding absorption permanent wilting is attained irrespective of the presence in the soil of more than the theoretical quantity of water which corresponds to the “wilting coefficient” of these authors. This excess of soil water is only effective temporarily to preserve the life of the root hairs; its amount is more or less definitely related to the aerial conditions prevailing throughout the period of wilting and rises with increase in the transpiration rate. Thus the only constant with which we have to deal in cases of wilting under widely varying conditions is a physiological constant, a condition of the plant protoplasm with respect to water, which arises as a result of the interaction upon the plant of a complex of external conditions—of these the soil moisture content is only one. The soil moisture content at permanent wilting is therefore a variable which increases with change in the value of the other terms of the equation, especially with increase in the evaporating power of the air beyond a certain limit; and it is not to be considered as independent of these other terms. In this respect the conclusion of Briggs and Shantz that the soil moisture residuum here considered is constant under a wide range of aerial conditions, must obviously be modified. The relatively constant moisture contents of the soil at permanent wilting that were obtained by these authors are precisely what should be expected for aerial conditions such as they describe as prevailing in the greenhouse where their experiments were carried on. Equally constant but quite different and higher values should be obtained wherever plants are wilted under conditions which maintain a relatively uniform but considerably higher rate of transpiration than prevailed in their experiments. It is only when the results of experiments made under widely varying conditions are compared that the relation

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