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TRANSPIRATION IN RELATION TO GROWTH AND TO THE SUCCESSIONAL AND GEOGRAPHIC DISTRIBUTION OF PLANTS.*

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In former publications (Botanical Gazette 49; 325-339, 1910; Ibid 54; 503-514; Bulletin 16, Geological Survey of Ohio, 1912) the writer invited a closer consideration of a number of points of interest to students of modern phases of Botany. Among other matters, attention was called to the fact that while the presence of structural modifications is generally regarded as a condition in favor of certain plants which are limited to habitats favorable to them, the more noteworthy characteristic is very likely functional variability, when plants extend the areal range beyond their typical habitats. It is a well known fact that plant migrations are not completed as yet, and that vegetational limits are determined more frequently by developmental than by climatic or edaphic conditions. European ecologists especially have furnished notable instances of this character, and the more important results of the several International Phytogeographic excursions into various parts of the world tend to give prominence to the problem of functional plasticity in plants of the same species, but of ecologically and geographically separate regions. Relative power of endurance and acclimatization are questions of special significance also in the existing peculiarities of scattered geographical distribution as well as in physiological ecology.

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Examples of a more local nature are cited in Bulletin 16, in the chapters dealing with the historical factors of bog vegetation and the succession of vegetation upon peat soils. It is there shown that areal movements of vegetation during remote geological periods of time as well as to-day, are determined partly by the external conditions to which a plant or the social aggregate is exposed and partly by the functional limits of the organic units, these two sets of factors themselves progressively changing as vegetation types evolve. A further consideration of importance is the theory entertained that the change of conditions, in the remote past, following the accumulation of organic soil (peat-like in nature) and the invasion of it by organisms originally aquatic, had played a prominent part in the establishment of a land flora and the further differentiation of it into those alternating phases of the life cycle which are so characteristic of archegoniate plants.

In the work of an experimental nature, the writer brought out the fact that the point of most importance which should be noted in this connection is the difference in the water requirement of plants. The experiments cited showed clearly that transpiration is not a measure of growth even under the same atmospheric conditions, and can not be looked upon as the most striking criterion for such colonists among plants as are steadily coming into a new habitat and succeed to establish themselves as dominants or in competition with the plants constituting the association.

The term "water requirement" is a word which enjoys the advantage of brevity as well as euphony, but it is also another instance of the rather numerous cases in the literature of applied botany of the misleading use of terms. It is assumed by many writers that a definite and quantitative relation exists between transpiration and growth, and that hence the ratio of the weight of water absorbed and transpired by a plant during its growth to the green or dry substance produced is an adequate and simple measure of growth. The generalization from the data presented by them is too broad; it is seriously inadequate to account for numerous exceptions in the investigations bearing on this subject, and is certain to lead to error. It is needless to say that any measure of "the agricultural duty of water," of the water economy of crops or of native vegetation types; any action looking toward the better utilization and management of water resources for irrigation; any estimation of the capacity of a land area for crop production or for the probable future population it may support; any study of the geographical movement of vegetation, if made on the basis of this standard of water use in relation to plant growth, must be influenced by the congruity of the relationship and the magnitude of the value involved.

It is necessary either to abandon the term, because investigators are no longer certain of denoting consistent results obtained by means of the value, or to change the meaning of the term so that it may carry with it the implication which appears in the experimental results of various workers.

In most of the research that has been made on the water requirement of plants the investigators have not fully considered the relation of transpiration to growth. Transpiration is undoubtedly of value as an indicator of different soil and climate conditions and in exhibiting differences which exist between different species and varieties of plants. The general literature bearing upon transpiration has been so well brought together and summarized that a review of it need not be given here. Among the· different factors which are directly related to the problem and which affect physically the transpiration value of plants may be mentioned the water content of the soil, the saturation deficiency of the air, and the character of the plant, length of active period, relative size, root and leaf area, morphological structure, etc. Of these factors the soil water content is considered to be the most important and more complex variable. Its value is a function of the structure, type and amount of soil, tillage, the per cent of humus and clay content, and the quantity of mineral salts (here considered merely as affecting the vapor pressure of water). These conditions modify also the rate of water movement. The value of the transpirational water loss may be determined and expressed as a ratio in terms of any one condition affecting it directly, but which of these is the better criterion may be left in abeyance for the present. The transpiration ratio may fittingly be called the ecological water requirement. As a criterion for comparing the available water of agricultural soils; as a measure of the quantity, the permanence or the fluctation of the water relation of plants in their habitat, transpiration under these conditions is very important, and an adequate and simple index of habitat conditions. It is greatly increased with the higher soil water content and decreases within limits as the soil moisture is lowered; where the range in soil water is small the effect is not marked. The loss of water from plants is inappreciable in saturated air, is greater in dry than in moist atmospheric conditions, and less for plants nearer the ground stratum. Under these conditions (assuming in all cases that secondary injurious conditions are eliminated) it indicates the continuity of the water relation between the soil, the plant and the air—the water is absorbed without greatly altering or expending the energy of cell constituents. The transpiration ratio indicates the magnitude of the water factor within the zone of shoot and root activity which controls the individual plant or the association; it further indicates the limiting

values that produce the effect of wilting and drought, and deter-
mine the differentiation of the vegetation by the local occurrence
of soil types. It enables to that extent a correlation between avail-
able water and the invasion, succession or reversion, under
natural conditions, of one vegetation type to another. The
formula unquestionably provides values which are sufficiently
distinctive to characterize diverse plants and diverse habitats,
and which may serve also as a criterion for the range of deviation,
the maximum and minimum transpiration value for the limits
of the existence of plants as individuals or as groups, and for
the geographical distribution of plants where this is determined
physically by soil, climate or competition. However, correlations
of transpiration with growth or green and dry weight of plants
are by no means as clear as they should be; they must be more
thoroughly tested.

Critical researches are required in at least three experimental
fields of investigation to determine (1) how far the observed
results in growth, structural character, size and weight of plants
depend on differences in the relation subsisting between absorption
from the soil and transpiration into the air, (2) how far they
are due to the differences in the amount of water present and
retained within the plant, i. e., to differences in the physiological
water balance in plants, and (3) how far they are determined
by the biochemical relations of the root-system with the soil-
water constituents and with metabolism. Here the growth
increment is the important criterion, and the ratio which is
used as the index of the physiological water requirement (to
distinguish it from the other term used on the basis of the environ-
mental water relation) may well be called the coefficient of growth.
To what extent the values of the coefficient may be a measure of
the relative nutrient efficiency of any salt, or may be determined
in terms of temperature or of the summation of atmospheric
factors, i. e., character of climate, and how far they hold out the
promise of being a standard, mathematically-expressed index
under soil, seasonal, and plant variations, and how far the range
of deviation and the minimum value will enable in detecting
physiological limits to plant processes, to morphogenesis, to
geographic distribution, or to zonation in montane regions,
remains to be determined. The problem is decidedly complex.
It is not the purpose of the present paper to enter into this phase
of the discussion, but rather to confine itself more closely to the
relation of transpiration to green and dry substance produced and
to growth.

There can be little, if any, doubt that the absorbing power
of the root system of a plant is not regulated by the amount
of water transpired, but rather by the differential permeability
of the absorbing epidermal root cells and the metabolic require-

ments during the life cycle.   The phenomena of selective absorption show that transpiration does not determine in these cases the amount of salts absorbed during metabolism and growth, that the time of maximum absorption for different salts varies, and that they are absorbed at independently varying rates.   Plants do not absorb mineral or organic constituents in the same concentration as exists in the solution in which the roots are found. The data from numerous experiments show that under certain conditions the roots of plants remove the solutes from a solution faster than the water, and in a different ratio than exists in the solution.   The process of absorption of inorganic and organic constituents is not connected with transpiration, but with the metabolism of the plant.   Hence, the value of the transpiration ratio is, under these conditions, more frequently inversely proportional to the amount of growth and the luxuriance of vegetation.   The marked difference exhibited by different plants in efficiency of growth under conditions of limited water supply is particularly a characteristic and striking feature of variability in nutritive metabolism, not in transpiration.   It is unnecessary to review such cases as include the action of mineral fertilizers— separately and as antagonistic or balanced solutions— the effects of organic compounds from peat and from mineral soils, the action of inorganic and organic acids and alkalies.   Such investigations are well known.   They are extremely important as they show that rapid production of green and dry substance of plants is not necessarily accompanied by a high relative or total transpiration value.   The conditions of water loss show extreme variations with respect to the total quantity of water available and required, and the amount of growth.

Under the circumstances it is unnecessary to discuss the problem as to what special demands on inorganic materials individual plants may make, wherein the use or advantage for necessary essential and nonessential constituents lies, or to differentiate nutritive materials from those functioning otherwise. The specific effects produced by these substances, either externally or after having entered the cells and there reacting with the contents, differ according to the nature of the compound and if derived from habitat conditions characteristic of unrelated vegetation types, e. g., those frequenting organic soils, such as peat, may even interfere with growth and normal development. The specific physiological effects produced may be more marked on the roots than on the green parts of plants, or may affect leaf tissue more strikingly than that of the stem.   These different reactions are due in part to modifying effects upon imbibition of cell colloids, largely to changes in the permeability of the protoplasmic membrane and in the metabolism accompanying the direct absorption of constituents in the soil solution.   In

some cases an insufficiency of any salt will operate as a limiting factor, the plants continue to transpire and yet make little growth, or may even show a loss in weight accompanied by a high transpiration; in other cases the conditions retard or inhibit growth as well as transpiration and produce the effect of physiological drought; still other cases exhibit no detrimental effect, but rather an increase in growth and in yield of plant material with little or no change of transpiration; stimulation may accelerate or diminish the rate of transpiration, but not necessarily that of metabolism or growth. These phenomena have been shown repeatedly by the work in this laboratory (Bull. 16, 1912, Geological Survey of Ohio) and by the experimentation of various investigators elsewhere.

Variation in green and dry weight of plants and a great expenditure of energy often indicated by a loss in total weight, commonly occur during activity in spring while leaves are unfolding; the inequalities cannot be attributed to differences in rate or amount of transpiration. The greater absorption and distribution of mineral salts and organic material which has been reported under conditions of increased humidity, of shade, or at different periods of growth is not determined by an accelerating effect of the transpiration current. In autumn, following the death of leaves, when there is a relatively rapid migration of mineral and organic substances to other parts of the plant, it becomes obvious that the transpiration stream is not the medium by means of which a plant can obtain a better supply of the necessary nutrients. The translocation of organic or inorganic material to leaves, or from storage regions to places where they are used up, is a phenomenon of wide occurrence in aquatic plants, in underground parts of land plants, in plants occupying very humid and very dry land areas. Maximum growth is correlated with a large movement of materials, but the more vigorous translocation and absorption of salts and organic material can rarely be referred to a greater transpirational water loss or to a more vigorous transpiration current; the rate and the direction of the movement of the solutes and water is independent of one another. The causes of these phenomena are identical with those recorded for the selective absorption of roots. They are conditioned by the differential permeability of the protoplasmic membranes of cells, and are related and dependent upon the more complex metabolic influences of the entire organism. One can comprehend the advantage which plants with woody tissue have over those in which the movement is wholly in the cortex, but the reasons advanced in support of the transpiration view do not appear quite sound. A number of plants show "preferences" for lime soils in one part of their areal range which are not typical in another habitat. Others thrive,

successfully reproduce themselves and constantly extend their range of distribution largely because the various responses in vegetative characters or reproduction, in differences in abundance, in effectiveness of competition, are more frequently matters concerned with inherent vitality, with endurance and acclimatization, with the physico-chemical complex of the plant itself, rather than with favorable habitat conditions. As one travels into the interior of a continent the increasingly continental character of the climate is accompanied by the appearance, on the whole, of open and woody plant associations which do not show growth or the strong development of woody tissue as a response to the influence of greater amounts of transpiration water. As has been pointed out elsewhere by the writer, the scattered types of geographical distribution and the trend of the migratory movement of individual species and of associations tend more frequently to indicate the importance of functional plasticity and the nature of the invasion level, i. e., whether the plants become dominant, or enter as dependent species and either become assimilated with the vegetation type or are slowly exterminated. At all events the facts cannot be related merely by taking into account the transpiration current or the quantity of water evaporated. The rate and character of growth, the demand for materials and the destination of the migratory materials of various kind are conditioned·usually upon the character of the constructive metabolism.

That no direct relation exists between growth, green and dry weight of plants and transpiration even under the same conditions of experiment is further illustrated by an examination of the quantity of water associated with metabolism. Water, in addition to its important physical influence in imbibition and turgor phenomena, has various other roles. In the living plant organisms are going on many chemical reactions within limited conditions of temperature and moderate concentrations of solutions. All these energy transformations take place in the presence of an excess of water within the plant. They come to an equilibrium point or to an end by the dilution or removal of the products of the reaction; the velocity of these reactions is regulated by the general physical factors governing such changes within a colloidal system. The most important reactions upon which the life and the growth of plants depend are those by which water is held and fixed in organic combinations (1) in the synthesis of food and body material, and (2) in hydrolytic reactions whereby water unites with insoluble carbohydrates as well as with fats and proteins to form diffusible products for translocation to active cells and to the growing region.

The quantity of water combined in synthetic reactions is fairly well known. Assuming that as much water is set free in the breaking

down as is fixed in the construction of these materials, i. e., that
the complete oxidation results in a quantity of water equal to that
required during photosynthesis and chemosynthesis, the amount
of water comprises but little more than three-fifths or 60 to 65
percent. of the weight of the dry matter of plants. The ecological
water requirement it will be seen is greatly in excess of the actual
quantity of water used; the quantity of water lost by transpira-
tion is not related to the synthetic process. Transpiration aids
the gaseous exchange, but the rate and amount of CO_2 entering
is not in proportion to the water evaporating through the stomata.
The diffusion of the gas is independent of it, and the supply of CO_2
is usually less than could be utilized by the chloroplasts. The
results obtained in green and dry weight of plant depend upon and
vary within the limiting conditions of the CO_2 gradient in the air,
the light intensity, and the general temperature conditions as
well as the duration of period of the growth.

Unfortunately the number of investigations on hydrolytic
reactions in plants during their entire life cycle is small, and it
would be therefore unsafe to make any extended discussion of
the results. The greater percentage of organic matter in tissues
is often due to hydrolytic reactions, but the total quantity of
water used in this manner is unknown, since no means are yet
available for the determining the extent and the degree of hydra-
tion, and the number of times which degradation or metabolic
transition products function in hydrolytic reactions. In many
cases the action consists merely in an absorption of water which
is followed by a splitting up of the substance. The different
hydrolytic enzymes which act upon glucosides, and such catalytic
agents as saccharase, amylase, cytase, lypase, protease are active
in this stage of metabolism. In other stages the hydrolytic pro-
cesses are reversible and accelerate synthetic combinations, some
of the products showing profound differences in reaction and with
relation to the influence of external factors. The number of such
intermediate compounds is large; their molecular structure is not
sufficiently well known, and the knowledge of this construction
action is yet very scanty. Hydrolytic reactions occur in all
stages of growth, from germination to maturity and decay.

The attention of physiologists has been attracted thus far
especially to the dependence of these reactions on temperature.
However, the principle of temperature coefficients fails to hold
rigidly, for wherever components are co-ordinated into a system
of reciprocal relations, and obscured by the effects of limiting
conditions, such as in the cycle of changes collectively spoken of
as growth, the character and the rate of any one single reaction
is not that of more elementary chemical processes. Beyond a
certain point, further temperature increases do not cause more
growth. The favorable range of temperature has not as yet been

correlated with the various functions of a plant or of different plants. On the other hand, plant temperature follows very closely that of the environment; hence, it seems likely that the effectiveness of temperature conditions upon the general development and growth of plants, from the time of germination to that of seed maturation, and the limits of temperature requirement (for morphogenesis and for plant distribution as well) may be measured. Indeed, values have been obtained in various ways and used as a fairly approximate criterion. But much needs yet to be determined empirically. Inquiries of the highest importance concern the relations between reaction activities and the regulative functions, and their degree of interdependence. A compact sturdy growth and a greater yield in seed can be obtained in most plants only over a comparatively restricted range of temperature, and hence only over a limited geographical range, if the water supply increases. Differences in the ability of species or of associations of plants to grow under conditions widely different from those of their typical habitat and thus the increase of their areal range, again point to the limit finally set by the relative ability of the protoplasmic functions in acclimatization or competition.

It seems to be known only in a general way that the greater the proportion of the water component in the plant, the nearer is the equilibrium point to the position of complete hydrolysis, thus affecting the concentration and the character of the food materials. It is well enough known that an increased water supply prolongs the vegetative period of growth and increases the forage value of the crop rather than the yield in grain, and that the less water used in growing grain, the greater is the percentage of gluten in the seed and the higher the food value. In recent years the tendency all over the western United States is toward a more economical use of water, even in localities where water for irrigation is still reasonably low in price. In the east correlation studies have been made between rainfall and the yield for a number of agricultural crops. The data indicate a general relation between yield and the water supply during the months of July and August,—during the intermediate period of active growth when the plants are undergoing hydrolytic changes in metabolism preparatory to building up seeds and fruit. A greater water content within the plant is required during this period for such purposes than is needed during germination or ripening or at any other stage in growth, and the danger of impairing the vitality of the plant is greater at this time if it lacks this physiological water requirement. It must be present in a certain minimum quantity before maturity and ripening can take place; otherwise the ripening processes are retarded and growth results in a small yield, in dwarfing of the whole plant, and in injuries when the maximum

quantity of water is exceeded.   The entire structure of land plants inhabiting dry climates shows the resistance to transpirational water loss and how far such limitations may go; and the plants possessing special body features for accelerating transpiration or for exuding water where transpiration is out of the question, indicate how fundamentally important is the maintenance of the water balance within the plant.   Artifical defoliation, an increased water supply or decreased transpiration are known to affect in a number of trees the thickening of cell walls during the formation of autumn wood; this is caused partly by inferior nutrition, largely by the increased amount of water in the plant.   The dearth of both exact knowledge and laboratory experiment make it impossible to state the amount of water involved in hydrolytic reactions and necessary as a constant quantity in the plant during its life cycle for vegetative or reproductive growth.

It will be seen from the brief remarks above that the rate of growth, the amount of it and the final size attained by a plant depend in part on favorable conditions of temperature, light intensity, food supply, and on the amount of water present in the plant.   The rate or the total amount of water transpired gives no indication as to the quantity which normally is required for metabolic processes and for growth.   Moreover, the chemical reactions associated with the growth of cells throughout the formative phase, the phase of enlargement of cells and that of maturation, by which food materials and other substances become incorporated into body tissue, are largely dehydrating in character. At the growing point it is chiefly a local production of originally combined water set free by dehydration processes and by respiration rather than the transpiration water which induces turgor and the elongation of new cells.   Many plants, aside from those carrying water in a special storage tissue, are able by means of dehydrating processes to withstand long periods of drought without permanent injury; and numerous cases are known of fruits, seeds and severed portions of living plant tissue which are able to maintain a certain quantity of intracellular water in this manner indefinitely, and for some time a constant loss of water incurred through transpiration.

It would certainly be quite wrong to conclude that transpiration is not essential to plants, merely because it is not directly related to absorption and translocation of solutes, to green and dry weight of plants, and not a measure of metabolism and growth or vegatative luxuriance.   The quantity of transpiration water in most plants is certainly not co-ordinated with or related to these functions.   The retention of water is the physiological function indispensable to growth in general, and to survival and greater areal distribution in regions of a continental climate. But there can be no doubt that transpiration is indicative of

the water relation of diverse habitats and diverse plants. The
incidental advantages associated with transpiration are
undoubtedly these: the water loss reduces the temperature of
the plant itself to that of the air about it, thus preventing injury
by overheating in direct sunlight; and it aids in the gaseous
exchange. The significance of transpiration as one of the forces
which bring about the ascent of water in plants cannot be ascer-
tained as yet. Data required for the solution of the question are
wanting. Other forces must be involved to effect, in humid
areas or during periods of defoliation, the lifting of water in the
stem to a certain height, and in sufficient quantity. Transpira-
tion may be to a certain extent a factor in determining the form
of the plant. The variability especially of the higher plants in
growth form and in anatomical structure has been shown to be
far greater in this respect than hitherto supposed; among all the
agencies that affect shape and structure in the plant none has more
formative influence than water. But here also critical researches
are still required to determine how far differences in the requisite
water content of the plant—the water equilibrium of the entire
plant—rather than differences in the rate or the amount of tran-
spiration are the causal conditions. The examination of these
relations must be more quantitative than has heretofore been
attempted to be of value to scientific agriculture and to plant
geography.