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PHYSICAL CHEMISTRY IN THE SERVICE OF PHYTOGEOGRAPHY[1]

BIOLOGISTS, grown in the present generation from a mere squad of determined scouts to a splendid army of disciplined investigators, increasing daily in rank and equipment, have as their greatest task the placing of biology alongside physics and chemistry in the ranks of the exact sciences.

In the title of this paper, *Phytogeography,* which even its most ardent disciples must confess is one of the least quantitative of the biological sciences, is coupled with *Physical Chemistry,* which is conceded by all to be one of the most precise of the physical sciences. This contrast has been made, not to magnify the chasm which conventionally has been assumed to separate the exact from the descriptive sciences, but to emphasize to biologists and to chemists and to physicists alike, the fact that the methods of the most advanced physical sciences can now be successfully employed in such a confessedly descriptive phase of biology as ecology and phytogeography.

In turning to the task of the moment, which is to consider how certain of the simplest physico-chemical methods may be of service in ecology and phytogeography, it is important to place the group of problems to be investigated in its proper biological setting, and to state these problems in such a form that their relationship to a physico-chemical method of investigation is quite obvious.

[1] A paper presented at the Symposium on Relations of Chemistry to Botany, before the joint session of Section G, American Association for the Advancement of Science, and the Botanical Society of America, December 27, 1916.

Phytogeography has two main phases, the historical and the physiological.

In the investigation of the historical factors involved in the geographical distribution of plants, the methods of physical chemistry can be of little service.

The physiological problems of ecology and phytogeography are essentially those of the relation of the organism to its environment. It is here that physical chemistry, along with other quantitative and experimental methods of research may be profitably applied.

It is a truism to say that the relations of the living protoplasm to its inert environment constitutes one of the most fundamental groups of biological problems. To cooperate in the solution of these problems is the greatest opportunity of ecologists. That the contribution of ecology has not already been greater is largely attributable to the non-quantitative character of most of the work hitherto done.

In the closer analysis of the relationship of the organism to its surroundings it is apparent that there are two planes of contact of protoplast and environment: that which lies between the protoplast and separates it from the outside world, and that which lines the vacuoles of the cell and separates the deeper-lying protoplasm from the internal environment of the vacuolar solution, just as the plasma membrane separates it from the external world.

The processes which are taking place in these two planes are presumably physicochemical processes. Certainly, physicochemical methods of investigation are those which may be applied with the greatest hope of advance in the solution of the problems presented by those planes of contact of organism and environment.

That these processes are of fundamental significance to the student of the complex problems of ecology and phytogeography of the higher plants should be evident from the fact that the differentiation of tissues in the vast majority of flowering plants, with which alone I am concerned in this paper, is such that the cell membrane comes into contact with two quite distinct phases of the environment. In water absorption, it separates the fluids of the cell from a soil solution of quite different properties. In water loss, it separates the fluids of another set of cells from an atmosphere varying enormously in its water absorbing capacity.

These two environmental factors, which stated in physiological terms may be referred to as the force with which the substratum withholds water from the plant and the force with which the atmosphere tends to withdraw water from the plant, have by common consent been given the place of first importance in the environmental complex.

The importance of a thoroughgoing investigation of the relationship of the plasma membrane to the concentration and the composition of the intracellular and the extracellular solution has long been recognized. Nor have physiologists interested in the problem of transpiration failed to recognize the fundamental significance of the membrane which separates the fluid contents of the cell from its gaseous environment.

It is quite natural that the problem of the permeability of the cell membrane should have been far more extensively investigated than that of the relationship of the protoplast to the cell sap. Experimental modification of the solution surrounding the cell is subject to only the limitations imposed by the solubilities and other properties of chemical reagents and the viability under the influence of these reagents of the cells or tissues employed. To determine the properties of the sap contained in the vacuole at any moment is a problem of some difficulty, to modify these properties at will is in itself an undertaking of no mean magnitude, while to investigate with any degree of completeness the relations of the properties of the sap of the vacuoles to the surrounding protoplasm would seem to be a task of almost unsurmountable difficulties.

Nevertheless, the time has come when an investigation of the properties of the sap of the vacuole in relation to the protoplast and in relation to the factors of the environment should be undertaken. It is inconceivable that the properties of the sap should be uninfluenced by the forces which are acting upon and through the living membrane surrounding the cell. It is difficult to think, for example, that the osmotic properties of the sap of the vacuoles should be independent of the forces which are tending to draw water from the cell in transpiration and of the forces in the substratum which oppose water absorption. If this be true, an investigation of the properties of the intracellular fluids of plants in various environments, in which the water-absorbing power of the air as well as the water-yielding capacity of the soil vary enormously, may throw much light upon the basic physiological problems of ecology and plant distribution.

If progress is to be made, it is not merely necessary that problems be clearly defined, but that methods which are adequate and practical for use under the conditions surrounding the investigation shall be found. The question of method becomes, therefore, one of paramount importance.

The phytogeographer must limit his choice to those methods which can be used under camp conditions. Otherwise he must be willing to forego work on phytogeography in the only regions in which it can be satisfactorily investigated, that is, in those which have not been completely modified by the activities of man. Fortunately the determination of the depression of the freezing-point of a solution below that of the pure solvent furnishes a relatively simple method of calculating its osmotic pressure or osmotic concentration. It is quite possible to make cryoscopic determinations sufficiently exact for phytogeographical problems in the field, and especially at the field laboratories which fortunately are becoming more numerous.

In addition to developing a simple technique for use in the field, one who hopes to convince botanists that the investigation of the physico-chemical properties of vegetable saps should form an essential part of a comprehensive ecological or phytogeographical study, must show that in any region the sub-habitats, formations, associations, plant societies or whatever the nomenclatorial specialist may call them, are measurably different in their sap properties, and that even more conspicuous differentiation exists in the sap properties of the larger phytogeographical regions. If he can also show that such ecological groups as the succulents, the epiphytes and the parasites are differentiated in the physico-chemical properties of their tissue fluids, the necessity for the use of physico-chemical methods in phytogeographical work will be self-evident.

The foregoing outline of the fundamental conceptions underlying the studies which my associates and I have carried out in various regions has of necessity been so detailed that it will be impossible at this time to give any adequate summary of the many hundreds of determinations of osmotic concentration of tissue fluids of plants growing in various environments which are now at my disposal.

The actual details, as far as published, are available in a series of technical papers.

How great the differences in the sap properties of the vegetations of various regions may be is illustrated by the accompanying table in which the average concentration in atmospheres for Long Island, Arizona and Jamaican regions studied by my associates and myself and for a series of determinations made for a quite different purpose by Ohlweiler at the Missouri Botanical Garden are laid side by side.

Region	Ligneous Plants	Herbaceous Plants
Montane rain forest:		
Blue Mountains, Jamaica...	11.44	8.80
Mesophytic regions:		
Long Island habitats	14.40	10.41
Missouri Botanical Garden.	14.96	——
Desert regions:		
Jamaican coastal deserts ...	30.05	——
Arizona deserts	24.97	15.15

Had it been possible to table the data of each of these regions, and that for others which are now available, according to local habitats it would have been seen that in any region the local habitats may be measurably differentiated with respect to the sap properties of their vegetation. Tabulation by local habitats would also have brought out clearly the fact that herbaceous and ligneous plants differ in the osmotic properties of their tissue fluids.

The averages in the table are not presented as complete descriptions of the sap of the plants of these regions, but merely as the simplest available means of summarizing their characteristics and emphasizing to the phytogeographer the fact that the vegetations are differentiated in the properties of their sap as well as in their taxonomic composition and ecological structure.

The explanation of such differences in vegetations as have just been demonstrated is by no means simple.

The most direct and obvious relationship of the properties of the sap of the organism to its environment is to be seen in halophytes. The leaves of many of these are salty to the taste. It is quite apparent that they must have a relatively high concentration due to the absorption of salts from the substratum. It is, however, a grave error to assume, as some botanists seem to have done, that the whole problem of sap concentration is one of the absorption of electrolytes from the soil—to assume in fact, that the plant organism stands in the relation of a sponge to the solution around it. Zoologists, who have devoted much attention to the relationship between the concentration of the blood of the marine organisms and that of the water in which they live, have long recognized that the osmotic concentrations of the two fluids may be identical but that the solutes to which these concentrations are due may be very different indeed.

Even in the succulent halophytes, the leaves of which are essentially reinforced water bags, there appears to be by no means an identical capacity for adjustment to the concentration of their substratum or for the occupation of available areas. Thus, for example, *Sesuvium Portulacastrum* and *Batis maritima* both occur on the highly saline flats of the southern shore of the island of Jamaica. *Batis* shows a far higher osmotic concentration than *Sesuvium*, 49.7 as compared with 38.3 atmospheres on the average, and is seen in the obviously more saline localities.

Now differences in the concentration of the soil solution may not be the determining factor in the distribution of these two halophytes. Other factors require far more detailed investigation than any one has been able up to the present time to give them. The point to be emphasized here is that two species of halophytes, not without several points of similarity, differ in both sap concentration and in local distribution. The chemical method has given us at once measures of the physiological characteristics of these two forms. These quantitative measures furnish a first definite step towards the solution of the problem of their distribution.

To discuss adequately the many problems presented by a comparison of the sap properties of the vegetations of diverse local habitats or phytogeographical regions would carry us far beyond the limits of this address. Before leaving this phase of the subject it is important to point out that in its relationship to plant distribution, sap concentration may have a dynamic as well as a static significance.

If the differences in the sap properties of the vegetations of various habitats be in part due to fixed hereditary differences in the species, instead of merely a resultant of local environmental conditions, and if one of the factors determining the capacity for survival in a given habitat be the osmotic concentration of the cell sap, it is clear that sap properties may be a factor in the migration of species.

The factor of osmotic concentration would be active in two ways. First, in the determination of migration from warmer into colder regions, by virtue of capacity for frost resistance. Second, in migration from mesophytic into desert regions.

The problem of the relationship of sap concentration to frost resistance need not delay us long. The freezing-point of plant tissues has been the subject of scores of investigations, most of which have been of a purely physiological or of an economic nature.

The studies of Ohlweiler, Chandler and others render it highly probable that the osmotic concentration of the tissue fluids is one of the factors involved in the capacity for frost resistance. Such determinations as Mr. Popenoe and I have been able to make on the sap of the varieties of avocado (*Persea americana*) which have been introduced into the United States, indicate that the Mexican and Guatamalan types, which have been found by practical horticulturists to surpass the so-called West Indian type in capacity for frost resistance, have a slightly higher osmotic concentration of their cell sap.

Concerning the rôle of osmotic concentration in the survival of plants introduced into xerophytic regions we have as yet practically no information.

It is perhaps evident that the factors which limit the artificial introduction of species would also be active in determining the survival of species introduced into any region by hurricanes, ocean currents or by any other natural causes. Upon some of these questions I hope to be able to furnish more satisfactory information on a later occasion.

We must now turn to a discussion of certain of the ecologically more interesting groups of plants. Among these may be mentioned the succulents, the epiphytes and parasitic plants.

The studies of succulent physiology which have been carried out in recent years, and especially at the Desert Laboratory by MacDougal, Spoehr, Richards, Mrs. Shreve and others, have been far too detailed to make possible any adequate discussion of succulency at this time. It is interesting to note in passing that the succulents are characterized by two quite different types of sap. On the one hand are the desert species with generally low osmotic concentration, on the other the halophytes with high osmotic concentration. The physiological interpretation of this condition presents a most interesting problem for future research.

Among the most characteristic, and ecologically most fascinating features of tropical regions is the burden of epiphytes borne by the trees. If one turns to the literature in search of work of a quantitative nature on the physiology of this taxonomically and morphologically diversified group of plants, his search will be practically in vain. Material progress has already been made in the study of the sap properties of some of the representative types, although it is quite too early to discuss in detail even this phase of the physiology of these plants.

Osmotic concentration in these forms is generally exceedingly low, Orchidaceæ from the Jamaican rain forest show an average of 3.34 atmospheres, those from the Florida hammocks an average of 4.88 atmospheres. Tank epiphytes from the Blue Mountains of Jamaica show concentrations ranging from 2.8 to 5.5 atmospheres. Comparable values are found in subtropical Florida.

The succulent Peperomias and some other epiphytic species are also characterized by a concentration of their tissue fluids only a fraction of that obtaining in the foliage of the arborescent plants of the same forests.

Thus, in general, epiphytic species are characterized by low osmotic concentration. This is not, however, a necessary condition of epiphytism. Determinations are available for at least one species of epiphytic fern showing a sap concentration roughly three times as high as that generally characteristic of the succulent Orchidaceæ and Piperaceæ and the tank Bromeliaceæ.

The keen botanical interest aroused by parasitic flowering plants has found expression in an enormous number of macroscopic and microscopic morphological and life-history investigations. Yet it should be clear that the problem of the distribution of parasitic forms, both among the possible host plants of a particular region and from region to region, is primarily a physiological one. Among the possible factors, the relative concentration of the tissue fluids of the photosynthetic and transpiring organs of the host and parasite seems on *a priori* grounds one of the greatest importance. Studies on the osmotic concentration of the tissue fluids of Jamaican Loranthaceæ on various hosts have shown that in general but not invariably, the osmotic concentration of the fluids of the leaves, or of the leaf homologs, of the parasite is higher than that of those of the host.

In the foregoing discussion only a portion of the results of studies already made, but as yet largely unpublished, have been lightly touched upon. They are illustrative merely. For the mass of facts justifying generalization, the published tables must be consulted. Enough has, perhaps, been said to indicate the fundamental significance for the physiological phases of phytogeography of the physico-chemical measurements. As phytogeography becomes more and more a problem of the physiology of individual species of plants, investigated in their own environment, as methods become more precise, and as results are recorded and discussed in more quantitative terms, the ecologist's sector of the attack upon the great problem of the relationship of the organism to its environment will be increasingly successful. Concurrently, the relations of chemistry to botany will become more clearly defined in a field in which its existence has heretofore been little recognized, and the service of chemistry to botany will be increasingly great.

J. Arthur Harris

SCIENTIFIC EVENTS

MEMORIAL TO SIR WILLIAM RAMSAY

The following appeal has been issued by a committee formed to raise a memorial to the late Sir William Ramsay.