SCIENCE

Friday, August 31, 1917

CONTENTS

MSS. intended for publication and books, etc., intended for review should be sent to Professor J. McKeen Cattell, Garrison-On-Hudson, N. Y.

LIEBIG'S LAW OF THE MINIMUM IN RELATION TO GENERAL BIOLOGICAL PROBLEMS[1]

The Law of the Minimum has never been accurately defined, although the idea that it involves is relatively simple. Professor B. E. Livingston says in a recent paper[2] that "this principle is still quite incomplete logically and its statement will assuredly become much more complex as our science advances." In order to get a clear understanding of the law so that it may be stated accurately, we will begin with a simple application to chemical reactions.

One molecule of KOH reacts with one molecule of HCl to form one molecule of KCl and one of H_2O. If only one molecule of KOH is present, only one molecule of KCl can be formed, no matter how many molecules of HCl are present; and likewise if only one molecule of HCl is present, only one molecule of KCl can be formed, no matter how many molecules of KOH are present. By considering the weights of the reacting substances, the situation is somewhat complicated: 56.1 grams of KOH react with 36.5 grams of HCl to form 74.6 grams of KCl and 18 grams of H_2O. In round numbers 3 parts by weight of KOH and two of HCl give 4 parts by weight of KCl and one of H_2O: 3/4 gr. of KOH and 1/2 gr. of HCl are necessary to form a gram of KCl. Let us call these fractions, 3/4 and 1/2, the specific reactive weights of KOH and HCl in respect to the formation of a unit quantity of KCl. Suppose x amount of KOH and y of HCl are given. If x and

[1] Paper read before the Biological Club of Yale University, April 19, 1917.

[2] *Plant World,* 20: 1–15, 1917.

y are divided by their respective specific reactive weights, we get $\frac{4}{3}x$ and $2y$. The smaller of these quantities is a direct measure of the weight of KCl that can be formed from x KOH and y HCl. If, for example, x and y are both equal to three grams, four grams of KCl can be obtained.

These facts can be generalized. If A, B and C are substances which react to form S and u A, v B and w C are necessary for the formation of a unit amount of S, then u, v and w may be called the specific reactive values of A, B and C, respectively. They may be weights, volumes, numbers of molecules or what not. In any particular case, where pA, qB and rC are reacting, the amount of S formed is the smallest of the fractions p/u, q/v, r/w. When the amounts of the reacting substances are divided by their specific reactive values, the smallest quantity so obtained is equal to the amount of the product formed.

This conclusion is directly applicable to the problem of fertilizers. It is known that most of the higher plants must obtain seven elements in combined form from the soil. They are S, P, N, K, Ca, Mg and Fe. If αS, βP, γN, δK, ϵCa, ζMg and ηFe are required for a unit amount of growth in some particular plant, say wheat, and if aS, bP, cN, dK, eCa, fMg and gFe are present in a particular soil in available form, the maximum amount of wheat that can be grown in that soil will be the smallest of the fractions a/α, b/β, c/γ, d/δ, e/ϵ, f/ζ, g/η. In this case α, β, γ, etc., may be called specific growth values for the plant under consideration. When the available amounts of the essential inorganic food constituents are divided by their respective growth values, the smallest quantity obtained gives the maximum amount of growth possible.

It was in this connection that Liebig[3] first formulated the Law of the Minimum which, as commonly stated,[4] says that "the yield of any crop always depends on that nutritive constituent which is present in minimum amount." The use of the term minimum is not strictly accurate, as can be seen from the example of KOH and HCl. If three grams of each are present, the amount of KOH determines the yield of KCl, although both HCl and KOH are present in equal amount. However, the above statement of the law is convenient because of its simplicity.

A much broader application of the Law of the Minimum was indicated by the work of F. F. Blackman, whose conclusions are summarized in his paper on "Optima and limiting factors."[5] Blackman called attention to the complexity of the process of carbon assimilation, the rate of which depends on at least six factors—

1. Temperature,
2. Light intensity,
3. Carbon-dioxide supply,
4. Water supply,
5. Chlorophyll,
6. Enzymes.

Where it is possible to vary one of these factors independently of the rest, its effect on the rate of assimilation can be measured, under suitable conditions, and a curve plotted. In this way a temperature-assimilation curve, a light-assimilation curve and a carbon-dioxide-assimilation curve can be constructed. The other factors are more difficult to control. The following curves were constructed by Blackman and Smith[6] from a study of the rate of assimilation in *Elodea*.

The light curve and the carbon-dioxide curve are straight lines. The rate of assimilation varies directly with the inten-

3 "Die Chemie in ihre Anwendung auf Agricultur und Physiologie," 7te Auflage, 2: 225, 1862.

4 *Cf.* F. Czapek, "Biochemie der Pflanzen," 2: 841, 1905.

5 *Annals of Botany*, 19: 281–295, 1905.

6 *Proc. R. Soc., B.*, 83: 389–412, 1910.

sity of light and the supply of carbon dioxide. The temperature curve shows that the rate of assimilation is an exponential function of the temperature. In fact the process of assimilation obeys van't Hoff's

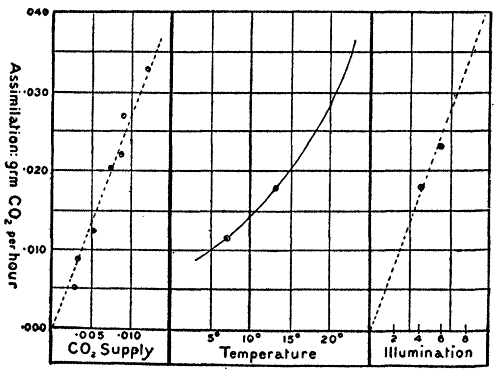

FIG. 1. Effect of external factors on assimilation in *Elodea*. (After Blackman and Smith.)

law of reactions for temperatures under 30° C. Above this, the rate of assimilation at first rises and then falls off, the process being complicated at high temperatures by a "time factor." The same effect has been observed at high light intensities, and with strong concentrations of carbon-dioxide which have a narcotic effect.

Disregarding these complications, we will confine our attention to the first parts of these curves. The ordinates of all three curves are the same, namely, rates of carbon assimilation, which can be measured in terms either of CO_2 absorbed or of sugar produced. The former happens to be the more convenient measure. At any given temperature, the rate of assimilation which is a function of that particular temperature can be determined directly by the curve and is equal to a certain distance measured off from the origin on the Y-axis. Similar distances are given for any definite supply of carbon dioxide and for any degree of illumination. In any actual environmental complex, where the temperature, light and carbon-dioxide supply are known, the rate of assimilation is equal to the shortest distance measured on the Y-axis. This is stated as a general principle by Blackman as follows: "When a process is conditioned as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the 'slowest' factor." The factor which gives the shortest distance on the Y-axis—that is, the "slowest" factor, he calls the limiting factor.

As a matter of fact the carbon assimilation of green plants is usually limited by the seasonal variation in temperature and the diurnal variation in light, the CO_2 content of the air being constant. Nothing has been said of the other factors that effect carbon assimilation—the water supply, chlorophyll and enzymes. These so-called "internal" factors, as well as the "external" factors, are governed by the Law of the Minimum. Of the internal factors, water and chlorophyll are present in excess in healthy green plants, the amount of assimilatory enzymes being the only probable limiting factor.

It is not necessary to adduce additional examples to show that the Law of the Minimum is a *universal* law, affecting not merely the concentration of reacting substances, but *all* factors that in any way influence a reaction or process. The law is applicable to physical, chemical and geological as well as biological problems.[7] An interesting instance of its application to a problem in physics is the determination of the magnitude of a thermionic current. This varies with changes in temperature, and also with changes in the voltage applied. The temperature formula gives one value, the voltage formula may give another; the lesser value determines the current flowing. The

[7] A timely application may be made which is worth bearing in mind. The efficiency of a nation at war is subject to the Law of the Minimum. Defeat, in the last analysis, may be attributed to the effect of some limiting factor.

application of the Law of the Minimum has been worked out in many cases and has been of great use in the interpretation of complicated relations; but it has been recognized as a law and has been consciously applied by plant physiologists and physiological chemists only.[8] Without doubt it can be used to advantage in many problems of the physiology, morphology and ecology of both plants and animals.

The Law of the Minimum must be taken into account in all experimental work, for which it serves both as a precaution and a guide.[9] When investigating the effect of an external factor such as temperature, light, etc., on any given process, it is necessary to keep all other variable factors constant, and then to determine the effect of changes in the factor under consideration. What results might be obtained when this method is used in studying carbon assimilation? Suppose the CO_2 supply and the light are kept constant, while the temperature is varied. If the CO_2 supply is such that it becomes a limiting factor when the temperature rises above 10° C. then the rate of assimilation will rise with the temperature up to this point, but will remain constant at all higher temperatures, until the destructive effect of the high temperature is manifested and the curve again falls off. Above 10° C. variations in the temperature have no apparent effect under these experimental conditions. But if the CO_2 supply is increased so as to permit more rapid assimilation, then the temperature curve can be extended. Negative results from such an experimental method are therefore without significance. It is not enough that the experiment be conducted under constant conditions; the constant factors must not interfere in any way with the carrying out of the process; that is, they must not be limiting factors. On the other hand, it is a simple matter to determine by the shape of the curve whether any other factor than the one under investigation is a limiting factor. Such is always the case when a break occurs in the curve; usually the curve rises at first and later runs parallel with X-axis. Such curves were obtained by Miss Matthaei[10] in studying the carbon assimilation of cherry laurel at varying temperatures with unit light intensity. The problem is much more complicated, however, when variation of one factor is accompanied by changes in one or more other factors. This complication arises in plotting the temperature curve for enzyme activity. The curve rises at first according to van't Hoff's law of reactions, but eventually a maximum value is reached and the curve falls off. At some point near the end of the ascending portion of the curve a break occurs: for all temperatures below this point, temperature is the limiting factor and determines the activity of the enzyme; for all temperatures above this point, not temperature, but the amount of enzyme is the limiting factor. The higher temperatures cause a permanent inactivation or decomposition of the enzyme so that its activity is conditioned only secondarily by the temperature. There is also a time factor involved here; the longer the temperature acts, the more the enzyme is decomposed, within certain limits. The study

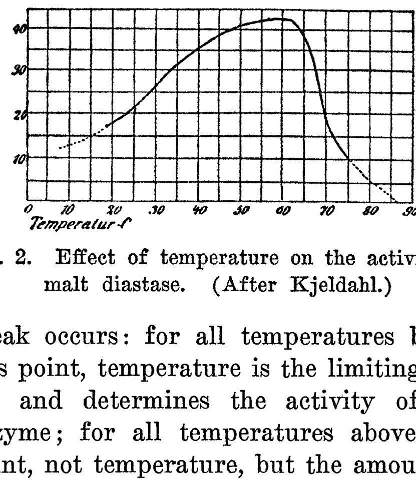

FIG. 2. Effect of temperature on the activity of malt diastase. (After Kjeldahl.)

[8] *Cf.* the work of L. B. Mendel, T. B. Osborne and their pupils.

[9] *Cf.* B. E. Livingston, *loc. cit.*

[10] *Phil. Trans.*, B, 196: 47–105, 1904.

of the action of salt solutions on permeability, growth, etc., involve even greater complications produced by the interrelation of conditioning factors.

In order to get an accurate statement of the Law of Minimum, it is necessary to get away from the custom of discussing causes, however difficult this may be.[11] The idea of causation invariably indicates *incomplete analysis*. A biological phenomenon is dependent not on a single variable, but on a complex or constellation of factors, as we have seen in the case of carbon assimilation. It should be discussed therefore in terms of all the conditioning factors, not in terms of that one which temporarily happens to be a limiting factor. The term "function" is valuable in this connection. The amount of carbon assimilation is a function of the temperature; it is another function of the illumination, etc. With this idea of function in mind, the Law of the Minimum may be stated in the following form. *When a quantity is dependent on a number of variable factors and must be a function of one of them, the quantity is that function which gives the minimum value.* Expressed in plain English this means that a chain is no stronger than its weakest link. The Law of the Minimum is only too obvious. Its application is often so self-evident that it is made as a matter of course.

But the most interesting thing about the law is not how it works, but when it does not work. There is a fundamental discrepancy between the Law of the Minimum and Galton's Law of averages. In the current text-books on genetics and plant physiology[12] the following ingenious explanation of Galton's Law is given. Assume that the size of a bean is determined by only five variables, each of which must occur in one of two categories; in one case the size of the bean will be increased by one unit of size, in the other it will be decreased by the same amount. Considering all the possible permutations of these five variables, we get the following arrangement:

I	II	III	IV	V	Sum	I	II	III	IV	V	Sum
+	+	+	+	+	+5	+	+	−	−	−	−1
+	+	+	+	−	+3	+	−	+	−	−	−1
+	+	+	−	+	+3	+	−	−	+	−	−1
+	+	−	+	+	+3	+	−	−	−	+	−1
+	−	+	+	+	+3	−	+	+	−	−	−1
−	+	+	+	+	+3	−	+	−	+	−	−1
+	+	+	−	−	+1	−	+	−	−	+	−1
+	+	−	+	−	+1	−	−	+	+	−	−1
+	+	−	−	+	+1	−	−	+	−	+	−1
+	−	+	+	−	+1	−	−	−	+	+	−1
+	−	+	−	+	+1	+	−	−	−	−	−3
+	−	−	+	+	+1	−	+	−	−	−	−3
−	+	+	+	−	+1	−	−	+	−	−	−3
−	+	+	−	+	+1	−	−	−	+	−	−3
−	+	−	+	+	+1	−	−	−	−	+	−3
−	−	+	+	+	+1	−	−	−	−	−	−5

The beans will be of six sizes, $+5$, $+3$, $+1$, -1, -3, -5, and out of a very large number (n), $n/32$ will be $+5$, $5n/32$ will be $+3$, $10n/32$ will be $+1$, $10n/32$ will be -1, $5n/32$ will be -3, and $n/32$ will be -5. The six sizes are in the ratio $1:5:10:10:5:1$. If we plot the sizes of the various classes of beans against the frequency of their occurrence, we get an approximation to the familiar curve of normal error. For the sake of simplicity, the number of variable factors was made five and the number of categories in which each might occur was limited to two. If the variables and the categories are made sufficiently numerous, the curve of normal error can be approximated within any desired degree of exactitude. It is unnecessary to point out the empirical fact that when the sizes, weights, etc., of organisms or their parts are divided into classes and the

[11] *Cf.* B. E. Livingston, *loc. cit.*

[12] E. Baur, "Einführung in die experimentelle Vererbungslehre," 2te Auflage, 1914. L. Jost, "Vorlesungen über Pflanzenphysiologie," 3te Auflage, 1913.

classes are plotted against the number of individuals in each class, the resulting curve approaches the normal curve of error, if a sufficiently large number of individuals are used. Exceptional instances of curves with more than one maximum, or only parts of curves, are easily accounted for and for convenience will be left out of consideration. Since the empirical data bear out the conclusions arrived at by the above procedure, the explanation may be considered valid.

However, the explanation involves the addition of the values of the various factors, which is in reality averaging them, since their value is measured in terms of net gain or loss. Although this process of averaging the various factors involved is borne out by comparing the results with empirical data, it is done, nevertheless, in contradiction to the Law of the Minimum. According to this law $n/32$ should be $+1$ and $31n/32$ should be -1, because *all* the factors are $+1$ in only one permutation, and -1 occurs in all the others and would be a limiting factor. The curve that would result if the Law of Minimum held would start from one at the upper end of the scale of sizes, weights or what not and would rise with great rapidity toward the lower end, where it would reach its maximum. This kind of curve is not the rule.

Every case where Galton's Law holds is a case where the Law of the Minimum does not hold. The resultant size or weight of an organism, which is a measure of its growth, shows that this is not determined by the limiting factor of its environment, but represents some sort of average between all the factors involved. In other words, a process of compensation or integration has taken place, the factors giving the largest values being utilized to some extent at least to alleviate the influence of the limiting factor—a utilization of surplus to cover deficit. Individual processes obey the Law of the Minimum; but the grand total is governed by what may be termed a principle of integration.

The means by which this integration is brought about are not hard to find. At least four important processes are at work in living organisms to this effect, namely—

1. Responses to stimuli,
2. Development,
3. Evolution,
4. Biotic succession.

A few examples will illustrate the way in which integration is effected by each of these. A seedling placed upside down is in the wrong position with respect to the center of the earth, its source of light, and moisture. Position with respect to gravity may be considered to be the limiting factor here; but the germinating rootlet is positively geotropic and bends toward the earth; the young shoot is negatively geotropic and bends away from the earth. In this way these responses to the geotropic stimulus counteract the influence of the limiting factor. Roots behave similarly in response to moisture content of the soil; stems and leaves in response to light.

In plants it is hard to draw a line between simple responses to stimuli and morphogenic responses which involve permanent changes of form and structure. The difference between sun leaves and shade leaves is a familiar example of a morphogenic response. The shape, size and structure of the leaf here counteract the limiting factor light. Again, plants which are shaded by others so that they receive insufficient light usually become etiolated, that is, the stems and leaf-petioles in many cases increase in length until some portion of the plant is brought to a position where it receives adequate illumination. Here again the limiting factor is light, and the result of etiolation is to overcome its effect.

Evolution is likewise an integrating process. Its results are not accomplished in the individual, but in the race, and are called adaptations. Adaptations are means of avoiding the effects of limiting factors.

Another means of integration is seen in biotic succession. Here the integration extends over a considerable period of time and its benefits do not accrue to the individual or the race, but to succeeding generations and different species. The integrative effect in succession may be largely produced by the death and decay of an association resulting in the accumulation of humus. Thus both xerophytic and hydrophytic plants prepare the way for a mesophytic flora. The limiting factor here is water, which is too scarce in the one case and too abundant in the other. By the accumulation of humus, the properties of the soil are so altered that a more favorable water supply is offered to later generations, and in this way the effect of the limiting factor is counteracted.

All these processes which bring about integration between the relations of living organisms to the factors of the environment that determine their growth and activity are evidently based on a single fundamental principle, to which Professor L. J. Henderson has applied the appropriate misnomer teleology.[13] Wherever integration is found in the factors influencing the individual, the race or the association, it is possible to define a closed system. Such a system includes all the factors which can be integrated, that is, all the possible limiting factors for any given process. These systems may focus about a single cell, an organ, an organism or a group of organisms. They are inclusive. The life of a plant, for example, is determined by a complex of factors between which integration is found to occur. At the same time the functional activity of the root system is determined by another complex of integrated factors, and the functional activity of the leaves by still a different set. Since the life of the root system is dependent on the products of the activity of the leaves, these represent members of the complex which conditions the growth and function of the root system. Such internal factors as enter into the complex of factors centering about the life of a portion of an organism are likewise subject to integration. In this way the condition of the root system affects the leaves and the condition of the leaves affects the root system. Correlations are therefore manifestations of the principle of integration.

The organic world can be analyzed into systems of various orders, those of a higher order being inclusive of, or divisible into, systems of a lower order. These systems are invariably overcoming the effects of limiting factors. The limiting factor is the stimulus to which the system reacts. The reaction places the organism in a more efficient relation with its environment, but no matter how many reactions are carried out, there is always some limiting factor left, and so the organism is kept constantly busy. The end result is to approximate more or less closely some kind of average of all the resources at its disposal.

I think it might be possible to go even further and get a quantitative measure of the degree to which the process of integration has been carried, by considering the number of factors integrated and how close an approximation to the normal curve of error had been obtained. Such a quantitative measure would likewise be an index of the stage of evolution that an organism had reached.[14] At the very least, the Law of the Minimum or the principle of limiting factors offers a sound basis from which such intangible processes as behavior, correla-

13 The order of nature, 1917.

14 Our criterion of "degeneracy" in a living organism is based essentially on a decrease in the number or range of factors between which integration is possible.

tions, evolution and ecological succession[15] can be viewed with a clear perspective, if it is not the only scientifically accurate point of view from which to attack such problems. HENRY D. HOOKER, JR.

OSBORN BOTANICAL LABORATORY,
YALE UNIVERSITY

THE PECK TESTIMONIAL EXHIBIT OF MUSHROOM MODELS

IT is peculiarly fitting at this time to describe rather briefly the exhibit of mushroom models, recently installed in the State Museum at Albany, N. Y., as a memorial to the life and service of the late Charles Horton Peck, state botanist of New York from 1867 to 1915, a period of forty-eight years, all except the last two years having been spent in active service.

The final installation of these remarkable mushroom models was completed only a few days prior to his death, which occurred on July 10, 1917. The models, fifty-seven in number and representing fifty-five species of edible and poisonous mushrooms, are the work of Mr. Henri Marchand, an artist and sculptor of rare ability. The models are made of wax from casts in the field and reproduce with perfect fidelity to nature, the form, coloring and habitat of each species.

Space need not be taken to enumerate the entire list of species represented by the models, but the variety of form and color may be suggested by the following species which are represented in the collection.

Poisonous:

Amanita phalloides
Amanita muscaria
Clitocybe illudens
Russula emetica
Inocybe asterospora

Edible or Harmless:

Amanita caesarea
Tricholoma sejunctum
Tricholoma personatum
Russula cyanoxantha
Lepiota procera
Lepiota naucina
Agaricus campester
Agaricus arvensis
Coprinus comatus
Morchella deliciosa
Gyromitra esculenta
Russula virescens
Strobilomyces strobilaceus
Pleurotus ostreatus
Fistulina hepatica
Armillaria mellea
Boletus cyanescens
Polyporus sulphureus

The services of Dr. Peck in the field of mycology are surpassed by no other American student of fungi. His work, although not confined to the fleshy fungi, is best known from the hundreds of species which he has described in the fleshy and woody groups of fungi (Agaricaceæ, Boletaceæ, Polyporaceæ, Hydnaceæ and Clavariaceæ).

Without the advantages of European travel and study and frequently working without access to the older European literature upon fungi, his work stands out with conspicuous individuality. That he has apparently described in some cases, species already described by the older mycologists of Europe is no reflection upon his remarkable ability in the discernment of specific and generic characters of our native species.

His work will stand for all time as the foundation upon which later students of the fungi may build with safety a more elaborate morphological and systematic revision of the fleshy and woody groups of fungi.

Those friends, admirers and fellow botanists, who have contributed toward bringing into existence this testimonial exhibit of mushroom models may well feel that there is no more suitable memorial possible. There are few pages of modern literature dealing with the fleshy and woody fungi that do not reflect in some degree the individuality of Dr. Peck's work, and looking at these models in the State Museum, with their exquisite variety of form and color, one may imagine with what pleasure and appreciation they would be viewed by him whom they memorialize. H. D. HOUSE

STATE MUSEUM,
ALBANY, N. Y.

[15] For an application of the principles enunciated in this paper to plant ecology see G. E. Nichols, *Plant World*, Sept., 1917.