Robertson, T. B., 1908a. "Further Remarks on the Normal Rate of Growth of an Individual, and Its Biochemical Significance," *Arch. Entwicklungsmech. der Organism.*, 26, 108–118.

Robertson, T. B., 1913. "On the Nature of the Autocatalyst of Growth," *Arch. Ent.-Mech.*, 37, 497–508.

Robertson, T. B., 1923. "The Chemical Basis of Growth and Senescence," Philadelphia.

Robertson, T. B., 1926. "The Analysis of the Growth of the Normal White Mouse into Its Constituent Processes," *J. Gen. Physiol.*, 8, 463–507.

[1] Conklin did not find this to be true in Crepidula plana; rather, he found comparatively little increase in nuclear material with each cell division. This, however, does not necessarily invalidate Loeb's conclusions.

[2] Pearl, however, asserts that the fit of Robertson's theoretical growth curves to the observed data is too poor "to afford evidence of any particular value in favor of Robertson's ingenious......hypothesis."

MacDowell, moreover, finds that when new-born mice are fed to the limit, their growth curve during the first fourteen days is parabolic rather than exponential. This one fact alone would compel a modification of the theories which Robertson and Crozier propose.

[3] As both Morgan and Crozier have pointed out, however, Robertson's assumption that the master reaction is monomolecular in both directions, an assumption to which he is forced in order to make the autocatalytic curve coincide with that of growth, is a rather improbable one. In a later paper (Robertson, 1926) a different equation is used to permit a slightly asymmetrical curve, but it does not remedy this defect, or any of the other defects that are here discussed.

[4] It is assumed that volume is proportional to mass throughout growth. While this is not strictly true, the deviation from proportionality is not sufficient to affect the present discussion.

CHLOROPHYLL CONTENT AND RATE OF PHOTOSYNTHESIS

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Two sets of factors are generally recognized as affecting the rate of photosynthesis in green plants: external factors, including light, temperature, and carbon dioxide; and internal factors. The latter is a vague group, the only obvious one being chlorophyll. Owing probably to the difficulty of experimentally controlling internal factors, little is known about them. The only work leading to definite information about an internal factor is that of Willstätter and Stoll (1918). They investigated the photosynthetic rates of a variety of leaves differing widely in chlorophyll content. They were able to determine chlorophyll accurately, but they could not control the amount of it present in the leaves. Thus in order to obtain leaves differing in chlorophyll content they were obliged to use leaves which were not at all comparable in other respects. This may be the

reason why they failed to find any correlation between chlorophyll content and rate of photosynthesis.

The chlorophyll content of *Chlorella vulgaris* may be controlled over a fairly wide range without materially disturbing its rate of growth or respiration. This is done by growing pure cultures of cells in a medium containing the appropriate salts, with about 1.5% glucose, and with the concentration of iron kept below that normally used.

The rate of photosynthesis of cells differing in chlorophyll content was determined at high light intensity in glass vessels attached to manometers, after a method described by Warburg (1924). Relative chlorophyll content per unit volume of cells was determined by 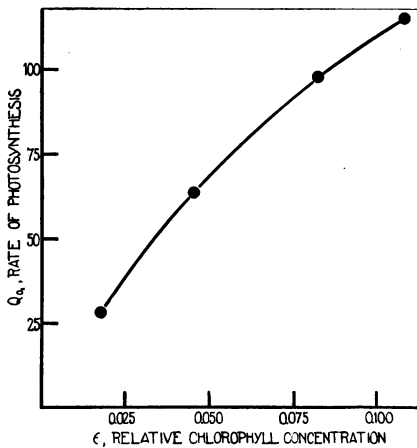extracting the cell pigments (green and yellow together) with methyl alcohol, the extract being made up to a definite volume in a volumetric flask. The extinction coefficient ϵ for the wavelength $\lambda = 670 \ \mu\mu$ was determined for each extract thus prepared. This wave-length was chosen because it is outside the region of absorption of the yellow cell pigments, and near the center of strong absorption by chlorophyll in the red.

FIGURE 1

The rate of photosynthesis plotted as a function of the chlorophyll content per unit volume of cells.

Figure 1 shows rates of photosynthesis plotted as ordinates against corresponding values of ϵ as abscissae. Q_{O_2} represents the number of cubic millimeters of oxygen produced by 10 cubic millimeters of cells in one hour at 20°C. ϵ represents the extinction coefficient of the extract of 10 mm.^{3} cells made up to 25 cc. with methyl alcohol.

The points, like those of several other similar series, lie on a smooth curve. The rate of photosynthesis at high light intensities is clearly a function of the chlorophyll content of the cells. This seems to be good experimental evidence that chlorophyll is really the pigment concerned in photosynthesis—a fact doubted by no one, but supported so far by inference only.

It is a familiar fact that cutting down the rate of photosynthesis by decreasing the light intensity causes a fundamental change in the character of the process. At low intensities of light the rate scarcely varies with temperature, while at high intensities it varies rapidly with temperature. Dilute prussic acid has practically no effect on photosynthesis at low in-

tensities of light, but inhibits the process considerably at high intensities. For these observations we are indebted to F. F. Blackman (1905) and O. Warburg (1919). The so-called "Blackman reaction," a reaction with a high temperature coefficient and sensitive to prussic acid, is supposed by Warburg to be limiting the rate of the photosynthetic process at high light intensities, while at low light intensities a photochemical reaction, relatively insensitive to changes in temperature and to prussic acid, governs the rate. The characteristics of the two reactions are well summarized by Warburg (1925). If this interpretation is correct, then it should be possible to separate the Blackman reaction from the photochemical reac-

tion either by reducing the light intensity, or by cutting down the chlorophyll content. The result in either case should be a decrease in the rate of the photochemical reaction until it is slower than the Blackman reaction, and becomes the "pacemaker" of the process.

Figure 2 shows two curves representing rate of photosynthesis as a function of temperature at widely different chlorophyll concentrations. For curve A, $\epsilon =$ 0.101, and for curve B, $\epsilon = 0.016$. The data for most processes, when plotted in this way (logarithm of the rate or frequency against reciprocal of the absolute temperature), usually show a straight line relationship. The peculiar shape of the curves presented will be discussed in a later paper. I
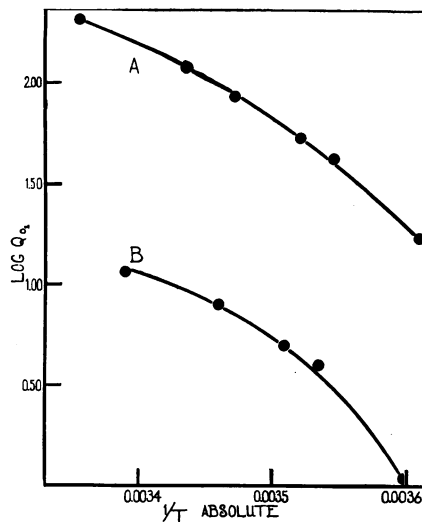

FIGURE 2

The rate of photosynthesis plotted as a function of temperature, at two different chlorophyll concentrations. For curve A, $\epsilon = 0.101$; for curve B, $\epsilon = 0.016$.

wish here to bring out the point that these curves are similar in form, showing that photosynthesis is the same function of temperature whether the chlorophyll concentration be high or low.

Table 1 shows the inhibition of photosynthesis by prussic acid at three different concentrations of chlorophyll. There is no tendency for the inhibition to be less at lower chlorophyll concentrations. On the contrary, at the lowest chlorophyll concentration the inhibition is 15 per cent more than at the highest.

Although either lowering the light intensity or decreasing the chlorophyll content decreases the rate of photosynthesis, the characteristics of the process are very differently affected in each case. It is unreasonable to

suppose that the light intensity affects anything but the photochemical part of the process. The amount of chlorophyll must also affect this part, and in the same way. However, since the characteristics of the process (sensitivity to temperature and to prussic acid) cannot be similarly altered by changing chlorophyll content and light intensity, it must be supposed that chlorophyll plays some other part in the process, besides its rôle in the photochemical reaction.

TABLE 1

THE EFFECT OF PRUSSIC ACID ON PHOTOSYNTHESIS AT THREE DIFFERENT CONCENTRATIONS OF CHLOROPHYLL

c	HCN CONCENTRATION	MM.^{3} O$_2$ PRODUCED	INHIBITION BY HCN
0.037	O	93.1	40%
	9×10^{-6} N	56.2	
0.060	O	122.0	32%
	9×10^{-6} N	82.7	
0.083	O	171.5	25%
	9×10^{-6} N	129.5	

A more detailed presentation of this work is in preparation, and will appear in the *Journal of General Physiology.*

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Blackman, F. F., *Ann. Botany,* 19, 1905.

Warburg, O., *Die Naturwissenschaften,* 49-50, 1925; *Biochem. Zeits.,* 100, 1919; 152, 1924.

Willstätter and Stoll, *Untersuchungen üder die Assimilation der Kohlensäure,* Berlin, 1918.

FUNCTIONAL DISTURBANCES OF HEARING IN GUINEA PIGS AFTER LONG EXPOSURE TO AN INTENSE TONE

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I.—Present controversy regarding theories of the perception of sound seems to be mainly concerned with two sharply defined views. One, the "frequency" theory, regards the basilar membrane as a vibrating unit, which responds in whole or in part in a way depending upon the energy of the stimulating force. A stimulus of great energy would disturb a relatively large part of the basilar membrane and a stimulus of less energy would disturb a relatively shorter section beginning at the base of the cochlea and extending upward. Under this theory pitch is correlated with