generalization concerning pathological pain from study of specific pathological pain is permissible. (iv) No such generalization from experimental pain in man to pathological pain in man is as yet permissible. There is some acceptable evidence that the response is comparable when a powerful anxiety component has been introduced into the experimental pain situation. How broad the limits of usefulness of this finding may be is yet to be shown. Other, as yet unknown, factors may be pertinent.

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Maximal Photosynthetic Rates in Nature

Abstract. It seems likely that turbulence under natural conditions, both aquatic and terrestrial, is higher than it is in the bottles or leaf chambers used when photosynthesis is measured experimentally. Most of the maximal photosynthetic rates reported in the literature are probably lower than those which occur in nature.

Most previous estimates of photosynthetic yield in aquatic habitats have been based on experiments involving enclosure of phytoplankton communities in clear and dark bottles and exposure of these communities to light of various intensities by suspension at different depths in a lake. The data so obtained are considered representative of the photosynthetic activity of the phytoplankton under natural conditions, and these data are inserted in equations containing factors for light penetration, day length, and phytoplankton abundance (*1*) to provide estimates of yield per unit of water surface. The average hourly yield obtained when the exposure period was long (8 hours or more) was lower than that obtained in exposures of a few hours' duration (*2*), and yields obtained when bottles were agitated exceeded those in quiet bottles (*3*). Doty (*3*) considered the quiet bottle a closer approach to natural conditions than the agitated bottles, and most of the studies in the literature are based on data from quiet bottles. It seems likely, however, that confinement of a phytoplankton community in bottles represents a significant departure from the natural condition and may have a considerable influence on photosynthetic rate. During the summer of 1958, a study (*4*) was carried on in western Lake Erie in which photosynthesis was measured under completely natural conditions and the observed rates were compared with data from parallel experiments in which clear and dark bottles were utilized.

The clear- and dark-bottle experiments were conducted as described in previous papers (*1, 2*). Phytoplankton communities at natural densities were confined in clear and dark bottles, suspended at various depths (0 to 3 m) at 0.5-m intervals, and exposed for 3 hours. The difference in *p*H (*4*) in the clear and dark bottles was used to determine CO_2 absorption by reference to a differential titration curve for the natural water (*2*).

The measurements made under completely natural conditions were made by sampling at approximately 4-hour intervals. Samples were taken from five depths (0.1, 1, 3, 5, and 8 m) at a station in the channel between South Bass and Middle Bass islands where the water was 9 m deep. The samples were returned to the laboratory for *p*H determination, and the change in *p*H during a given time interval was used to compute the change in CO_2 concentration. Table 1 shows an example of the data obtained and of computed values for the CO_2 change for the water column.

In this study no corrections were applied for CO_2 exchange between air and water. The surface water usually was slightly supersaturated in the morning and undersaturated in the afternoon. Bohr (*6*) has shown that when water is stirred vigorously the rate constant for CO_2 transport across the gas-liquid boundary layers is about 2×10^{-3} cm/sec. Thus, the maximal rate of CO_2 entry would be of the order of 9 mmole/m^2 per 12 hours (*7*) if free CO_2 concentration in water were zero. But the actual free CO_2 concentration is not zero, and the water is not stirred so vigorously as in Bohr's experiments. The CO_2 equilibrium between air and water was usually reached during the morning hours (the average time of this occurrence was 0800), so the net diurnal CO_2 exchange must have been in the direction of CO_2 absorption from the atmosphere, and neglecting this process makes our estimates of photosynthesis too low. It seems likely that the error is less than 2 percent.

The computations in Table 2 also assume that the *p*H changes due to the influx of different water between sampling times will not introduce a systematic error. Random errors will, of course, be introduced by this factor, so the rate computed from a single day's work may be too large or too small, depending on whether the change of water masses increased or decreased the *p*H value. In the average from several days' work, however, such random errors will cancel out. Values for individual days ranged from 0 to 620 mmole/m^2 day.

Students of photosynthesis have usually considered two quantities, (i) total or gross photosynthesis and (ii) apparent photosynthesis (that is, photosynthesis in excess of the respiratory processes of the plants which carry on the photosynthetic activity). When one is measuring CO_2 change in a natural aquatic environment, a third quantity must be considered—namely, net photosynthesis (that is, photosynthesis in excess of the respiratory contributions of the entire aquatic community). Computations like those in Table 1 represent diurnal net photosynthesis. Because the nocturnal CO_2 production is practically equal to the diurnal CO_2 uptake (the *p*H value at 0630, for example, shows no consistent trend from day to day), we can obtain an approximate estimate of the gross

Table 1. Carbon dioxide change as computed from *p*H change under completely natural conditions.

Depth (m)	*p*H		ΔCO_2 (mmole/m^3)	Cubic meters* represented in water column	ΔCO_2 for entire water column (mmole/m^2)
	Time				
	0600	1100			
0.1	8.24	8.42	24	1	24
1.0	8.23	8.40	24	1	24
3.0	8.21	8.35	19	2	38
5.0	8.20	8.31	15	2	30
8.0	8.19	8.28	12	3	36
Total					152

* The first two samples are considered representative of the first two meters; the 3- and 5-m samples, of the next 2-m intervals, respectively; the 8-m sample, of the last three meters in the water column.

Table 2. Photosynthetic yields under completely natural conditions compared with yields computed from light- and dark-bottle data (see *13*).

Time interval	Rate of photosynthesis (mm/m²/day)*		
	Under natural conditions		Computed from bottle data
	Net	Gross	Gross
17 June–18 July	225	450	187
19 July–22 August	288	576	242

* The difference between 225 and 288 is not statistically significant with the number of samples used (14 in each period), but the differences between 450 and 187, 576, and 242 are significant beyond the 1 percent level.

photosynthetic rate by doubling the observed diurnal net rate, for the respiration rate indicated by the nocturnal CO_2 gain must continue throughout the daylight hours.

Table 2 shows the average daily CO_2 uptake, net and gross, computed in this way and compared with daily gross yields estimated from light- and dark-bottle data. Note that the diurnal net yields exceed the gross yields computed from the bottle data. It is evident that enclosing the aquatic community in bottles reduces photosynthetic activity to less than half that maintained under natural conditions (*8*). One factor which may contribute importantly to the reduced rates in bottles is the greatly reduced turbulence. Eddy diffusivities in western Lake Erie in summer are of the order of 25 cm²/sec; this must be at least 10^4 times greater than the values for unagitated bottles.

Photosynthetic rates for terrestrial plant leaves have usually been measured by determining CO_2 absorption from an air stream passing through a leaf chamber. The highest rates of air flow routinely used have been about 2.5 lit. of air per square centimeter of leaf per hour (*9*). Heinicke and Hoffman (*9*) state that they chose a flow rate of 2.5 lit./cm² hr because they observed that a hydroxide surface when exposed to such a flow rate absorbed CO_2 at the same rate as did a hydroxide surface standing open in the room. Such a flow rate, therefore, represents conditions of air turbulence much quieter than those prevailing outdoors.

Heinicke and Hoffman observed an increase in photosynthetic rate (in apple) from 22.1 to 30.8 mg of CO_2 per square decimeter per hour when they increased the rate of air flow from 2.5 to 7.5 lit./cm² hr, although the CO_2 content of air at this flow rate did not fall below 80 percent of that in normal air. More recently Burnside (*10*) observed that increasing the flow rate from 1 to 6 lit./cm² hr increased the photosynthetic rate (in cotton, and sunflower) from 20 to 37 mg/dm² hr. Most of the maximum yields in Rabinowitch's (*11*) Table 28.VI are less than 20. The rates reported by Russian workers represent notable exceptions. Kursanov's rate for *Pyrus malus* is 35, closely similar to the rate obtained by Heinicke and Hoffman with their high flow rate. Perhaps the higher yields reported by Russian workers reflect higher turbulence in their leaf chambers. A relation of photosynthetic rates to eddy diffusivity in leaf chambers might contribute to our understanding of the problem. Verduin (*12*) has published some computations of probable CO_2 concentrations within leaf chambers, but we have found no quantitative study of eddy diffusivity in leaf chambers.

It seems likely that most of the maximal terrestrial photosynthetic rates appearing in the literature are considerably lower than the maximal rates attained under completely natural conditions; the reduced turbulence of the medium in the experimental apparatus may be primarily responsible for the reduced rates.

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7. This computation is made as follows:

$$\underset{\text{(cm/sec)}}{2 \times 10^{-3}} \times \underset{\substack{\text{Concn. differ-}\\ \text{ence across}\\ \text{boundary layers}}}{13 \times 10^{-6}} \times \underset{\substack{\text{Partition}\\ \text{coeff.}}}{0.8} \times \underset{(\text{cm}^2/\text{m}^2)}{10^4} \times \underset{\text{sec/12 hr}}{4.3 \times 10^4}$$

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13. A sample computation from bottle data is as follows:

$$\underset{\substack{(\text{mm/m}^3/\text{hr})\\ \text{Optimal}\\ \text{light}}}{4.8} \times \underset{\substack{\text{Ratio of}\\ \text{optimal}\\ \text{value}\\ \text{to av. in}\\ \text{euphotic}\\ \text{zone}}}{0.65} \times \underset{\substack{(\text{m})\\ \text{Depth of}\\ \text{euphotic}\\ \text{zone}}}{5} \times \underset{\substack{\text{Hours of}\\ \text{daylight}}}{12}$$

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Magnitude of Reinforcement and Consummatory Behavior

Abstract. The rates at which white rats licked saline, sucrose, and saccharin solutions, respectively, were measured by cumulative recording of tongue contacts with the solution in question. The local rate of licking was constant for all solutions, but differences in the distribution of sustained periods of licking were related to the type and concentration of the fluid consumed.

In place of Hull's (*1*) original associative interpretation, Spence (*2*) has recently argued for a motivational theory of the effects on behavior of different reward magnitudes. Spence bases part of his argument upon empirical data collected in his own and other laboratories. But greater attention is given to indirect evidence derived from a theoretical analysis of runway behavior. According to this theory, part of an animal's consummatory behavior in a goal box becomes conditioned to stimuli in that goal box, and ultimately, through generalization, anticipatory goal responses (r_g) are elicited by stimuli in the runway. When s_g represents feedback stimulation from the response r_g, the mechanism r_g-s_g is said to maintain running in the alley. In particular, this r_g-s_g mechanism is assumed to possess motivational properties "that vary with the magnitude or vigor with which it occurs" (*2*, p. 135).

Whether or not this assumption is necessary is not certain (see *3*), but it is inadequate as stated, owing to the ambiguity of the term ***vigor***. The vigor of a response might, for instance, refer to the magnitude, or strength, of the response—that is, the amount of effort that goes into a single occurrence of that response; it might refer to the rate at which that response occurs (when it does occur); or it might refer to the persistence of that response in competition with other responses. Thus, *vigor* might refer to the intension, tempo, or perseveration of a response, or to any combination of these and other response dimensions (*4*). Only the first and second of these dimensions appear to have been considered by Spence—that is, he questions whether different magnitudes of reward produce different r_g's in terms of strength or intension (*3*, p. 137) or whether the effect is on the tempo of a single r_g (*2*, p. 147), and, with some reservations, he concludes that the second alternative is correct—on the basis of experiments reported by Guttman (*5*) and by Sheffield, Roby, and Campbell (*6*). However, neither of these studies is pertinent, because although they show that different reward conditions lead to different operant and consumption rates, there is no indication whether these were due to the tempo, perseveration, or latency of the consummatory behavior. That is, the consummatory response may have oc-