EFFECT OF 2,4-DICHLOROPHENOXYACETIC ACID ON PHOTOSYNTHESIS AND RESPIRATION[1,2]

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Early work with plant growth regulators offered only indirect evidence regarding their effect on photosynthesis. Mitchell *et al.* (15) showed that starved bean leaves exposed to light after they had been sprayed with α-naphthaleneacetic acid accumulated less starch, sugar, and dextrin than unsprayed leaves, and thus indicated the possibility of a decrease in photosynthesis. Freeland (13, 14), measuring photosynthesis directly by gas exchange, found that 2,4-dichlorophenoxyacetic acid (2,4-D) and other plant growth regulators inhibited apparent photosynthesis in Anacharis and in bean leaves. In bean, 2,4-D in a concentration of 100 ppm caused an inhibition of photosynthesis amounting to approximately 20% over the 4-day experimental period; respiration was first inhibited and then stimulated during the same period. In Anacharis, 30 and 100 ppm of 2,4-D caused a decrease in the rate of photosynthesis, the reduction being greater at the higher concentration. Respiration was at first inhibited by 2,4-D, but showed a partial or complete recovery at the end of 48 hours. Rhodes (20) showed that 2-methyl-4-chlorophenoxyacetic acid reduced apparent photosynthesis of tomato plants.

Nickell (16) reported stimulation of respiration of tumor tissue of *Rumex acetosa* at very low concentrations of 2,4-D, with progressive inhibition of respiration at higher concentrations. Growth of the tumor tissue responded to the application of 2,4-D in much the same manner as respiration.

The dependence of the growth-promoting effect of naturally occurring auxin upon the concentration of the undissociated auxin molecule was established in 1934 (6), after Dolk and Thimann (12) had demonstrated that auxin activity was highest in an acid medium. This relationship has since been verified for synthetic plant growth regulators and other weak acids and bases by observing their effect in a variety of growth and respiration responses (2, 4, 5, 21, 22, 23, 25, 26). Albaum *et al.* (1) showed that the relation of the pH of the medium to the effect of externally applied indoleacetic acid on Nitella was due to the penetration of the indoleacetic acid, the coincidence of the curves for penetration of indoleacetic acid and its dissociation, plotted against pH, indicating that it entered as the undissociated acid.

Audus (3) found the inhibition of root growth to be proportional to the logarithm of the concentration of undissociated 2,4-D acid present, whether the range of concentrations of this molecule was achieved by varying the pH or by increasing the concentration at a constant pH.

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The widespread use of 2,4-D in citrus culture for such purposes as increasing fruit size, delaying leaf and fruit abscission, and prolonging storage life of harvested fruit (24) has resulted in a situation in which a great deal of practical knowledge concerning the effects of the growth regulator on citrus is available, whereas little is known regarding the means by which 2,4-D alters the functioning of the plant to produce the observed responses. The present investigation is concerned with a quantitative study of the effect of 2,4-D on photosynthesis and respiration of citrus leaves and, for comparative purposes, its effect on the same processes in the unicellular green alga *Chlorella pyrenoidosa*.

MATERIALS AND METHODS

EXPERIMENTS WITH CITRUS LEAVES: To reduce variation of the experimental material to a minimum, leaf samples were taken from a single Washington Navel orange tree growing in the field. The leaves selected were of a comparable physiological age, being those of the most recent growth flush, which had reached their full expansion and color development.

After harvesting, the leaves were brought into the laboratory in a closed container lined with moistened paper. For treatment and measurement of photosynthesis, 12 disks were cut from each leaf with a sharpened cork borer having an inside diameter of 8 mm. The 12 disks from each leaf were distributed among 12 beakers, 1 disk to each beaker. Six leaves were used for each run. The 6 disks in each beaker were then covered with solutions of buffer, or of buffer plus 2,4-D, prepared as described below. Circular pieces of stainless steel screen were placed over the leaves to ensure their remaining immersed in the solutions during the treatment. The beakers were then placed in a desiccator fitted with a stopcock and were subjected to a vacuum for 30 minutes. The vacuum was then released, and the infiltrated disks were removed from the solutions and placed on absorbent paper, to remain until the water-soaked appearance of the tissue disappeared, usually about 30 minutes. The disks were then transferred individually to 16-ml Warburg flasks having two side arms, the 6 disks from each treatment being arranged with their upper (non-stomate-bearing) surfaces downward around the center well of the flask so that there was no overlapping. One ml of a diethanolamine-carbonate buffer (18) of a composition that maintained a constant partial pressure of approximately 1% CO_2 in the flask was distributed, 0.3 ml to each side arm and 0.4 ml to the center well. A fluted filter paper was then placed in the center well, and the system was closed.

Measurements of photosynthesis, as evidenced by evolution of oxygen, were carried out in an illuminated

Warburg respirometer (27) at a temperature of 25°C, with a light intensity of approximately 1200 fc, for a period of 1 hour. A one-hour measurement of respiration in darkness completed the determination. The sum of the light and dark readings gave an approximation of true photosynthesis. The manometric assemblies were not shaken, thus avoiding the need for adding water or an adhesive to the flask to prevent the disks from overlapping during the determinations.

Buffer solutions of various H^+ concentrations were prepared by diluting a stock solution of phosphate buffer with water (for the controls) or with a solution of recrystallized 2,4-D acid brought to the desired pH by the addition of KOH, to give a final concentration of 0.04 M phosphate. The final concentration of 2,4-D in those buffers containing it was 2×10^{-3} M. This procedure was used to minimize the change in pH of the solutions containing 2,4-D as a result of the increased H^+ concentration due to the acid.

For treatments with a range of 2,4-D concentrations at pH 4.5, solutions were prepared in the same manner with a concentrated phosphate buffer solution at pH 4.5 diluted with solutions of 2,4-D at the same pH to give a final phosphate concentration of 0.04 M and 2,4-D concentrations in the desired range.

The buffer concentration of 0.04 M was selected after preliminary experiments indicated that over the range of 0.01–0.05 M PO_4 there was very little effect of buffer concentration on the rate of photosynthesis of the leaves, whereas concentrations higher than 0.1 M inhibited the process appreciably, and those below 0.005 M did not have sufficient buffering capacity to resist changes in pH during the treatments.

To place the solutions in intimate contact with the cells and thus reduce to a minimum the time required for penetration into the cells, materials were applied to the leaves by infiltration. Day (10) has found that 2,4-D will penetrate through the cuticle and epidermis of bean leaves at approximately 30 μ/hr. Under the conditions of the present work, this rate would more than ensure that 2,4-D would penetrate from the intercellular spaces into the cells before photosynthesis measurements were started. The fact that penetration had reached a maximum before measurements were begun was also indicated by the fact that there was no significant change in the rate of photosynthesis of any of the treatments during the period in which determinations were made. Leaf disks which were infiltrated with water alone or with 0.04 M phosphate buffer did not differ significantly in their rates of photosynthesis from noninfiltrated leaf disks.

The leaf-disk infiltration technique was used to eliminate as many as possible of the side effects of 2,4-D, such as an effect on translocation which would in turn change the rate of photosynthesis. The short period of exposure and the unnatural conditions prevailing during the treatment and during the measurement of photosynthesis do not allow direct comparison with field applications of the growth regulator, but do permit a more critical study of the effect on photosynthesis alone.

EXPERIMENTS WITH CHLORELLA: To eliminate inaccuracies resulting from failure to maintain a 2,4-D solution of known concentration in contact with the cells of the orange leaf, owing to change in concentration of the infiltrated solutions by water loss, and, particularly, to eliminate the possible effect of 2,4-D on stomate opening (7), a parallel series of experiments was run, using *Chlorella pyrenoidosa*.

The technique used for treatment and measurement of photosynthesis with Chlorella cells was of necessity somewhat different from that employed with the orange leaf disks. Chlorella was cultured aseptically in flasks containing 50 ml of nutrient solution. These flasks were shaken continuously in a greenhouse. After approximately 2 weeks, samples were removed into centrifuge tubes and centrifuged for 3 minutes. The cells were then resuspended in 3 ml of the buffer solution or of the buffer plus 2,4-D solution used for treatment and were transferred to Warburg flasks having two side arms. One ml of diethanolamine-carbonate buffer was then distributed in the side arms and center well, as indicated above. Photosynthesis and respiration were measured as in the preceding experiments except the flasks were shaken at 100 cycles per minute. Replications were obtained by successive runs using the same treatments.

DETERMINATION OF DISSOCIATION CONSTANT OF 2,4-D: The 2,4-D acid [3] used in these experiments was recrystallized twice from hot water, yielding odorless white crystals with a melting point of 138.6° to 139.6°C. The dissociation constant of this material was determined with the use of 0.003 and 0.004 M solutions. The hydrogen-ion concentrations of these solutions were measured with a Beckman model G pH meter after calibration with a solution of 0.05 M KH phthalate, the pH of which was taken as 4.005 (11). The pK'_a value for 2,4-D acid, calculated from the equations

$$\frac{[H^+][A^-]}{[HA]} = K'_a;\ pK'_a = \log \frac{1}{K'_a},$$

was found to be 2.96. This compares with the values of 3.28 and 2.81–2.89 determined by Audus (3) and van Overbeek (26) respectively.

[3] Provided by The Dow Chemical Co.

RESULTS

EFFECT OF HYDROGEN-ION CONCENTRATION ON INHIBITION OF PHOTOSYNTHESIS BY 2,4-D: The uppermost curve of figure 1 shows the effect of H^+ concentration, over the range from pH 3.10 to pH 8.05, on the photosynthesis of navel orange leaf samples infiltrated with 0.04 M phosphate buffer. There is a tendency for the highest rate to be achieved between pH 5 and 6, with the low point of the curve at the greatest H^+ concentration and no detectable difference between the rate at pH 7 and that at pH 8. The addition of 2×10^{-3} M 2,4-D to the buffer solutions at the various pH values caused a change in the slope of the curve, as indicated in the second curve of figure 1. The continuing downward trend of this curve, from pH 8.05 to a low point at pH 3.10, indicates

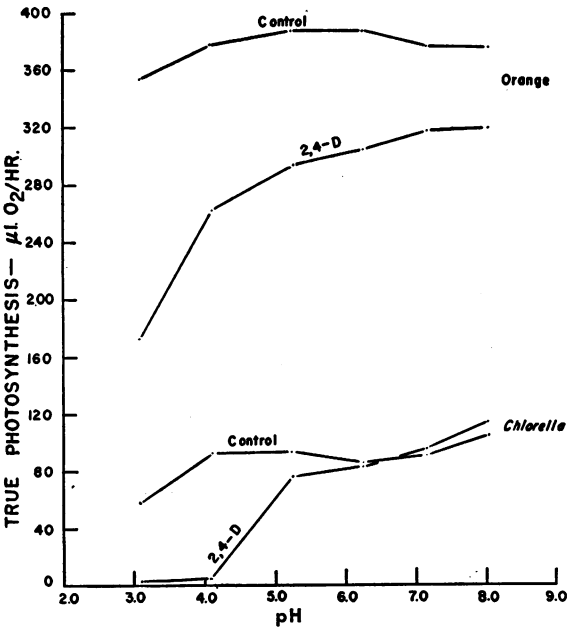

FIG. 1. Photosynthesis of Washington Navel orange leaves and of the green alga *Chlorella pyrenoidosa*, as affected by H^+ concentration, alone, and with the addition of 2×10^{-3} M 2,4-D.

that with a decrease in pH the same concentration of 2,4-D caused an increasing inhibition of the process of photosynthesis.

The two lower curves of figure 1 show the effect of the same range of hydrogen-ion concentrations, with and without the addition of 2×10^{-3} M 2,4-D, on the true photosynthesis of *Chlorella pyrenoidosa*. Photosynthesis was inhibited at pH 3.10 but showed very little effect of H^+ concentration over the rest of the pH range, with the possible exception of a tendency for a stimulation to occur above pH 7.

The 2,4-D curve shows a somewhat different effect than was found with the orange leaves. With Chlorella, inhibition was almost complete at pH 4.10 and 3.10, while at pH values above 7 the cells exposed to 2,4-D actually had a stimulated rate of photosynthesis, as compared with the controls.

Figure 2 represents the same data recalculated so that the percentage inhibition of photosynthesis by 2,4-D is plotted against the logarithm of the concentration of the undissociated acid present in each of the H^+ concentrations used. With both orange leaves

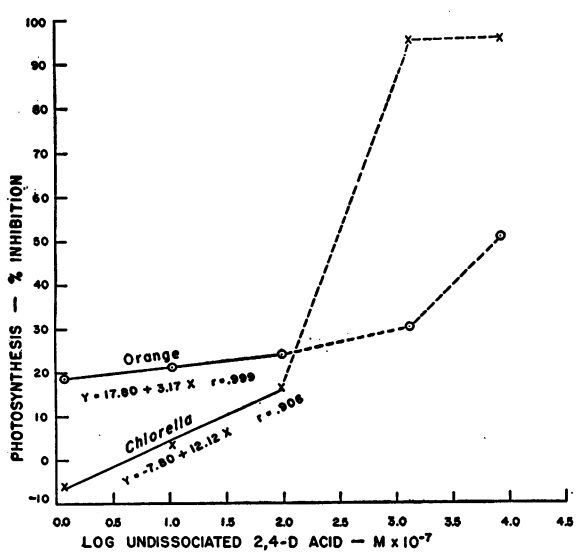

FIG. 2. Percentage inhibition of photosynthesis of Washington Navel orange leaves and of *Chlorella pyrenoidosa* by a range of undissociated 2,4-D acid concentrations obtained by varying the H^+ concentration of buffers containing a constant amount (2×10^{-3} M) of 2,4-D.

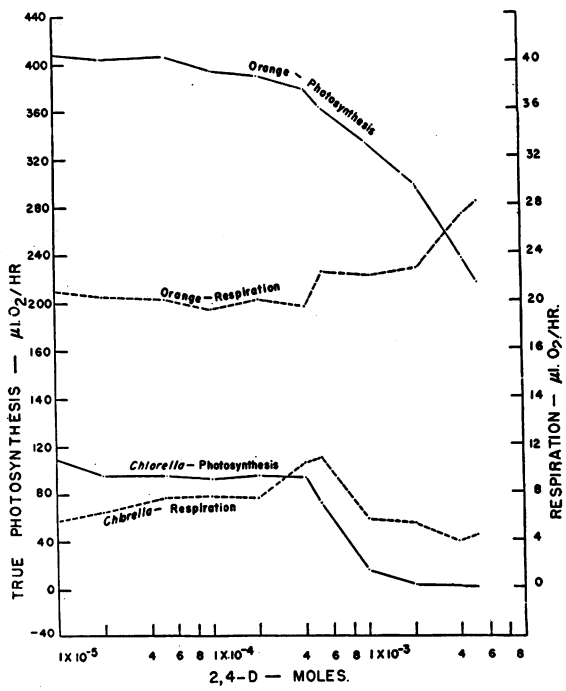

FIG. 3. Photosynthesis and respiration of Washington Navel orange leaves and of *Chlorella pyrenoidosa*, as affected by concentrations of 2,4-D from 1×10^{-5} to 5×10^{-3} M at pH 4.5.

and Chlorella, in the lower range of undissociated acid concentrations (1.22×10^{-7} to 9.55×10^{-6} M, corresponding to pH 7.18 to 5.28), the data fit straight lines when plotted against the logarithm of the concentration of undissociated acid. The inhibition of photosynthesis in the orange leaves gives a line with the formula $Y = 17.80 + 3.17\,X$, with a correlation coefficient $r = 0.999$; in Chlorella, the line of best fit is $Y = -7.80 + 12.12\,X$, with a correlation coefficient $r = 0.906$. Attempts to fit the portions of the curves mentioned, and the entire range of concentrations, to an arithmetical relationship gave very low correlation coefficients. The higher range of undissociated acid concentrations (9.55×10^{-6} to 8.37×10^{-4} M, corresponding to pH 5.28 to 3.10) failed to fit adequately either a logarithmic or an arithmetical regression.

These parts of the curves are indicated in the figure by means of dashed lines connecting the mean values.

EFFECT OF 2,4-D CONCENTRATION ON INHIBITION OF PHOTOSYNTHESIS: The effects of 2,4-D, in concentrations ranging from 1×10^{-5} M to 5×10^{-3} M at pH 4.5, on photosynthesis of navel orange leaves and of Chlorella cells are shown in figure 3. The values for the control treated with buffer at pH 4.5 (not shown on the chart) were 402 μl O_2/hr for the orange leaves and 108 μl O_2/hr for the Chlorella cells.

The fairly smooth curve for orange leaves when rate of photosynthesis is plotted against molar concentration of 2,4-D on a logarithmic basis, indicates a continuous decrease in rate of photosynthesis with increasing concentration.

In the case of the Chlorella cells there is very little effect of 2,4-D on photosynthesis over the range 1×10^{-5} to 4×10^{-4} M, with a rapid decrease brought about by an increase in concentration to 2×10^{-3} M, at which point inhibition of photosynthesis appeared to be complete. Although photosynthesis was completely inhibited, the cells were apparently still alive, as evidenced by the fact that respiration continued, although oxygen uptake was at the same rate in both light and darkness. This oxygen uptake may, of course, have been due to some oxidative processes in nonliving cells.

Figure 4 shows the data of figure 3 plotted as percentage inhibition of photosynthesis against concentration of undissociated 2,4-D. In this case the inhibition of photosynthesis in both Chlorella and navel orange leaves by 2,4-D over the range of concentration of undissociated acid molecules from 5.4×10^{-6} to 1.40×10^{-4} M, fit straight lines calculated against concentration of undissociated 2,4-D. These curves—that of the orange leaves with the formula $Y = 4.38 + 3.01\,X$ and $r = 0.977$, and that of Chlorella with the formula $Y = 5.36 + 19.22\,X$ and $r = 0.924$—correspond

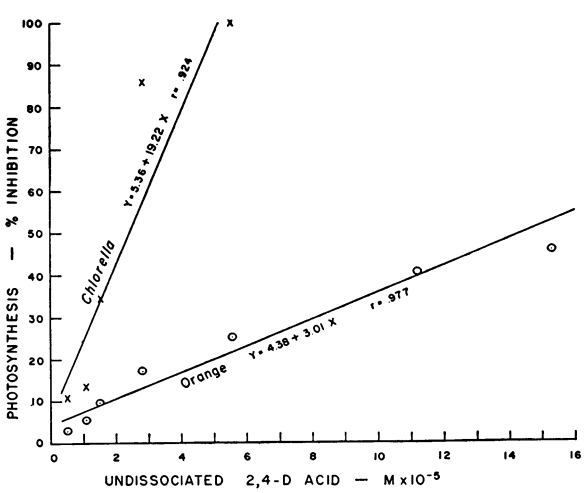

FIG. 4. Percentage inhibition of photosynthesis of Washington Navel orange leaves and of *Chlorella pyrenoidosa* by a range of undissociated 2,4-D acid concentrations obtained by varying the concentration of 2,4-D added to buffers at pH 4.5.

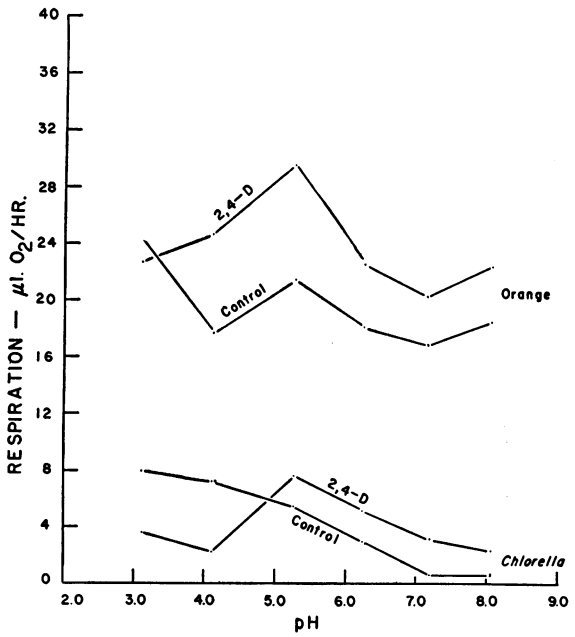

FIG. 5. Respiration of Washington Navel orange leaves and of *Chlorella pyrenoidosa*, as affected by H^+ concentration, alone, and with the addition of 2×10^{-3} M 2,4-D.

to those portions of the curves in figure 2 which are drawn with dashes. They have good fit when calculated on an arithmetical basis and have low correlation coefficients when calculated on a logarithm of concentration basis.

EFFECT OF 2,4-D CONCENTRATION ON RESPIRATION: Respiration measurements made on the orange leaves and Chlorella cells at the time photosynthesis was determined are shown in figures 3 and 5. The curves in figure 3 show that with an increase in 2,4-D concentration at a constant H^+ concentration there is a tendency toward an increase in respiration. In the orange leaves this tendency continues to the highest concentration, but in Chlorella the stimulation is found only over a narrow concentration range and is followed by a progressive inhibition of respiration. Curves in figure 5 show that over the range from pH 3.10 to pH 8.05, there is inhibition of respiration in both orange and Chlorella only at the lower pH values, with a more or less constant stimulation of respiration in the higher pH values.

Since the mass of tissue used in these determinations was limited by the need for limiting the total oxygen evolution by photosynthesis to a value which could easily be determined in the Warburg apparatus, and since the respiration values are approximately one-tenth of those for photosynthesis, they are so low that it is difficult to draw valid conclusions from the small differences which occurred during these experiments.

DISCUSSION

Although growth responses of plants to various growth substances, both naturally occurring and syn-

thetic, have frequently been shown to depend on the concentration of the undissociated molecule (2, 25), the present authors have found no previous reference to similar effects of a growth substance on photosynthesis.

The inhibition of photosynthesis by cyanide has recently been shown (17, 28) to be a function of the concentration of undissociated HCN. The concept of undissociated auxin as the controlling factor in pH-growth curves has recently been challenged on the basis that the pH of the bathing medium controls the ionization of plant proteins and thus controls the response to added growth regulators (8). Burström (9) suggests that calcium rather than undissociated auxin controls the response of root growth to pH, but he attributes this to a hardening of the cell wall by calcium, which counteracts the softening effect of auxin.

It nevertheless appears that the data presented here can best be interpreted by assuming that the undissociated 2,4-D molecule is the effective agent in inhibiting the photosynthesis of Chlorella and of navel orange leaves under the conditions of these experiments. This relationship seems to be best explained by the assumption that only the undissociated molecule penetrates (1) into the cell and thus is the effective form of the compound. These data indicate, however, that there may be at least two separate types of inhibition involved, and that, in addition, at least in orange leaves, part of the inhibition may be due to an indirect effect on photosynthesis through gas exchange, or to an effect of the ionized form of the acid.

The two sets of data presented here cover parts of the same range of undissociated acid concentration obtained in two different ways. The experiments summarized in figure 2 cover undissociated acid concentrations ranging from 9.05×10^{-8} to 8.37×10^{-4}, while those in figure 4 range from 5.42×10^{-6} to 1.40×10^{-4}, giving an expansion of a portion of the curves of figure 2. As shown in figure 2, only the lower concentration range can be fitted significantly to the logarithm of undissociated 2,4-D concentration, with a sharp break in the curve for Chlorella and a less obvious change for navel orange leaves at a value corresponding to 9.50×10^{-5} M of undissociated acid.

Considering only the portion of the curve (fig. 2) which is presented as a solid line, the relationship indicates the possibility of an effect of 2,4-D on some rate-limiting enzyme reaction concerned with photosynthesis, making the rate of photosynthesis inversely proportional to the logarithm of undissociated 2,4-D acid. Since the undissociated acid is assumed to be the form which penetrates, the concentration within the cells depends on the concentration of undissociated acid in the medium, and the slope of the curve thus represents the proportionality of reacting molecules or the affinity of 2,4-D for the substance with which it is reacting. The difference in slope of the orange leaf curve might be due either to a lower effective concentration within the cells as a result of the different method used for treatment, or to a greater adsorption of 2,4-D by some nonactive material within the cells (8), or to a combination of these two with other factors.

The intercept of the Chlorella curve indicates a stimulation of photosynthesis by the lower range of concentrations of 2,4-D, but the same proportionality would not necessarily be carried through the concentration range lower than that used here. The intercept of the orange leaf curve indicates an appreciable inhibition at extremely low concentrations of undissociated 2,4-D. This might be due to one or more of a number of factors, such as closure of the stomates, which has been shown to be one of the effects of 2,4-D application (7, 19), or to an effect of the dissociated form of the growth regulator such as has been postulated (8, 23), or, more likely, to a different level of undissociated acid within the cell, governed by the pH of the cell itself. The continuous bathing of the Chlorella cells in the solution would render them likely to undergo a greater change in their internal pH than the orange leaves. Due to lack of any means for accurate determination of the internal pH of the cells, the question of whether or not the undissociated acid is the only form which reacts within the cells, as well as the only form which penetrates into the cell, cannot be settled, and effects which might arise out of this relationship must remain speculative.

The portions of the two curves which do not fit the same relationship as those discussed above, and which are indicated in figure 2 by dashed lines, are thought to represent a different type of inhibition. A part of the same concentration range used in figure 2 is covered by the curves in figure 4, where the different concentrations of undissociated acid were obtained at a constant pH by a change in total concentration of 2,4-D. This range, from 5.42×10^{-6} to 1.40×10^{-4} M of undissociated acid, corresponds approximately to the range of log concentration of undissociated acid in figure 2 from 2.0 to 3.0. In this case, the data can be fitted most accurately to an arithmetical relationship in which the inhibition of photosynthesis is dependent on the concentration of undissociated 2,4-D acid. Here again the curve for Chlorella has a much steeper slope than the one for orange leaves, but in this case the intercepts are rather close, and both fall near zero. The area in which the curves for the two types of inhibition cross is rather indefinite, the inhibition being somewhat less in figure 4 than in figure 2 for the same concentration of undissociated acid. Investigations are presently underway to give further experimental points for this region of the curve and to elucidate the role which the hydrogen ion itself may play in determining the response of photosynthesis to 2,4-D through an effect on the dissociation of the cell constituents (8).

Observations of Chlorella cells after the conclusion of photosynthesis and respiration determinations indicated that the cells which had been exposed to concentrations of undissociated 2,4-D higher than 9.35×10^{-5} M were progressively decolorized by higher concentrations, the difference being obvious to the unaided eye, with a complete lack of green color in those cells in which photosynthesis had been completely inhibited.

This suggests that the second type of inhibition being dealt with here, over the range from 4.52×10^{-6} to 1.36×10^{-4} M of undissociated acid, may be due to a progressive destruction of chlorophyll, or to inhibition of chlorophyll synthesis by the 2,4-D, resulting in a decreased photosynthesis.

Summary

The effect of 2,4-dichlorophenoxyacetic acid on photosynthesis and respiration of leaves of Washington Navel orange and of the unicellular green alga *Chlorella pyrenoidosa* has been studied.

The inhibition of photosynthesis by 2,4-D is shown to be related to the concentration of undissociated 2,4-D acid molecules in the solution used for treatment, regardless of whether the difference in undissociated acid concentration was obtained by varying the pH of buffer solutions containing a constant amount of 2,4-D, or by varying the concentration of 2,4-D added to buffers of the same pH.

Two phases of inhibition are shown: one, in a low range of undissociated acid concentration, is proportional to the logarithm of this concentration; the other, covering a higher concentration range, is proportional to the concentration of undissociated 2,4-D and is thought to represent a direct or indirect destruction of chlorophyll by the 2,4-D.

The effect of the same concentrations of 2,4-D on respiration of the plant tissues was slight, but tended to show stimulation in intermediate ranges of undissociated acid concentration and inhibition in the higher concentration ranges.

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