THE EFFECTS OF 2,4-DICHLOROPHENOXYACETIC ACID ON MUSTARD PLANTS AS MODIFIED BY LIGHT QUALITY

GEORGE WILLIAMS JR.

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University of New Hampshire, Ph.D., 1963
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THE EFFECTS OF 2,4-D ON MUSTARD PLANTS
AS MODIFIED BY LIGHT QUALITY

BY
GEORGE WILLIAMS, JR.
B.S., Southern University, 1957
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INTRODUCTION

For the past decade the effects of 2,4-dichloro-phenoxyacetic acid (2,4-D) on plant growth have been widely investigated. Nevertheless, the overall mechanism by which 2,4-D kills plants is still a problem to plant scientists. It is well-known that 2,4-D may affect plants in many ways. One of the first obvious effects is that of a change in the water relations of tissues. 2,4-D has been observed to cause an initial increase in the moisture content of numerous plants followed by a definite decline until death. The absorption of mineral ions is often depressed by 2,4-D and changes are induced in the amino acid and protein contents. Also, 2,4-D has an effect on the carbohydrate content, photosynthesis, respiration, etc.

The fact that 2,4-D may either promote or retard photosynthesis and/or respiration is well established. However, the exact nature of its initial effects is debatable because numerous investigators have observed that it interferes with many plant mechanisms. Crafts (22) sums up this point as follows:

Many of the mechanisms being studied may have only a remote relation to the actual method by which the lethal action of a herbicide is brought about. For example, it is tempting to suggest that because the substituted urea and triazine herbicides block photosynthesis, the plants die of starvation. However, if seedlings are placed in complete darkness at the same time that others are treated with these herbicides, the chemically treated seedlings die much before those placed in the dark. And if the concentration of one of these herbicides is sufficient, seedlings of weeds are killed without emerging; in other words,
they die without ever starting photosynthesis. This emphasizes the point that the actual mode of lethal action is more basic than photosynthesis; the effects on photosynthesis may be secondary to some much more fundamental process that is upset by the herbicide.

Various environmental factors have been studied in relation to their influence on the effects of 2,4-D on plant growth. How different factors may modify the action of 2,4-D remains unclear. Of the many factors studied in relation to the effectiveness of 2,4-D and other herbicides, there is little doubt that light plays a very important role. In a recent monograph Audus (6) points out that the herbicidal action may be effected by a light effect on the absorption process of the plant. This would be an indirect action, accelerating the removal and distribution of auxin from the leaves, thus influencing translocation of food which 2,4-D accompanies, and finally, an activation of 2,4-D in the cell.

Many complications are met when modifying herbicidal action with light. In some instances low intensities have increased the effectiveness of a 2,4-D solution of a specific concentration, whereas the same solution with higher light intensities produced relatively little effect on the plants. In fact, they were almost insensitive to the herbicide. Often, it is important as to whether the plants receive light before or after 2,4-D treatment (6).

This dissertation is a report of a study designed to offer further elucidation of the modifying effects of light qualities on the action of the sodium salt of 2,4-D with the hope of achieving an increased understanding of how
different light colors influence the herbicidal activity of 2,4-D. Tibbits and Holm (69) emphasized the importance of an understanding of the physiological and morphological responses of plant tissues to phytotoxic compounds in order that new herbicides may be more intelligently selected and developed for weed control. The data presented are mainly measurements of CO₂ uptake (apparent photosynthesis), CO₂ output (respiration), and dry weight studies under specific conditions.
LITERATURE REVIEW

The diverse uses of 2,4-D as a growth-promoting or growth-inhibiting substance have caused numerous investigators to conduct many studies to evaluate the physiological response of plants when treated with 2,4-D. As a result of such broad and inquiring interest, innumerable reports have been published concerning the effects of 2,4-D and other chemicals on various plant processes.

Shaw, et al. (62), and Shaw and Danielson (63) have emphasized that for the most effective utilization of herbicides it is important to know their nature and properties, sites and mechanisms of action, metabolic fate in plants and soil, and the environmental influence on their performance. It is further pointed out by Shaw and Danielson (63) that herbicides kill weeds by their interference in such vital processes as respiration, photosynthesis, transpiration, and mitosis. As an example, 2-chloro-4,6-bis(ethylamino)-s-triazine (simazine) was listed as being very effective in inhibiting the ability of the chloroplast to function in the photosynthetic process, thereby causing insufficient production of sugar and starch.

Jukes (42) reported that 3-amino-1,2,4-triazole (amitrole) acts as an antimetabolite. He defined a metabolite as "a compound that occurs in living organisms and has an essential function in a biochemical process". The
action of amitrole as an antimetabolite is that of blocking the synthesis of vitamins and chlorophyll. McWhorter and Porter (48) reported that amitrole caused the production of chlorotic tissue in corn plants. In comparing untreated plants to amitrole treated plants they observed a much lower respiratory quotient with the treated plants. The assumption was made that untreated plants metabolized basically carbohydrates, whereas amitrole treated plants metabolized fats as a major respiratory substrate. They also observed that oxygen uptake in chlorotic tissue was inhibited by iodoacetate and malonate as compared to control tissue. Nevertheless, sodium fluoride caused nearly the same degree of inhibition in both tissues. The metabolism of amitrole in different plants was studied by Carter and Naylor (17). They noted that amitrole was metabolized very rapidly in plants from many families. It is suggested that some one or more of the compounds derived from amitrole in plants may possess phytocidal activity.

The fact that many physiological responses of plants to 2,4-D may be of a secondary nature was discussed by Mitchell (50). Among these possible secondary responses are an increase in the moisture content of tissues, hydrolysis of reserve carbohydrates, and depletion of sugars.

Numerous reports (21, 22) have been presented explaining the mechanisms of absorption, translocation, and mode of action of herbicides. The completion of any herbicidal action may involve penetration, absorption by cells, migration to the vascular system, translocation, and a final
toxic action generally involving the living protoplasm. Crafts (22) gives four possible fates of an applied herbicide in regards to penetration: (i) it may remain on the outer leaf surface either in a crystalline or liquid form; (ii) it may penetrate into the cuticle and remain there in solution; (iii) it may proceed into the cuticle and then into the aqueous portion of the epidermal cell walls and it may migrate via the anticlinal walls to the vascular system; and (iv) it may follow the latter route into the leaf and be absorbed into the symplast and then move to the phloem and out of the leaf into the assimilatory stream.

In a previous report Wiese and Rea (75) concluded that phenoxy herbicides are most effective in the control of bindweed when growth conditions are unfavorable. According to their report, temperature and humidity conditions at various times of the day had no effect on 2,4-D toxicity to bindweed. Foy (28) working with 2,2-dichloroproprionic (dalapon) emphasized two types of physiological action which he termed acute toxicity and delayed growth regulatory responses.

Baker (7) found that 1,2-dihydropyridazine-3,6-dione (maleic hydrazide) in concentrations of 0.01 M and above inhibited oxygen uptake by tobacco tissues to varying degrees depending upon the pH of the solution. No inhibitory effect on various plant dehydrogenases by maleic hydrazide was observed. However, maleic hydrazide inhibited diaphorase nearly to the same degree as it did respiration. This suggested the possibility of this enzyme being involved in the respiratory process but no proof was provided.
Weinstein (74) pointed out that both increased and decreased respiratory activity have resulted from the treatment of plants with fluoride. He emphasized the view that the effect of fluoride on tissue respiration was largely determined by the amount that reached the active cellular sites and that the conditions of light, temperature, time, etc. played an important role. The data in this report suggested the possibility of an uncoupling of phosphorylation or reduced transphorylation by fluorides or by a product of fluoride metabolism.

Ashton (4) by treating red kidney beans and Kanota oats with 2-chloro-4-ethylamino-6-isopropyl-amino-s-triazine (atrazine) demonstrated that characteristic leaf injury symptoms occurred specifically in light but not in dark. Employing different quantities of tungsten light he noted that less injury appeared with lower light intensity. Reductions in the rate of transpiration by atrazine treatment of soybeans and corn were observed by Smith and Buchholtz (64). These reductions were attributed to stomatal closure after atrazine treatment which indicated the inhibition of water uptake at the stomata. "Stomatal closure after treatment with atrazine would thus appear to be a result of increased CO₂ in the guard cells and substomatal cavities resulting from the inhibition of photosynthesis and increased respiration rate instituted by the herbicide".

Chrispeels and Hanson (18) noted an increase in the ribonucleic acid (RNA) content of soybean hypocotyl treated with 2,4-D. They reported that the increase was more rapid
during the second 24 hour period. More than half of the increased RNA occurred in the microsomal fraction. They proposed that the herbicide renewed nuclear activity leading to the synthesis of RNA and protein, thereby a reversion to meristematic metabolism took place.

Pallas (58) reported that increased temperatures from 20 to 30°C increased absorption and translocation of 2,4-D and benzoic acid by red kidney beans. However, less 2,4-D or benzoic acid was absorbed and translocated at low humidities (34-48%) than at high humidities (70-74%). He correlated the increased absorption and translocation at high humidities with the degree of stomatal opening. Pallas and Williams (59) have stated that the absorption and translocation of 2,4-D and P³² were markedly reduced in red kidney bean plants at high moisture tensions. However, soil-moisture stress had no effect on the absorption of 2,4-D and much more was translocated at 1/3-atm than at 4-atm. According to Wedding and Blackman (73) the uptake of 2,4-D by Chlorella may be suppressed in the presence of auxins, particularly, 2,4,5-trichlorophenoxyacetic acid (2,4,5-T), indoleacetic acid (IAA), and 4-chlorophenoxyacetic acid (4-CPA). These workers consider that the depressed uptake of 2,4-D in the presence of 2,4,5-T, IAA, and 4-CPA by Chlorella is of a competitive nature. It is postulated that either compound may replace the other.

Williams, Slife, and Hanson (77) found cocklebur was more sensitive to 2,4-D than smartweed, jimson weed or bur cucumber. From the results of their study they concluded that some factors
other than the amount of cellular absorption were responsible for the herbicidal activity in these weeds. The typical 2,4-D epinastic responses in leaves and stems were observed in all five weeds. Although these workers were able to induce injury with low and high concentrations of 2,4-D, complete kill was not effected because 2,4-D failed to be translocated to untreated branches. This was offered as an explanation for incomplete kill of close weed stands.

Wort (78) pointed out that 2,4-D may affect various enzymes in many different ways depending on the plant species, plant part, age, and physiological condition of the plant. Some enzymes are increased where others are decreased.

Lockhart (47) stated that gibberellic acid (GA) was the controlling factor in the regulation of stem growth by visible radiation. He pointed out that any increment in plasticity of the primary cell wall results in a growth increase. Thus, visible irradiation causes a decrease in plasticization resulting in the inhibition of stem growth through a decrease in cell elongation. However, GA or auxin appear to be the necessary growth factors essential for increasing plasticity. It is concluded that visible irradiation somehow reduces the amount of GA.

Employing flax in an intensive study relating the interaction of temperature and light intensity on the effect of 2,4-D, Jordan, Dunham, and Linck (41) demonstrated that the response of flax was affected by light intensity either before or after treatment with 2,4-D. They reported that the
greatest response was with low intensity and least with high intensity. Temperature affected the response of flax to 2,4-D in a somewhat different manner than did light, that is the higher temperature was more effective and the lower less effective. Some interaction occurred between light intensity and temperature. With high light intensity before and after 2,4-D treatment the response of flax at temperatures of 65, 75, and 85 F was quite similar. In the meanwhile, with low light intensity there were large differences in the response of flax to 2,4-D treatment with the above temperatures. The response of flax to 2,4-D under these conditions seemingly showed some unfavorable balance between photosynthesis and respiration.

Jansen, Gentner, and Shaw (40) using corn and soybeans tested 63 surfactants in aqueous spray systems on the effects of the herbicidal activity of dalapon, 2,4-D, amitrole, and 4,6-dinitro-o-sec-butylphenol (DNBP). These surfactants were representative of anionic, cationic, nonionic, ampholytic, and blended-surfactant classes. They noted both suppression and progression of herbicidal activity, as well as no effect. Some surfactants in high concentrations exhibited phytotoxic effects while others stimulated growth at lower concentrations. These workers concluded that the proper selection of surfactants would increase the herbicidal activity of specific herbicides. Thus, the increased efficiency of herbicides would lessen cost and possible damage to desired plants. Gentner and Hilton (30) reported that a 0.3 M sucrose solution reduced
the inhibition of new leaf development of barley plants treated with 3-phenyl-1,1-dimethylurea (fenuron), 3-(p-chlorophenyl)-1,1-dimethylurea (monuron), 3-(3,4-dichlorophenyl)-1,1-dimethylurea (neburon), and 3-(3,4-dichlorophenyl)-1-methylurea (DMU). However, as the concentration of herbicides was increased sucrose became less effective. These investigators thereby claimed that the toxic effect produced by the herbicides was a photosynthate deficiency. They further concluded that the reduced protective effect of sucrose with higher herbicide concentrations indicated the sensitivity of metabolic reactions other than photosynthesis.

Photosynthesis

In a recent review van Overbeek (71) stated that it seems quite conclusive from all available evidence that the urea herbicides interfere with the oxidation of H₂O in the noncyclic photosynthetic electron flow. There appears to be no interference with the reduction of triphosphopyridine nucleotide (TPN). However, he stated that these herbicides do interfere with the portion of electron flow system which provides low energy electrons to refill the holes in the chlorophyll. These so-called holes come about as a result of photons of light striking the chlorophyll apparatus setting free some electrons which leave behind holes. Thus, if the holes are not refilled and electrons are continually leaving, the chlorophyll eventually becomes oxidized.

The importance of photosynthesis and its relation-
ship to plant growth under natural and artificial conditions as influenced by light, temperature, CO₂, and various other factors is well discussed by several investigators (1, 16, 23, 29, 51, 68). Gaastra (29) emphasizes the implicit relationship between the origination of organic matter and energy from photosynthesis essential for the maintenance of higher plants. Sorokin (65) concluded the upward and downward trends often observed in gas exchange during photosynthesis experiments may be brought about by the building up or activation of some essential participants in the photosynthetic process and as a result of the destruction, consumption, or inactivation of some photosynthetic agents. Decker and Tió (23) compared the amount of photosynthetic work done by leaves of coffee plants to the net gain or dry weight increment. They concluded that the major part of the photosynthetic work was immediately cancelled by photorespiration since the dry weight increment was low. These workers stressed that dry weight increment is directly proportional to the excess of photosynthesis over respiration. It has been found that the leaf polysaccharides are linked to the early products of photosynthetic assimilation of CO₂ (52).

Ormrod (57) found that the photosynthesis of rice plants with low light intensity was not harmed so long as the temperature remained low. However, high temperature with low light intensity for extended durations may have significant effects on CO₂ uptake and output. He concluded that vast losses of carbohydrates could occur resulting in a
dry weight decrease. Yet, the photosynthetic rates of rice plants were not extensively reduced nor was the photosynthetic mechanism injured by low temperature with or without low light intensity. Rhykerd, Langston, and Peterson (61) using three different light treatments for alfalfa, red clover, and birdsfoot trefoil found the uptake of CO2 by a plant under a specific light environment apparently was affected by the previous light environment in which it had grown. Illumination with a constant light intensity was more favorable for CO2 uptake than one of the same length and quantity but at several different light intensities. In their experiments CO2 uptake by birdsfoot trefoil seedlings was lower than that of alfalfa and red clover under all light treatments. Black, Turner, and Gibbs (10) stated that CO2 assimilation by photosynthesis in plants is dependent on adenosine triphosphate (ATP) and reduced triphosphopyridine nucleotide (TPNH) formation. They observed a lag in CO2 fixation at low light intensities, whereas increased light intensities resulted in rapid assimilation of CO2. A similar lagging was observed in ATP formation with low light intensities. Therefore, it was suggested that at low light intensities ATP formation may be a limiting factor in CO2 fixation by chloroplasts.

It is reported that leaves illuminated with red light generally absorb larger amounts of CO2 than leaves illuminated with blue light (70). These reporters (70) found that the wavelength of light had no effect on the distribution of absorbed CO2 between the ethanol-soluble and -insoluble
products of photosynthesis in tobacco leaves.

Berrie (9) supplying tomato plants with an exogenous supply of sucrose found that plants sprayed 10 to 20 times gave the greatest dry weight increment. Little difference was observed whether the sprays were given in the evening, that is, at the end of the illumination period, or in the morning, prior to illumination. Plants sprayed with the sucrose solution were exposed to various temperatures and light intensities under 8 hour day and 16 hour day. In all instances there was nearly a doubling of the total dry weight increment of sucrose sprayed plants over control plants at the end of the 8 hour day experimental period. However, with the 16 hour day only high temperatures and/or low light intensities produced any substantial increase in dry weight of the sucrose sprayed plants over controls. Therefore, day-length is reported to be the most important factor determining the degree of utilization of the applied sucrose. With daylight, gold, and green light qualities no differences between sucrose sprayed and control plants were noticed among the different types of light in the case of the 8 hour day. Nevertheless, under the 16 hour day the plants exposed to green light were generally much smaller, and those illuminated with yellow (gold) light made better use of the applied sugar.

Hayashi (35) reported that there was no significant difference in the photosynthetic activity between gibberellic acid treated and control rice and tomato plants on a unit leaf area basis. Nevertheless, the photosynthetic activity of the whole plants increased 10 to 18% in a period of one week after
the treatment with GA. He concluded that the most reasonable explanation for this increase was "the photosynthetic activity per unit leaf area does not change as the result of the GA treatment; but owing to the increase in leaf area, the photosynthetic activity of the whole plant increases". Similar results were obtained by Alvim (2) who tested red kidney bean seedlings with GA. He observed an increase in the photosynthetic rate which he presumed to be due to the rapid translocation of photosynthates from the leaves to the stem. Both Hayashi (35) and Alvim (2) noted a decrease in root dry weight resulting from treatment with GA.

Petroleum oils have been demonstrated to suppress photosynthesis in the leaves of mustard and parsnip plants (37). The suppression or decline in photosynthesis is attributed to the interference with the CO₂ supply. However, parsnip recovered from treatment with both petroleum naphtha and paraffinic oil, whereas mustard recovered only from treatment with the paraffinic oil.

Certain triazine herbicides may inhibit CO₂ fixation of red kidney bean plants in light according to Ashton, Zweig, and Mason (5), and Zweig and Ashton (79). The degree of inhibition varied with the concentration of the herbicide, increasing with an increased concentration.

The effects of monuron on plant growth have been investigated by several workers (34, 49, 67). Both Minshall (49) and Sweetser and Todd (67) presented data which support the suggestion that monuron interferes with some phase of photosynthesis. Yet, Hassall (34) reported that photosynthetic
conditions had no influence on the growth-retarding effect of monuron. Thus, light has been emphasized as influencing the action of monuron by some investigators while others presume it is ineffective.

Huffaker and Miller (39) reported that in cell-free extracts from bean plants, growth-stimulating concentrations of 2,4-D increased the activity of several enzymes essential for CO₂ fixation. However, the activity of the same enzymes was decreased by growth-inhibiting concentrations of 2,4-D. Wedding and Black (72) found that 2,4-D was effective in inhibiting the incorporation of P₃₂ into ATP and adenosine diphosphate (ADP) stimulating oxygen uptake by Chlorella.

Respiration

Recently, Hackett (31) extensively reviewed a large number of reports on the respiratory mechanisms in higher plants. He stated that "respiration, or "life with air", involves the breakdown and oxidations of organic compounds, the transfer of hydrogen (electrons) to molecular oxygen, and the release of utilizable energy within the cell".

Hartman (33) found that post-harvest ripening tomatoes treated with several synthetic growth substances produced more CO₂ than did similar untreated fruits during the ripening period. Thus, it is recognizable that these growth substances caused an increase in the metabolic activity within the fruits. Yet, CO₂ evolution from freshly harvested asparagus spears was shown to be inhibited by post-harvest application of N⁶-benzyladenine (24). Norris and Foulds (56)
reported that GA in concentrations of 1 to 200 ppm had no significant effect on the oxygen uptake of onion root tips whereas IAA in concentrations of 10, 50, and 100 ppm caused inhibition of oxygen consumption of the apical segment of onion roots.

Farkas, Konrad, and Kiraly (26) found that illumination of etiolated wheat seedlings increased their sensitivity to malonate, a specific and potent inhibitor of succinic dehydrogenase. Such inhibitory action could bring about an interference in the rate of respiration. Green seedlings previously illuminated exhibited an increased respiratory rate. Both stimulatory and inhibitory effects were observed as a result of treating mustard and parsnip plants with various petroleum oils (36).

According to Applegate, Adams, and Carriker (3) fluoride solutions, depending on the concentration, promoted or inhibited oxygen uptake of intact bush beans. In contrast, Hill, et al. (38) noted that fluoride had no effect on the respiration of seven species of plants with either low or high fluoride concentrations.

The effects of 2,4-D on respiration in plants have been discussed by Klingman (45). He stressed that the rate of respiration may either be stimulated or retarded by 2,4-D. The threshold concentration which may cause an increase or inhibition in CO₂ output depends upon the plants' tolerance to 2,4-D. Generally, low concentrations are assumed to stimulate, where high concentrations are observed to inhibit
respiration. 2,4-D is reported to cause closure of the plant's stomates, which causes reduction in the CO₂ uptake and output. Black and Humphreys (11) reported that etiolated corn seedlings treated with 2,4-D prior to the preparation of cell-free extracts resulted in a general increase of enzymic activity associated with the pentose phosphate cycle. They found an increased utilization of ribose-5-phosphate and 6-phosphogluconate in cell-free extracts from 2,4-D treated corn seedlings. They concluded that 2,4-D treatment of etiolated corn seedlings affected glucose catabolism as a result of an increase in the amount catabolized via the pentose phosphate cycle.

Photosynthesis and Respiration

Brix (14) studied the effect of water stress on the rates of photosynthesis and respiration by tomato plants and loblolly pine seedlings. He observed decreases in the rates of photosynthesis and respiration with increasing water stress which he related to the diffusion pressure deficit. He also found similar changes in the rates of transpiration and photosynthesis during increasing water stress indicating that photosynthesis was affected by an increased resistance to gaseous diffusion. Moss, Musgrave, and Lemon (53) tested the effects of several environmental factors on photosynthesis, respiration, and transpiration of corn. They reported that the intensity of solar radiation was the predominant factor affecting the rate of photosynthesis. With increased CO₂
concentrations about the plants they noted an increase in assimilation, particularly with high light intensity. Increasing night temperatures caused increased respiratory activity. These workers also noticed a reduced rate of assimilation with water stress conditions.

Gibberellic acid was observed to cause a rapid increase in the rates of respiration, photosynthesis, and transpiration (20). After a maximum rate was reached a sudden decline took place. The rate of transpiration returned to its initial whereas that of respiration and photosynthesis of the treated plants remained higher than that of untreated plants. Kandler (43) reported that 2,4-dinitrophenol (DNP) in concentrations which inhibited oxidative phosphorylation and increased respiration did not inhibit photosynthesis.

Nieman (55) working with 12 crop plants found that NaCl did not appreciably suppress the photosynthetic activity of leaf samples on an unit area basis. On the other hand, respiration was slightly increased in both tolerant and sensitive species. The growth, in general, ranged from stimulated to severely depressed depending on the sensitivity of the plants to NaCl.

The sodium salt of 2,4-D is reported to have a specific effect on the photosynthetic and respiratory processes of plants (60). It is pointed out by these workers (60) that the herbicide causes a suppression of photosynthesis and respiration as well as some stimulation depending on the dosage of the chemical preparation.
MATERIALS AND METHODS

Experimental Growth Room and Equipment

The growth room utilized in this study is a concrete basement, except for the ceiling, located below the ground level under the plant physiology laboratory in the greenhouse. Temperature and lights are automatically controlled by time clocks giving a temperature of 21°C during the photo-period (16 hrs) and 16°C during the dark period (8 hrs). Daily temperature cycles are maintained by a Westinghouse Unitaire. A thermograph centrally located provides a continuous temperature record. Although the room is without humidity control this did not vary significantly from one day to the next because of the continuous air-conditioning.

Light sources. Fluorescent lamps of two types were used in this study. General Electric 96-inch T-8 slimline fluorescent lamps in warm white, cool white, blue, green, yellow (gold), pink, and red were used. Also, Sylvania Electric 96-inch T-12 Very High Output (VHO) fluorescent lamps in warm white, cool white, blue, and red were used. The spectral distribution curves of these lamps may be seen in Figures 1 and 2. See Table 1 for the various symbols used to designate the different lamps.

Measurement of the light intensity. Light intensity was measured in foot-candles and microwatts per square centimeter using a General Electric multi-cell light meter and an Eppley thermopile connected to a Kintel Electronic Galvanometer,
Fig. 1. Spectral distribution curves for General Electric fluorescent lamps.
Fig. 1. -- Continued.
Fig. 2. Spectral distribution curves for Sylvania Electric fluorescent lamps.
Table 1. Symbols used

<table>
<thead>
<tr>
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<th>Explanation</th>
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</tr>
<tr>
<td>W</td>
<td>Warm white fluorescent lamp</td>
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<tr>
<td>CW</td>
<td>Cool white fluorescent lamp</td>
</tr>
<tr>
<td>B</td>
<td>Blue fluorescent lamp</td>
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<tr>
<td>Y</td>
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<td>Pink fluorescent lamp</td>
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<td>R</td>
<td>Red fluorescent lamp</td>
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<tr>
<td><strong>Sylvania Electric Lamps</strong></td>
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<tr>
<td>VW</td>
<td>VHO warm white fluorescent lamp</td>
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<tr>
<td>VCW</td>
<td>VHO cool white fluorescent lamp</td>
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<tr>
<td>VB</td>
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<tr>
<td>VR</td>
<td>VHO red fluorescent lamp</td>
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<tr>
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<tr>
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<td>Foot-candle</td>
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<tr>
<td>μw/cm²</td>
<td>Microwatt per square centimeter</td>
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<tr>
<td>p:</td>
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</tbody>
</table>
respectively. However, for high intensities in foot-candles a Spectra Professional exposure light meter was used. The light intensities used were measured as the incident light intensity upon the plant at the beginning of any light treatment. Intensity readings in foot-candles were corrected using the correction factors shown in Table 2 for each light quality used. Thus, the corrected light intensities were the meter readings multiplied by the correction factors. Intensity readings in microwatts per square centimeter were first taken in microvolts and converted to microwatts per square centimeter by dividing by the factor, 0.05 μV/μW/cm².

Experimental set-up for testing light effects. A wooden frame consisting of three similar compartments separated by white plastic curtains was used to measure the effects of different light qualities (Fig. 3). Six circular rotating tables were located in each compartment. A neoprene belt, which went around the base of the tables to provide rotation, was run by a 1/3 hp electric motor coupled to a gear reducer which reduced the speed of revolution to 8-10 rpm. Rotation was solely to minimize any positional effects and provide equal distribution of illumination on the plants.

An adjustable luminaire was suspended with ropes and pulleys above the row of rotating tables in each compartment. Each luminaire could hold from 1 to 6 fluorescent lamps, the number depending on the desired light intensity to be used.

Experimental set-up for measuring CO₂ exchange. The CO₂ exchange measurements were made with a Liston-Becker In-
Table 2. Correction Factors

<table>
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<td>Cool white</td>
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<tr>
<td>Blue</td>
<td>0.46</td>
</tr>
<tr>
<td>Green</td>
<td>1.45</td>
</tr>
<tr>
<td>Yellow (Gold)</td>
<td>1.33</td>
</tr>
<tr>
<td>Pink</td>
<td>0.94</td>
</tr>
<tr>
<td>Red</td>
<td>0.58</td>
</tr>
<tr>
<td>VHO warm white</td>
<td>1.13</td>
</tr>
<tr>
<td>VHO cool white</td>
<td>1.00</td>
</tr>
<tr>
<td>VHO blue</td>
<td>0.99</td>
</tr>
<tr>
<td>VHO red</td>
<td>0.89</td>
</tr>
</tbody>
</table>
Fig. 3. Experimental set-up for testing light effects.
Infrared Analyzer Model 15A incorporated in a closed system. The importance of a closed system for studying assimilation and respiration was emphasized in 1926 by Bolas (13). Numerous investigators (12, 15, 46, 54) have used infrared analyzers to measure CO$_2$ exchange for determining photosynthetic and respiratory activities of plants and plant parts. The experimental set-up for these experiments consists of an L/B Infrared Analyzer (Amplifier and Analyzer), Esterline-Angus Recorder, Brooks Sho-Rate "50" flow meter, Dyna-Pump, and a plexiglas plant chamber (Fig. 4). Also tanks of gas (prepurified N$_2$ and CO$_2$ blended in prepurified N$_2$) of known concentration were connected in the set-up, which could be opened and closed for calibration and for increasing or decreasing the concentration of CO$_2$ in the system when necessary. Tygon tubing was used to connect the parts of the closed system. Air was circulated in the closed system by the Dyna-Pump at a rate of 4 cubic feet per hour. Figure 5 shows a close up view of the plexiglas plant chamber with a container of 20 plants enclosed in a test run. Whenever measuring the CO$_2$ exchange the top of the chamber was sealed with Dow Corning high vacuum grease and clamped across each end, thus providing an airtight plant chamber. Inside dimensions of the chamber are 23.5 x 13.3 x 14.3 cm, thus having a volume of approximately 4.5 liters. It could hold one or two containers of plants.

Descriptions and operation procedures of the Infrared Analyzer are outlined in the Beckman Instruction Manual (8).
Fig. 4. CO₂ exchange measuring set-up.
Fig. 5. Plastic plant chamber used in measuring CO$_2$ uptake and output.
Figure 6 shows a diagrammatic view of the analyzer portion of the L/B Infrared Analyzer. As seen in the figure, the analyzer consists of two infrared radiation sources, an energy beam chopper, sample cell with CO$_2$ present, reference cell, and a detector with a sensitive diaphragm. Equal amounts of infrared energy are emitted from both radiation sources, which are interrupted by the chopper. One beam of infrared energy passes through the reference cell while the other beam passes through the sample cell. The gas (CO$_2$ in these experiments) in the sample cell absorbs some of the infrared energy. No absorption takes place in the reference cell, which is filled with N$_2$. As a result, unequal beams of infrared energy emerge, striking the detector, which consists of two chambers filled with CO$_2$ at equal pressures. The two chambers are separated by a sensitive diaphragm. When unequal beams of energy strike the detector unequal pressures are produced in the chambers. The diaphragm moves in the direction of the chamber with the lesser pressure. The movement of the diaphragm produces an electrical output signal which is sent to the amplifier. The amplifier contains the operating controls.

General Procedures

Experimental plants. All plants were obtained from seeds of mustard (Brassica juncea (L.) Coss. cultivar Florida Broadleaf) carefully sown in polyethylene containers (1 pint) filled with vermiculite. Each container had four perforations in the bottom for drainage. A sufficient number of seeds
Fig. 6. Diagram of infrared carbon dioxide analyzer.
were sown to obtain 20 plants per container after thinning. Sowing was done at intervals since all plants could not be transferred to the lights at one time. This was done because when measuring CO$_2$ exchange the time required to do so would not permit all tests to be completed in one day. However, for dry weight studies all seeds were sown at one time for any one experiment.

**Nutrition.** A modification of Hoagland's nutrient solution (Table 3) was used to provide proper nutrients for the plants. The nutrient solution was applied to the surface of the vermiculite 17 days from sowing and thereafter every 4 days in 40 ml portions per container. The plants were watered with tap water as needed to maintain a moist medium.

**Light treatment.** The plants were grown in the greenhouse under natural daylight conditions until transferred to the experimental growth room for a particular light quality treatment. Two different light conditioning treatments were used. One is referred to as "short-term light" and a second as "long-term light". With the short-term light the plants were grown in the greenhouse for 32 days and under the light qualities for 5 days, while the plants for the long-term light were grown in the greenhouse for 17 days and under the light qualities for 20 days. Sufficient containers of plants were placed under each light quality to have six replications of any one treatment used in an experiment. That is, one replication of each treatment was placed on all six rotating tables under any particular light quality.
Table 3. Nutrient Solution*

Major elements: Weights in grams for one liter of nutrient solution.

<table>
<thead>
<tr>
<th>Substance</th>
<th>Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ca(NO$_3$)$_2$·4H$_2$O</td>
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</tr>
<tr>
<td>KNO$_3$</td>
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</tr>
<tr>
<td>MgSO$_4$·7H$_2$O</td>
<td>0.490</td>
</tr>
<tr>
<td>KH$_2$PO$_4$</td>
<td>0.140</td>
</tr>
</tbody>
</table>

Minor elements: Weights in grams for a one liter "stock" solution, from which one ml is used for each liter of nutrient solution.

<table>
<thead>
<tr>
<th>Substance</th>
<th>Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>H$_3$BO$_3$</td>
<td>2.900</td>
</tr>
<tr>
<td>MnCl$_2$·4H$_2$O</td>
<td>1.800</td>
</tr>
<tr>
<td>ZnSO$_4$·7H$_2$O</td>
<td>0.220</td>
</tr>
<tr>
<td>CuSO$_4$·5H$_2$O</td>
<td>0.080</td>
</tr>
<tr>
<td>H$_2$MoO$_4$·H$_2$O</td>
<td>0.020</td>
</tr>
</tbody>
</table>

Iron: One ml of a 0.5% "stock" solution of Dow Versenol F (Iron Sodium N-Hydroxyethylethylene diamine triacetate) is used for each liter of nutrient solution.

*Modification of Hoagland’s nutrient solution (27).
**Herbicidal treatment.** At the end of the light treatment (light conditioning, whether 5 or 20 days) the plants were approximately 8 to 10 cm in height and still in the vegetative stage of growth. Solutions of the sodium salt of 2,4-D (hereafter referred to as 2,4-D) were applied as a fine mist from a hand sprayer, to thoroughly cover the foliage of the plants. In some instances sucrose was mixed with 2,4-D and applied to the foliage, while in other instances sucrose solutions alone were applied. For CO₂ exchange measurements all plants were not treated at one time. Instead, the containers of plants were treated at intervals to allow a 24-hour post-spray period under the lights before measuring the CO₂ exchange. For dry weight studies all plants were treated at one time and given a post-spray period of 10 days under the lights. The various solutions were applied to the plants outside the experimental growth room. After the plants had dried they were returned to their original position under the lights.

**CO₂ analyses.** As pointed out under "Experimental set-up for measuring CO₂ exchange" an Infrared Analyzer was used to measure the changes in CO₂ concentration. Prior to measurement of CO₂ output and uptake the Infrared Analyzer was calibrated with gases of known concentration. However, before calibration the entire analyzer was warmed-up over night in the experimental growth room with all switches in the "on" position. N₂ was used to obtain the zero point on the recorder and 600 ppm of CO₂ was used to obtain the 100 point (full scale) on the recorder. In calibrating, the
"closed system" was left open and the gas allowed to flow through at a rate of 4 cubic feet per hour. Both the zero and 100 points were rechecked several times to correct for any drift that might have occurred during the process of calibrating. After this, two lower concentration of CO₂ (300 and 500 ppm) were used to obtain two intermediate points. A calibration curve was drawn based on these four points (0, 65, 91, 100, recorder deflection) obtained on the recorder from which the concentration of CO₂ in the range of 0 to 600 ppm could easily be read.

After the instrument was calibrated a container of 20 plants was sealed in the plant chamber (See Fig. 5). In measuring CO₂ output (respiration) N₂ was flushed through the system to reduce the level of CO₂ in the system to 170 ppm. This level was chosen because it represented the compensation point under these experimental conditions. Upon reaching 170 ppm the N₂ was cut-off, the system closed and the Dyna-Pump started. Immediately the lights were switched-off and CO₂ output measured for one hour. At the end of this period CO₂ concentration was raised or lowered to 500 ppm and the lights switched-on permitting CO₂ uptake for an hour. This was repeated for a container of treated plants and a container of control plants for each of the six positions under all the different lights used.

The lines on the recorder charts for the divisions of time are curved, thus points for each ten minutes are read and replotted on straight--line graph paper (20 squares per
inch) in terms of ppm based on the calibration curve. Figure 7 shows a typical set of curves for warm white light. The areas a and b shown in Figure 7 are regarded as the 2,4-D effect as influenced by light quality upon respiration and apparent photosynthesis respectively. These areas were measured in square centimeters with a polar planimeter and converted to microliters of CO₂. This was done for six replications in each treatment of an experiment.

**Dry weight analyses.** After the plants of various treatments had been subjected to the specific light conditions for the required pre- and post-spray periods, the tops of the 20 plants per container were harvested and dried for 10 days at 50°C in a drying oven, then the dry weight was determined. There were six replications in each experiment for all treatments, except in one experiment in which there were twelve replicates. Representative samples of the plants were harvested at the beginning of the light treatments and the mean dry weight determined and later subtracted from the dry weight of each replicate in the experiment. Therefore, the values given represent the dry weight increase of each replicate. However, some values shown represent differences between specific treatments.

**Statistical evaluation of the effectiveness of light qualities.** The differences in CO₂ uptake and output between control and treated plants in microliters were subjected to analysis of variance as outlined by Steel and Torrie (66), and Duncan's (25) multiple range test applied using the critical
Fig. 7. Typical curves showing the effect of warm white light at 600 μw/cm² on CO₂ exchange (--- Control; —— Treated).
values suggested by Harter (32).

The suggestions presented in the style manual for biological journals (19) were followed in the preparation of this manuscript.
RESULTS AND DISCUSSION

Effects of Light Quality and 2,4-D on Photosynthesis and Respiration

It is evident from the curves in Fig. 8 that with extended post-spray periods 2,4-D increasingly suppresses CO₂ uptake and promotes CO₂ output by mustard plants grown under the experimental conditions described earlier in the materials and methods. The slope and magnitude of the curves showing CO₂ uptake and output by mustards depend greatly upon the concentration of 2,4-D and light treatment.

Although results obtained using different light intensities are presented in the data, the main emphasis is placed on the effect of different light qualities. Nevertheless, comparisons are made between light intensity measured in foot-candles and microwatts per square centimeter. Such comparison is of particular interest because recent advances in phytoillumination stress the importance of light measurements in incident energy and not illuminance, especially so when comparing various light colors.

Plants used as controls and test plants (treated) were selected for uniformity of size, age, and appearance. From the data reported it is evident that in many instances considerable variability exists between replications for any one light treatment under the conditions of the experiment. In fact, some of the differences between replicates exceeded the differences between the means for light qualities.
Fig. 8. Effect of short-term warm white light at 600 μW/cm² on the action of 2,4-D on CO₂ exchange by mustard plants with different post-spray periods.
According to the procedure (see Materials and Methods) used to collect the data some variability were expected. In statistical analyses of the data presented below no correction was established for the variability in replication. Thus it is possible that if some modification of the method of analysis had been established to correct for variability between replicates more significant differences might have been observed among light qualities.

Low light intensity and 100 ppm 2,4-D. Experiments were designed to test the effects on photosynthesis and respiration of light quality using low light intensity measured in foot-candles and 100 ppm 2,4-D. Short-term and long-term light conditioning were used in these experiments. Results are shown in Tables 4 and 5. These results indicate that there are generally no really significant differences among light qualities in modifying the effects of 2,4-D, at such low concentration, either on CO₂ uptake or output. However, with short-term light condition the effect of blue was significant over pink at the 5% level.

Differences between mean microliters of CO₂ output for different light qualities (Tables 4, B and 5, B) for short-term light conditioning are much less than those for the long-term light conditioning. Apparently the short-term light eliminates some of the sharp differences among light qualities found when using long-term light. More morphological differences of plants occurred under light qualities with long-term light. Plants illuminated with blue, and red light are usually short and stalky with rather thick leathery leaves.
Table 4. Effects of short-term (5 days) light at 300 ft-c and 100 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO₂ uptake between control and treated plants (20 plants each) in microliters for one hour.

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<thead>
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<td>28</td>
<td>72</td>
<td>26</td>
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</tr>
</tbody>
</table>

Mean 98 132 89 82 65 112

p: (2) (3) (4) (5) (6)

LSR*: 49 51 53 54 55

Lights: P Y G W R B

Means: 65 82 89 98 112 132

B. "Respiration"- Differences in CO₂ output between control and treated plants (20 plants each) in microliters for one hour.

<table>
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Mean 77 74 71 46 63 51

p: (2) (3) (4) (5) (6)

LSR*: 69 73 75 76 78

Lights: Y R P G B W

Means: 46 51 63 71 74 77

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
Table 5. Effects of long-term (20 days) light at 300 ft-c and 100 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis" - Differences in CO₂ uptake between control and treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
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<td>88</td>
<td>85</td>
<td>154</td>
<td>94</td>
</tr>
</tbody>
</table>

*p: (2) (3) (4) (5) (6)  
LSR*: 81 85 88 90 91  
Lights: Y G R B P W  
Means: 85 88 94 151 154 166  

B. "Respiration" - Differences in CO₂ output between control and treated plants (20 plants each) in microliters for one hour.

<table>
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*p: (2) (3) (4) (5) (6)  
LSR*: 112 118 121 124 126  
Lights: Y G P W B R  
Means: 71 86 92 117 128 144  

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
A similar type of plant response is observed with plants illuminated with pink, and warm white light but to a lesser degree than that of plants under blue, and red. Green, and yellow usually cause an attenuation in stems and leaf blades. Also the leaves are thin as compared to leaves of plants grown under blue, red, pink, and white lights. Thereby, the long-term light is presumed to be the main factor in causing large differences in CO$_2$ uptake among different light colors.

Low light intensity and 500 ppm 2,4-D. To evaluate the effects of light quality on the 2,4-D effect, several experiments were conducted using an increased concentration (500 ppm) of 2,4-D. In one experiment light intensity was 600 µw/cm$^2$ with short-term light conditioning. Table 6 shows the results of gas exchange measurements made in this experiment. Among light qualities the interference of pink light with CO$_2$ uptake by 2,4-D treated plants over control plants was statistically significant at the 5% level above warm white, blue, and green. Although non-significant, the differences between yellow, red, and pink were appreciably large (Table 6, A). At the 1% level the effects of pink light were significant over warm white in causing 2,4-D to inhibit CO$_2$ uptake.

The respiratory process was stimulated by 2,4-D under each light quality. Nevertheless, there were no significant differences in CO$_2$ output among light qualities (Table 6, B).

In a second experiment the light intensity was 300 ft-c using long-term light conditioning. Results of this ex-
Table 6. Effects of short-term (5 days) light at 600 μw/cm² and 500 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO₂ uptake between control and treated plants (20 plants each) in microliters for one hour.

<table>
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<tr>
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<td>(4)</td>
<td>(5)</td>
<td>(6)</td>
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<td>Means:</td>
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<td>158</td>
<td>173</td>
<td>199</td>
<td>224</td>
<td>361</td>
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</tbody>
</table>

B. "Respiration"- Differences in CO₂ output between control and treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
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<th>B</th>
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<th>P</th>
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<td>Means:</td>
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<td>147</td>
<td>184</td>
<td>193</td>
<td>205</td>
<td>232</td>
</tr>
</tbody>
</table>

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
periment are presented in Table 7. As seen in part A of Table 7, warm white, and blue light reduced the CO₂ uptake in 2,4-D treated plants, as compared to control plants, to a greater extent at the 5% level than yellow and pink. Green was significant over yellow in its effect on the inhibition of apparent photosynthesis by 2,4-D. White was significantly effective at the 1% level over yellow in modifying the effect of 2,4-D in CO₂ assimilation.

Among light qualities, only red showed any significance in the promotion of CO₂ output. Thus, red was significant at the 5% level above pink. This type of difference between red and pink is unexpected since pink has a great deal of red in its spectral makeup (see Fig. 1, Spectral Distribution curves for pink and red lamps).

From the results of these experiments it is apparent that certain aspects of the 2,4-D effect on photosynthesis and respiration are extended more with the long-term light conditioning than with the short-term light conditioning.

Low light intensity and 1000 ppm 2,4-D. Two experimental tests were performed to determine the effect of light quality on the action of 1000 ppm 2,4-D. The short-term light conditioning period was used in each experimental test. The intensity in the first experiment was 600 µw/cm². Results (Table 8, A) of CO₂ uptake measurements based on the difference between 2,4-D treated and control plants exhibited no statistically significant differences among light qualities. Although non-significant, warm white and red light caused
Table 7. Effects of long-term (20 days) light at 300 ft-c and 500 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis" - Differences in CO₂ uptake between control and treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
<th></th>
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<td>58</td>
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<td>134</td>
<td>235</td>
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</table>

p: (2) (3) (4) (5) (6)
LSR*: 153 161 166 170 172
Lights: Y P R G B W
Means: 102 134 235 277 320 346

B. "Respiration" - Differences in CO₂ output between control and treated plants (20 plants each) in microliters for one hour.

<table>
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<td>110</td>
<td>190</td>
<td>102</td>
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<td>222</td>
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</table>

p: (2) (3) (4) (5) (6)
LSR*: 124 130 135 137 139
Lights: P Y B W G R
Means: 76 102 110 184 190 222

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
Table 8. Effects of short-term (5 days) light at 600 \(\mu W/cm^2\) and 1000 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO\(_2\) uptake between control and treated plants (20 plants each) in microliters for one hour.

<table>
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Mean 238 126 130 186 185 202

\(p:\) (2) (3) (4) (5) (6)

\(LSR^*:\) 101 106 110 112 114

Lights: B G P Y R W

Means: 126 130 185 186 202 238

B. "Respiration"- Differences in CO\(_2\) output between control and treated plants (20 plants each) in microliters for one hour.

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Mean 182 60 104 102 79 202

\(p:\) (2) (3) (4) (5) (6)

\(LSR^*:\) 89 94 97 99 100

Lights: B P Y G W R

Means: 60 79 102 104 182 202

\*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
greater interference in CO₂ uptake by 2,4-D than any of the other light qualities used.

Red was found to be significantly more effective in promoting a 2,4-D stimulatory effect on respiration above blue, pink, yellow, and green at the 5% level. Warm white was significant over blue and pink in promoting respiration by 2,4-D at the 5% level. Red irradiation was also significant at the 1% level over blue in its promotive effect (Table 8, B).

The light intensity in the second test was 300 ft-c. Blue was markedly effective in causing a reduction in CO₂ uptake in 2,4-D treated plants. At the 5% level blue was significant over all light qualities except pink. Both pink and red were significant over green, yellow, and warm white in inhibitory effects on photosynthesis (Table 9, A). Differences in CO₂ uptake between 2,4-D treated and control plants were significantly influenced by blue over green, yellow, and warm white at the 1% level. Pink and red were significant over green and yellow light.

No significant differences were observed among light qualities in their effect on the differences in CO₂ output between 2,4-D treated and control plants (Table 9, B).

The influence of blue light at low intensity in promoting the interference of 1000 ppm 2,4-D with CO₂ uptake was presented in an earlier report (76). However, in those studies long-term light conditioning periods were used. Blue was found to be highly significant compared to all other
Table 9. Effects of short-term (5 days) light at 300 ft-c and 1000 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis" - Differences in CO₂ uptake between control and treated plants (20 plants each) in microliters for one hour.

<table>
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<td>82</td>
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<td>(3)</td>
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Lights: G Y W R P B
Mean: 80 82 117 217 237 315

B. "Respiration" - Differences in CO₂ output between control and treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
<th>Light</th>
<th>W</th>
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Lights: R G Y B W P
Mean: 42 70 70 82 85 129

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
portions of the spectrum.

In comparison of the mean values for apparent photosynthesis in these two experiments (Table 8, A and 9, A) it is well exemplified that with light intensity measurements in energy there are less differences among light qualities than when light intensity measurements are in ft-c. Thus, these results (Tables 8, A and 9, A) indicate that the action of 2,4-D is equally modified by all light qualities where the light intensity is adjusted at equal energy levels. On the other hand, where ft-c are used some light colors are more effective in promoting the action of 2,4-D on CO₂ uptake.

Low light intensity and 2% and 5% sucrose:500 ppm 2,4-D mixtures. Experiments were designed to test the effects of sucrose:2,4-D mixture solutions. The short-term light conditioning period was used with a light intensity of 600 μw/cm².

With the use of 2% sucrose:500 ppm 2,4-D mixture only red showed any significance in influencing the uptake and output of CO₂. Red was significant over warm white and green in interfering with CO₂ uptake at the 5% level (Table 10, A).

In promoting respiration, red was significant over warm white at the 5% level (Table 10, B). No other significance was observed among light qualities.

No significant differences were observed among light qualities in their effect on CO₂ uptake and output when the 5% sucrose:500 ppm 2,4-D mixture was used (Table 11). The
Table 10. Effects of short-term (5 days) light at 600 μw/cm² and 2% sucrose:500 ppm 2,4-D mixture on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis" - Differences in CO₂ uptake between control and treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
<th></th>
<th>W</th>
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<th>G</th>
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</table>

p: (2) (3) (4) (5) (6)

LSR*: 96 101 104 106 108

Lights: W G B Y P R
Means: 109 110 144 172 207 231

B. "Respiration" - Differences in CO₂ output between control and treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
<th></th>
<th>W</th>
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<th>Y</th>
<th>P</th>
<th>R</th>
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<td>109</td>
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<tr>
<td>Mean</td>
<td>44</td>
<td>62</td>
<td>60</td>
<td>90</td>
<td>80</td>
<td>99</td>
</tr>
</tbody>
</table>

p: (2) (3) (4) (5) (6)

LSR*: 45 48 49 50 51

Lights: W G B P Y R
Means: 44 60 62 80 90 99

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
Table 11. Effects of short-term (5 days) light at 600 µw/cm² and 5% sucrose:500 ppm 2,4-D mixture on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO₂ uptake between control and treated plants (20 plant each) in microliters for one hour.

<table>
<thead>
<tr>
<th></th>
<th>W</th>
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<td>243</td>
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<td></td>
<td>306</td>
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<td>123</td>
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<td>285</td>
<td>250</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td>190</td>
<td>405</td>
<td>111</td>
<td>213</td>
<td>171</td>
<td>222</td>
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<td>Mean</td>
<td>210</td>
<td>216</td>
<td>176</td>
<td>183</td>
<td>207</td>
<td>227</td>
</tr>
</tbody>
</table>

p: (2) (3) (4) (5) (6)

LSR*: 136 142 147 150 152

Lights: G Y P W B R

Means: 176 183 207 210 216 227

B. "Respiration"- Differences in CO₂ output between control and treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
<th></th>
<th>W</th>
<th>B</th>
<th>G</th>
<th>Y</th>
<th>P</th>
<th>R</th>
</tr>
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<tbody>
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<td></td>
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<td></td>
<td>196</td>
<td>184</td>
<td>97</td>
<td>155</td>
<td>30</td>
<td>106</td>
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<td></td>
<td>95</td>
<td>448</td>
<td>221</td>
<td>86</td>
<td>157</td>
<td>90</td>
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<tr>
<td>Mean</td>
<td>130</td>
<td>204</td>
<td>159</td>
<td>136</td>
<td>147</td>
<td>169</td>
</tr>
</tbody>
</table>

p: (2) (3) (4) (5) (6)

LSR*: 133 140 144 147 149

Lights: W Y P G R B

Means: 130 136 147 159 169 204

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
results indicated that 5% sucrose added to 2,4-D lessened the effects of 2,4-D sufficiently to eliminate any significance among light qualities.

Results of these experiments are, in general, in agreement with the findings of Gentner and Hilton (30) who observed some reduced herbicidal effect of five phenylurea herbicides on barley plants with sucrose. Alvim (2) was able to control bean root dry weight reduction caused by GA with 10% sucrose sprays. Sucrose also lessened the injury from 2% urea spray.

**Low light intensity and 5% sucrose:500 ppm 2,4-D vs. 500 ppm 2,4-D.** This experimental test consisted of two chemical treatments and a light treatment. The light intensity was 600 µw/cm² using the short-term light conditioning period. Under each light quality one half of the plants (6 containers) were treated with a mixture of a solution of 5% sucrose:500 ppm 2,4-D, while a second half (6 containers) were treated with a 500 ppm 2,4-D solution alone. CO₂ exchange measurements were made, and the differences in microliters of CO₂ between the two treatments determined for each light quality used. The results are presented in Table 12. Among light qualities there were no significant differences at the 5% level for either CO₂ uptake or output. Yet, it may be noted that in a former test there were significances among light qualities in promoting 500 ppm 2,4-D interference in CO₂ uptake (Table 6, A). Therefore, the 5% sucrose:500 ppm 2,4-D mixture eliminated any significance among light qualities in
Table 12. Effects of short-term (5 days) light at 600 μw/cm² 5% sucrose:500 ppm 2,4-D mixture and 500 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis" - Differences in CO₂ uptake between the mixture treated and 2,4-D treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
<th></th>
<th>W</th>
<th>B</th>
<th>G</th>
<th>Y</th>
<th>P</th>
<th>R</th>
</tr>
</thead>
<tbody>
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<td>21</td>
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<td>35</td>
<td>46</td>
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<td>49</td>
<td>106</td>
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<td>111</td>
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<tr>
<td>44</td>
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<tr>
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<td></td>
</tr>
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<td>37</td>
<td>39</td>
<td>266</td>
<td>150</td>
<td>26</td>
<td></td>
</tr>
</tbody>
</table>

Mean: 45 166 46 145 139 90

p: (2) (3) (4) (5) (6)

LSR*: 137 144 148 151 154

Lights: W G R P Y B

Means: 45 46 90 139 145 166

B. "Respiration" - Differences in CO₂ output between the mixture treated and 2,4-D treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
<th></th>
<th>W</th>
<th>B</th>
<th>G</th>
<th>Y</th>
<th>P</th>
<th>R</th>
</tr>
</thead>
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<td>32</td>
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<td>67</td>
<td>189</td>
<td>60</td>
<td></td>
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<td>28</td>
<td>51</td>
<td>65</td>
<td>14</td>
<td>74</td>
<td>247</td>
<td></td>
</tr>
<tr>
<td>42</td>
<td>5</td>
<td>86</td>
<td>39</td>
<td>218</td>
<td>185</td>
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<tr>
<td>100</td>
<td>0</td>
<td>229</td>
<td>67</td>
<td>70</td>
<td></td>
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<td>44</td>
<td>46</td>
<td>466</td>
<td>139</td>
<td>58</td>
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</tr>
</tbody>
</table>

Mean: 58 80 66 158 139 118

p: (2) (3) (4) (5) (6)

LSR*: 118 124 128 130 132

Lights: W G B R P Y

Means: 58 66 80 118 139 158

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
inhibiting CO₂ uptake (Table 11, A). These results show that with 500 ppm of 2,4-D the 5% sucrose lessens the interference in CO₂ uptake. Thus in some manner the sucrose has decreased the effectiveness of the herbicide in disrupting the metabolic reactions involved in CO₂ uptake.

**High light intensity and 1000 ppm 2,4-D.** An experiment was designed to study the effects of high light intensity. The highest light intensity obtainable was used. This intensity was measure in ft-c and the long-term light conditioning period used. The lamps used were the only type available for obtaining high intensity at the time this experiment was conducted. The intensities for blue (VB), and red (VR) were highest while the intensity for pink was lowest. CO₂ exchange measurements were made on control and 1000 ppm 2,4-D treated plants. The differences in CO₂ uptake and output between control and treated plants in microliters are shown in Table 13.

Among light qualities pink was most effective in promoting 2,4-D interference with CO₂ uptake. Pink was significant above all lights except yellow at the 5% level. Yellow was significant over warm white. No significant differences were observed among blue, red, green, and yellow lights. Although blue and red light had the highest light intensities, they were only slightly more effective than warm white in causing 2,4-D to inhibit CO₂ uptake (Table 13, A).

The stimulatory effect of 2,4-D on CO₂ output was significantly influenced only by red light. Red was significant
Table 13. Effects of long-term (20 days) light at high intensities and 1000 ppm 2,4-D on photosynthesis and respiration by mustard plants.

### A. "Apparent Photosynthesis" - Differences in CO₂ uptake between control and treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
<th></th>
<th>W</th>
<th>VB</th>
<th>G</th>
<th>Y</th>
<th>P</th>
<th>VR</th>
</tr>
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<tbody>
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<td>(954)</td>
<td>(1710)</td>
<td>(954)</td>
<td>(954)</td>
<td>(465)</td>
<td>(1480)</td>
<td></td>
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<td>341</td>
<td>539</td>
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<td>403</td>
<td>529</td>
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<td>262</td>
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<td>275</td>
<td>525</td>
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<td>203</td>
<td>224</td>
<td>272</td>
<td>360</td>
<td>432</td>
<td>233</td>
</tr>
</tbody>
</table>

*Least significant range at the 5% level.

### B. "Respiration" - Differences in CO₂ output between control and treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
<th></th>
<th>W</th>
<th>VB</th>
<th>G</th>
<th>Y</th>
<th>P</th>
<th>VR</th>
</tr>
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<tbody>
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<td>(954)</td>
<td>(1710)</td>
<td>(954)</td>
<td>(954)</td>
<td>(465)</td>
<td>(1480)</td>
<td></td>
</tr>
<tr>
<td>99</td>
<td>162</td>
<td>37</td>
<td>138</td>
<td>90</td>
<td>412</td>
<td></td>
</tr>
<tr>
<td>178</td>
<td>261</td>
<td>222</td>
<td>150</td>
<td>211</td>
<td>68</td>
<td></td>
</tr>
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<td>48</td>
<td>62</td>
<td>92</td>
<td>150</td>
<td>116</td>
<td>194</td>
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<td>148</td>
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<td>225</td>
<td>180</td>
<td>490</td>
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<tr>
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<td>196</td>
<td>128</td>
<td>175</td>
<td>177</td>
<td>262</td>
</tr>
</tbody>
</table>

*Parentheses enclose ft-c intensities.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
over warm white at the 5% level (Table 13, B). No signi-
nificance was observed in any other comparison among light qualities.

Several workers (53, 57, 61) using different plants have reported increased CO\textsubscript{2} uptake and output with rather high light intensity. In fact, intensities ranged from 0 to 6000 ft-c. For this reason more significant differences among light qualities with high light intensity were expected in causing 2,4-D inhibition of CO\textsubscript{2} uptake and output than observed in the data presented (Table 13). No reasonable explanation is offered for the absence of more significant differences among light qualities. It is possible that species differences are responsible for the lack of more significant differences.

Long-term light conditioning vs. short-term light conditioning at 1000 ft-c and 1000 ppm 2,4-D. This test was concerned with an evaluation of the effects of yellow and green lights as compared to warm white on CO\textsubscript{2} exchange of 2,4-D treated and control plants. The experiment was designed to incorporate both long-term and short-term light conditioning periods. The corrected light intensity for all light qualities was 1000 ft-c. A 1000 ppm 2,4-D solution was used. Table 14 shows the results of the CO\textsubscript{2} exchange measurements as differences in CO\textsubscript{2} uptake and output between control and 2,4-D treated plants.

No significant differences in CO\textsubscript{2} uptake were observed for the different spectral regions either with the long-term light conditioning period or the short-term light conditioning
Table 14. Effects of long-term (20 days) and short-term (5 days) light at 1000 ft-c and 1000 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis" - Differences in CO₂ uptake between control and treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
<th></th>
<th>W¹</th>
<th>Y¹</th>
<th>G¹</th>
<th>W²</th>
<th>Y²</th>
<th>G²</th>
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</thead>
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<td>Mean</td>
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<td>164</td>
<td></td>
<td>216</td>
<td>226</td>
<td>171</td>
</tr>
<tr>
<td>p: (2) (3) (4) (5) (6)</td>
<td>LSR#: 127 134 138 141 143</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lights: Y¹ Y² G² G¹ W² W¹</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Means: 164 171 208 216 226 258</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

B. "Respiration" - Differences in CO₂ output between control and treated plants (20 plants each) in microliters for one hour.

<table>
<thead>
<tr>
<th></th>
<th>W¹</th>
<th>Y¹</th>
<th>G¹</th>
<th>W²</th>
<th>Y²</th>
<th>G²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>114</td>
<td>75</td>
<td>76</td>
<td>151</td>
<td>118</td>
<td>148</td>
</tr>
<tr>
<td>p: (2) (3) (4) (5) (6)</td>
<td>LSR#: 67 71 73 75 76</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lights: Y¹ G¹ W¹ Y² G² W²</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Means: 75 76 114 118 148 151</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Least significant range at the 5% level.
¹Long-term light.
²Short-term light.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
period. Also, no significant differences were observed for the same light quality with either light conditioning period. In fact, the difference between the means for the same light quality for both light conditioning periods was small for each of the light qualities used (see Means in Table 14, B).

CO₂ output was enhanced more by 2,4-D with the short-term light conditioning period than with the long-term light conditioning. Only warm white of the short-term was slightly significant over yellow of the long-term light conditioning.

Generally, yellow and green light are accepted to be poor for plant growth. Berrie (9) in a study relating the effect of sucrose sprays on the growth of tomato plants found poor growth under green light as compared to daylight and yellow light. A suppressive nature of green light has been emphasized by Klein (14).

Effects of Light Quality and 2,4-D on Dry Weight

Since dry weight increment is due to the excess of photosynthesis over respiration, any conditions favorable for high photosynthetic efficiency should result in an increase in dry weight. Since many investigators have concluded that light qualities may influence the effect of 2,4-D on photosynthesis, several studies were conducted to determine how some favorable photosynthetic conditions would modify the action of 2,4-D on dry weight yield. Also, comparisons were made of dry weight yield among light qualities where the
light intensity was measured in microwatts per square centimeter.

**High light intensity and 1000 ppm 2,4-D.** Six different kinds of fluorescent lamps were used. Two were General Electric T-8 slimline fluorescent lamps (R and W, see Table 1 and Fig. 1) and four were Sylvania Electric VHO fluorescent lamps (VR, VB, VW, and VCW, see Table 1 and Fig. 2). The long-term light conditioning period was employed in this test. The light intensity was 1500 ft-c for all qualities except General Electric red (R), which was 454 ft-c since this was the maximum obtainable with this quality. At the conclusion of the light conditioning period, twelve replicates, two from each of the six rotating tables, were treated with the solution of 2,4-D while twelve replicates were retained as controls (untreated) for each light quality. The containers of plants were returned to their original positions under the lights after the spray solution dried on the foliage. A post-spray period of ten days was given all plants (control and treated). Plant tops were harvested at the end of the post-spray period and the dry weights taken after drying for ten days. The percentage reduction in dry weight by 2,4-D was determined. Results are shown in Table 15.

Blue light was statistically less effective in promoting the 2,4-D effect on mustard than the other five light qualities at the 5% level. Both red light qualities were significantly more effective than blue at the 1% level in causing dry weight reduction by 2,4-D. No significant differences existed at the 1% level between any of the other
Table 15. Effects of long-term (20 days) light at high intensity and 1000 ppm 2,4-D on dry weight of mustard plants.

Percentage reduction in dry weight of 2,4-D treated plants (20 plants each) below that of control plants (20 plants each).

<table>
<thead>
<tr>
<th>VR (1500)</th>
<th>R (454)</th>
<th>VB (1500)</th>
<th>VW (1500)</th>
<th>W (1500)</th>
<th>VCW (1500)</th>
</tr>
</thead>
<tbody>
<tr>
<td>19.1</td>
<td>50.5</td>
<td>29.1</td>
<td>26.6</td>
<td>6.3</td>
<td>45.7</td>
</tr>
<tr>
<td>46.2</td>
<td>38.8</td>
<td>30.0</td>
<td>37.5</td>
<td>35.6</td>
<td>33.0</td>
</tr>
<tr>
<td>44.8</td>
<td>53.0</td>
<td>38.9</td>
<td>27.2</td>
<td>40.8</td>
<td>42.1</td>
</tr>
<tr>
<td>44.7</td>
<td>53.7</td>
<td>26.1</td>
<td>36.0</td>
<td>45.6</td>
<td>43.7</td>
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p: (2) (3) (4) (5) (6)

LSR*: 9.7 10.2 10.5 10.8 10.9

Lights: VB VW W VCW VR R

Means: 26.7 37.4 39.6 40.4 41.9 45.6

*Least significant range at the 5% level.

aParentheses enclose ft-c intensities.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
light qualities. The choice of lamps for this experiment was based on the fact that generally 2,4-D was most effective in the presence of red and blue light with somewhat low light intensities. Because the maximum obtainable light intensity for General Electric red (R) was very low, this permitted a very substantial comparison with higher light intensity. The greatest reduction in dry weight yield was obtained with the low intensity red light. These results indicate that low light intensities are most effective in influencing the action of 2,4-D.

Low light intensity, 1000 ppm 2,4-D, and 5% sucrose.

An experiment was conducted to measure the effects of light quality in relation to its modification of the 2,4-D action with and without sucrose. There were four treatments: (i) control; (ii) 5% sucrose; (iii) 1000 ppm 2,4-D; and (iv) 5% sucrose:1000 ppm 2,4-D mixture. In evaluating the light qualities the light intensity was 600 μw/cm² for all light colors and the short-term light conditioning period was used. A post-spray period of ten days was given all plants resulting in a total of fifteen days illumination.

Control (Table 16, A). All plants grew very well under lights of all qualities. The greatest increase in dry weight occurred in plants illuminated with red light. Red was significant over blue, green, yellow, and warm white, while pink was significant only over blue at the 5% level. Blue was least effective in causing dry weight increase, followed by green, yellow, and warm white although differences between these lights were not significantly different (Table
Table 16. Effects of short-term (5 days) light at 600 μw/cm² of six different light qualities, and 5% sucrose, 1000 ppm 2,4-D, and 5% sucrose: 1000 ppm 2,4-D mixture on dry weight (mgms) production of mustard plants.

A. Control:

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<tr>
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<tr>
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Table 16. -Continued

C. 2,4-D Treated:

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<td>264</td>
<td>274</td>
<td>414</td>
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</table>

Mean 205 198 192 253 287 276

p: (2) (3) (4) (5) (6)

LSR*: 71 75 77 78 80

Lights: G B W Y R P

Means: 192 198 205 253 276 287

D. Sucrose:2,4-D Mixture Treated:

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</table>

Mean 196 231 214 253 305 367

p: (2) (3) (4) (5) (6)

LSR*: 88 93 96 98 99

Lights: W G B Y P R

Means: 196 214 231 253 305 367

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
16, A). At the 1% level red showed a similar significance over all lights except pink.

Sucrose (Table 16, B). The dry weight production of plants treated with sucrose was greatest in those plants irradiated with red light. At the 5% level red was significant over green, blue, yellow, warm white, and pink. No significance existed among green, blue, yellow, warm white, and pink (Table 16, B). Only plants illuminated with blue, and yellow gained in dry weight as a result of the exogenous sucrose supply. Berrie (9) found that tomato plants irradiated with yellow light made better use of applied sugars than did those irradiated with daylight and green light under a 16 hour daylength.

2,4-D (Table 16, C). Pink light was most efficient in causing dry weight increase in 2,4-D treated plants. Next was red, followed by yellow, warm white, blue, and green. At the 5% level pink was significant over green, blue, and warm white. Red was found to be significant over green and blue. No significant differences in dry weight yield was noted among green, blue, warm white, and yellow. The differences between warm white, yellow, and red were non-significant. Also differences found between red and pink were non-significant (Table 16, C).

Sucrose:2,4-D mixture (Table 16, D). Plants treated with a sucrose:2,4-D mixture produced the greatest dry weight under red, followed by pink, yellow, blue, green, and warm white. Red was significant over all lights except pink at the 5% level. Warm white was significantly less effective
than pink. There were no significant differences between warm white, green, blue, and yellow nor were there any significant differences between green, blue, yellow, and pink (Table 16, D). At the 1% level red was significant over warm white, green, and blue.

Control vs. sucrose (Table 17, A). The differences in dry weight production between control and sucrose treated plants were not significant among light qualities (Table 17, A). The sucrose sprayed plants irradiated with blue and yellow produced more dry weight than control plants under the same lights (Table 16, A and B).

Control vs. 2,4-D (Table 17, B). 2,4-D significantly reduced the dry weight yield of plants illuminated with red light. At the 5% level red was significantly more effective in promoting the 2,4-D effect on dry weight increase over blue, yellow, and green. The differences among means for warm white, pink, and red were statistically non-significant as were the differences among means for blue, yellow, green, warm white, and pink (Table 17, B). At the 1% level red was significant over blue and yellow.

Control vs. sucrose: 2,4-D mixture (Table 17, C). There was considerable reduction in dry weight by the sucrose: 2,4-D mixture treatment. However, differences among light qualities were statistically non-significant. The greatest reduction was found with red light, followed by warm white, pink, green, yellow, and blue (Table 17, C).

These results (Table 17, B and C) indicated that
Table 17. Comparisons between treatments presented in Table 16.

A. Control vs. Sucrose Treated (Differences in dry weight between control and sucrose treated):

<table>
<thead>
<tr>
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Mean 128 157 109 72 222 213

p: (2) (3) (4) (5) (6)

LSR*: 158 166 171 174 177

Lights: Y G W B R P

Means: 72 109 128 157 213 222

B. Control vs. 2,4-D Treated (Reduction in dry weight by 2,4-D below that of control plants):

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Mean 382 265 326 274 402 559

p: (2) (3) (4) (5) (6)

LSR*: 184 193 200 203 206

Lights: B Y G W P R

Means: 265 274 326 382 402 559
Table 17. -Continued

C. Control vs. Sucrose: 2,4-D Mixture Treated (Reduction in dry weight by mixture below that of control plants):

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Mean 390 262 304 274 385 468

p:    (2) (3) (4) (5) (6)
LSR*: 204 214 221 226 229

Lights: B Y G P W R
Means: 262 274 304 385 390 468

D. Sucrose Treated vs. 2,4-D Treated (Reduction in dry weight by 2,4-D below that of sucrose treated plants):

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</table>

Mean 358 322 278 308 314 541

p:    (2) (3) (4) (5) (6)
LSR*: 160 168 174 177 180

Lights: G Y P B W R
Means: 278 308 314 321 358 541
Table 17. -Continued

E. Sucrose Treated vs. Sucrose:2,4-D Mixture Treated
(Reduction in dry weight by mixture below that of
sucrose treated plants):

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<td>322</td>
<td>450</td>
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</table>

p: (2) (3) (4) (5) (6)
LSR*: 181 190 196 200 203

Lights: G B Y P W R
Means: 257 289 308 322 366 450

F. Sucrose:2,4-D Mixture Treated vs. 2,4-D Treated (Differences in dry weight between mixture treated and
2,4-D treated plants):

<p>| | | | | | | |</p>
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<td>70</td>
<td>20</td>
<td>35</td>
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<tr>
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<td>56</td>
<td>72</td>
<td>93</td>
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<td>96</td>
</tr>
</tbody>
</table>

p: (2) (3) (4) (5) (6)
LSR*: 55 58 60 61 62

Lights: B P G W Y R
Means: 55 65 71 75 93 95

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are
significantly different, whereas any two means underscored
by the same line are not significantly different.
yellow and green lights are equally effective as blue in promoting the 2,4-D effect on dry weight reduction where light intensity is measured as incident energy. This was true with 2,4-D alone and with the sucrose:2,4-D mixture (Table 17, B and C).

Sucrose vs. 2,4-D (Table 17, D). Red light was significant over green, yellow, pink, blue, and warm white in reducing dry weight of 2,4-D treated plants below that of sucrose treated plants at the 5% level. No significant reduction occurred among these latter five lights (Table 17, D). At the 1% level red was significant over green in promoting the 2,4-D effect.

Sucrose vs. sucrose:2,4-D mixture (Table 17, E). The differences among light qualities in causing a reduction in dry weight yield by the sucrose:2,4-D mixture below that of the sucrose treated plants were non-significant at the 5% level. Although non-significant, the greatest reduction was obtained with red light, followed by warm white, pink, yellow, blue, and green (Table 17, E). It is evident from these results that the addition of sucrose reduced the effect of 2,4-D under red light in the reduction of dry weight yield of 2,4-D treated plants below that of sucrose treated plants (see Table 17, D).

Sucrose:2,4-D mixture vs. 2,4-D (Table 17, F). Differences among light qualities of the differences in dry weight yield between the sucrose:2,4-D mixture treated and 2,4-D treated plants were non-significant (Table 17, F).
Although the sucrose:2,4-D mixture was not significantly less in its effect on dry weight production than 2,4-D alone there was a general reduction in the 2,4-D effect by the addition of sucrose under all lights (Table 16, C and D).

**Low light intensity, 1000 ppm 2,4-D, and 10% sucrose.** Since 5% sucrose lessens the 2,4-D effect under various light qualities a similar experiment was conducted using a higher sucrose concentration (10%). With the exception of an increase in the sucrose concentration all other conditions were precisely the same as those for the test conducted with 5% sucrose.

**Control (Table 18, A).** Dry weight in mustard was greatest under red light, followed by pink, yellow, green, warm white, and blue. Statistically, red was significant over all light qualities in promoting dry weight yield at the 5% level. The differences in yield obtained under pink and yellow were significant over blue at the 5% level. There were no other significant differences among light qualities (Table 18, A). At the 1% level dry weight production was significantly greater under red than under blue, warm white, green, and yellow. Pink was more efficient than blue in enhancing dry weight production at the 1% level.

**Sucrose (Table 18, B).** The results (Table 18, B) showed that red light was more efficient in promoting dry weight production of sucrose treated plants. The order of efficiency for light qualities on dry weight yield of sucrose treated plants was the same as with control plants (Table 18, A). The decreasing order of efficiency was: red, pink, yellow,
Table 18. Effects of short-term (5 days) light at 600 µw/cm² of six different light qualities, and 10% sucrose, 1000 ppm 2,4-D, and 10% sucrose:1000 ppm 2,4-D mixture on dry weight (mgms) production of mustard plants.

A. Control:

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p: (2) (3) (4) (5) (6)
LSR*: 173 182 168 191 194

Lights: B W G Y P R
Means: 953 1070 1102 1192 1253 1450

B. Sucrose Treated:

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<td>1624</td>
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p: (2) (3) (4) (5) (6)
LSR*: 185 194 200 204 207

Lights: B W G Y P R
Means: 955 1130 1211 1266 1443 1624
Table 18. -Continued

C. 2,4-D Treated:

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<tr>
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<td>524</td>
<td>459</td>
<td>562</td>
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</table>

Mean 458 405 554 540 527 634

p: (2) (3) (4) (5) (6)

LSR*: 86 91 94 96 97

Lights: B W Y G R

Means: 405 458 527 540 554 634

---

D. Sucrose: 2,4-D Mixture Treated:

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<tr>
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<th>Y</th>
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<td>739</td>
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<td>492</td>
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<td>684</td>
<td>579</td>
<td>469</td>
<td>682</td>
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</table>

Mean 591 484 650 626 690 664

p: (2) (3) (4) (5) (6)

LSR*: 112 118 122 124 126

Lights: B W Y G R P

Means: 484 591 626 650 664 690

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.
green, warm white, and blue. The plants illuminated with red yielded significantly greater dry weight than those illuminated with blue, warm white, green, and yellow. Pink exhibited significance over blue, warm white, and green in the production of dry weight. Both yellow and green were found to be significantly more efficient in causing dry weight increase than blue at the 5% level (Table 18, B).

2,4-D (Table 18, C). In this test also, the red light produced the greatest dry weight. The next greatest yield was obtained with green, followed by yellow, pink, warm white, and blue. The mean dry weight yield produced under red light was significantly higher than that of blue, warm white, pink, and yellow. Green was significantly more effective than blue and warm white. Yellow and pink showed significance over blue (Table 18, C).

Sucrose: 2,4-D mixture (Table 18, D). When the mean dry weight yields (Table 18, D) of the sucrose: 2,4-D mixture treated plants were compared among light qualities the greatest dry weight increase was found under pink light. Following pink in order of effectiveness were: red, green, yellow, warm white, and blue. Blue was significantly less effective in promoting dry weight increase than all lights except warm white at the 5% level.

Control vs. sucrose (Table 19, A). The 10% sucrose treatment was found to be more effective in causing dry weight increase than 5% sucrose under all lights except blue (Tables 17, E and 19, E). The mean dry weight of sucrose treated plants was greater than that for control plants under all
Table 19. Comparisons between treatments presented in Table 18.

A. Control vs. Sucrose Treated (Differences in dry weight between control and sucrose treated):

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<td>135</td>
<td>135</td>
<td>135</td>
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<td>155</td>
<td>135</td>
<td>220</td>
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<tr>
<td>150</td>
<td>10</td>
<td>160</td>
<td>35</td>
<td>750</td>
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<td>30</td>
<td>160</td>
<td>160</td>
<td>220</td>
<td>130</td>
<td>20</td>
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Mean 187 91 160 119 352 226

p: (2) (3) (4) (5) (6)
LSR*: 155 163 168 172 171*
Lights: B Y G W R P
Means: B Y G W R P

B. Control vs. 2,4-D Treated (Reduction in dry weight by 2,4-D below that of control plants):

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<td></td>
<td>670</td>
<td>390</td>
<td>570</td>
<td>845</td>
<td>610</td>
<td>760</td>
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<td>570</td>
<td>685</td>
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<td>760</td>
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<td>820</td>
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<td>1045</td>
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<td>635</td>
<td>675</td>
<td>655</td>
<td>760</td>
<td>595</td>
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<td>265</td>
<td>330</td>
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<td>295</td>
<td>760</td>
<td>810</td>
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</table>

Mean 612 548 548 652 726 816

p: (2) (3) (4) (5) (6)
LSR*: 186 195 202 205 209
Lights: B G W Y P R
Means: 548 548 612 652 726 816
Table 19. -Continued

C. Control vs. Sucrose: 2,4-D Mixture Treated (Reduction in dry weight by mixture below that of control plants):

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<td>225</td>
<td>250</td>
<td>240</td>
<td>750</td>
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</table>

Mean 478 469 452 566 563 785

p: (2) (3) (4) (5) (6)

LSR*: 184 194 200 204 207

Lights: G B W P Y R

Means: 452 469 478 563 566 785

D. Sucrose Treated vs. 2,4-D Treated (Reduction in dry weight by 2,4-D below that of sucrose treated plants):

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<td>515</td>
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<td>790</td>
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</table>

Mean 672 550 657 727 916 990

p: (2) (3) (4) (5) (6)

LSR*: 208 219 226 231 234

Lights: B G W P Y R

Means: 550 657 672 727 916 990
Table 19. -Continued

E. Sucrose Treated vs. Sucrose:2,4-D Mixture Treated  
(Reduction in dry weight by mixture below that of  
sucrose treated plants):

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<td>620</td>
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<tr>
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<td>561</td>
<td>640</td>
<td>753</td>
<td>959</td>
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p: (2) (3) (4) (5) (6)  
LSR*: 203 213 220 224 228

Lights: B W G Y P R  
Means: 471 538 561 640 753 959

F. Sucrose:2,4-D Mixture Treated vs. 2,4-D Treated  
(Differences in dry weight between mixture treated and  
2,4-D treated plants):

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<td>45</td>
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<td>75</td>
<td>230</td>
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<td>Mean</td>
<td>152</td>
<td>74</td>
<td>118</td>
<td>88</td>
<td>162</td>
<td>62</td>
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</table>

p: (2) (3) (4) (5) (6)  
LSR*: 108 113 117 119 121

Lights: R B Y G W P  
Means: 62 74 88 118 152 162

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are  
significantly different, whereas any two means underscored  
by the same line are not significantly different.
light qualities (Table 18, A and B). Plants illuminated with pink most effectively utilized sucrose. Pink was followed by red, warm white, green, yellow, and blue in mean dry weight increase of sucrose treated plants above that of control plants. At the 5% level pink was significant over blue, yellow, green, and warm white. Red was significant only over blue (Table 19, A).

Control vs. 2,4-D (Table 19, B). Among light qualities red was more effective in promoting 2,4-D interference with dry weight increase. The next most effective lights were in the following order: pink, yellow, warm white, green, and blue. At the 5% level only red was significant over blue, green, and warm white (Table 19, B).

Control vs. sucrose:2,4-D mixture (Table 19, C). Table 19, C shows the reduction in dry weight by the sucrose:2,4-D mixture below that of controls. The greatest reduction was found in plants illuminated with red light. The next greatest reductions in dry weight were obtained in the following order: yellow, pink, warm white, blue, and green. Red was significant over all lights in promoting the reductive effect on dry weight by the sucrose:2,4-D mixture below that of controls. At the 1% level only green, blue, and warm white were less effective than red.

Sucrose vs. 2,4-D (Table 19, D). The reduction of dry weight by 2,4-D below sucrose treated plants was markedly influenced by light quality. The greatest difference in dry weight yield between sucrose treated and 2,4-D treated
plants occurred in plants irradiated with red and pink. Following these in order of effectiveness were: yellow, warm white, green, and blue. Red was shown to be significantly more effective than blue, green, warm white, and yellow. Pink was significant over blue, green, and warm white at the 5% level (Table 19, D). At the 1% level red was significant over blue, green, and warm white, while pink was significant only over blue.

Sucrose vs. sucrose:2,4-D mixture (Table 19, E). The presence of sucrose lessened the reductive effect of 2,4-D under all light qualities. Although dry weight reduction was decreased, red light remained most effective in promoting the effect of 2,4-D, followed by pink, yellow, green, warm white, and blue. Red was significantly more influential in promoting 2,4-D interference in dry weight production than all lights at the 5% level. Pink was significantly more influential than blue (Table 19, E).

Sucrose:2,4-D mixture vs. 2,4-D (Table 19, F). Differences among light qualities for differences in dry weight yield between sucrose:2,4-D mixture treated plants and 2,4-D treated plants were non-significant. The greatest difference was found with pink illumination. The next greatest was found with warm white, followed by green, yellow, blue, and red (Table 19, A).
CONCLUSIONS

The modifying effect of light quality of 2,4-D action with mustard plants has been shown to be variable. Here, the "2,4-D action" or "2,4-D effect" refers to the inhibition of photosynthesis, stimulation of respiration, and reduction in dry weight of mustard plants by 2,4-D. In most of the experiments conducted, where light intensity was measured as ft-c, generally red, and blue light were most effective in promoting the action of 2,4-D. On the other hand, yellow, and green were generally least effective. However, with light intensity measured as incident energy the influence of light quality on the 2,4-D action varies greatly with different colors. For example, green light is often more effective than blue. Since illuminance measurements (ft-c) are based on the sensitivity curve of the human eye which has its maximum in the green, equal intensities in ft-c for light qualities would definitely give different energy levels for light qualities being compared. No evidence has been offered that plants respond to light the same as the human eye, but it is generally accepted that plants respond to all portions of the visible spectrum. Thus it is evident from the results of these experiments that light intensity should be measured in energy and not illuminance for the better evaluation of light quality effects.

It may be concluded that the action of 100 ppm 2,4-D on CO₂ uptake and output was not significantly influenced by light quality at low light intensity. This non-significant
effect of light quality was found with both short and long-term light conditioning.

Results from experiments with low light intensity and 500 ppm 2,4-D showed that pink light was most effective in promoting 2,4-D interference in CO₂ uptake, next was red, followed by yellow, green, blue, and warm white. Here the light intensity was measured as incident energy using the short-term light conditioning period. However, with long-term light conditioning and light intensity measured in ft-c warm white light was most effective, followed by blue, green, red, pink, and yellow. Respiration was stimulated by 500 ppm 2,4-D under all light qualities, but significantly so only under red light.

Light quality was very effective in modifying the action of 2,4-D at 1000 ppm, with low intensity light measured in ft-c, and when short-term light conditioning was used. Blue light was most effective in promoting 2,4-D interference in CO₂ uptake. Following blue in order of effectiveness were: pink, red, warm white, yellow, and green. CO₂ output was enhanced by 2,4-D under all lights, but differences between light qualities were non-significant. On the other hand, where low light intensity was measured as incident energy with short-term light conditioning, light quality was less effective in promoting 2,4-D interference with CO₂ uptake. However, CO₂ output was significantly enhanced by 2,4-D under red, and warm white light.

The fact that lower concentrations of herbicides
have less effect on CO₂ uptake and output than higher concentrations was pointed out by other workers (5, 45, 79). A similar conclusion is reached here based on the fact that the degree of effectiveness of 2,4-D under different light qualities increased with an increase in concentration of 2,4-D.

The presence of 2% sucrose mixed with 500 ppm 2,4-D lessened the effect of 2,4-D interference in CO₂ uptake and output by mustard plants under all light qualities. Only red light promoted a significant 2,4-D interference in CO₂ uptake and output. With a higher sucrose concentration (5%) the significant modifying effects among light qualities on the 2,4-D action were eliminated. Thus the 2,4-D effect on mustard plants observed under different light qualities may be decreased with the addition of sucrose. It may be that the effect of 2,4-D on photosynthesis reduces the production of carbohydrates by inhibiting CO₂ uptake which could possibly be associated with the opening and closing of the stomates. The addition of sucrose supplies carbohydrates which the plants assimilate, thereby the effect of 2,4-D is overcome. However, stimulation of respiration by 2,4-D would result in considerable depletion of the added carbohydrate. Although 5% sucrose eliminated significant differences among light qualities in modifying the 2,4-D action, the reduced effect was not significant over the 2,4-D effect without sucrose added. A similar reduction of an inhibitory effect of several urea herbicides at low concentration on leaf development by
Sucrose was reported by Gentner and Hilton (30).

The influence of light quality on the 2,4-D action was not greatly enhanced with high light intensity and long-term light conditioning. In fact, 2,4-D inhibition of CO₂ uptake was least with light qualities having the highest intensities except for warm white. The order of decreasing effectiveness in promoting the action of 2,4-D was: pink, yellow, green, red, blue, and warm white. However, the greatest 2,4-D stimulation of CO₂ output was found in plants under light qualities with the highest intensities. This conclusion is partly in agreement with the findings of Jordan, Dunham, and Linck (41) in that they observed the greatest response of flax to 2,4-D with low intensity and least with high intensity.

Among light qualities with high intensity, dry weight reduction by 2,4-D was greatest with red (VR), and least with blue (VB). This agrees with the report of Tregunna, Krotkov, and Nelson (70) that leaves illuminated with red light generally absorbs larger amounts of CO₂ than leaves illuminated with blue. Thus the greatest reduction in dry weight by 2,4-D under red light indicate a greater interference in CO₂ uptake with red irradiation than with blue irradiation of mustard plants treated with 2,4-D. The greatest dry weight reduction occurred in plants illuminated with low intensity red light (R). Again, light of low intensity was more effective in promoting the 2,4-D effect on plant growth.

Red, and pink light with some exceptions were most effective in promoting dry weight increase over other light
colors in experiments with low intensity measured as incident energy. This was for 2,4-D treated plants with and without 5% and 10% sucrose, and short-term light conditioning. The 2,4-D effect was lessened by 10% sucrose under all light qualities.

The fact that considerable external morphological differences usually appear with long-term light conditioning may be an important factor when large differences in CO₂ uptake and output are found among light qualities. It is very likely that with an increased leaf area more stomates are present which would have a direct relation to the CO₂ exchange. Also, the possibility of more cells per unit leaf area would have some bearing on the photosynthetic and respiratory activities. Future studies of the effect of light quality on plant morphology should yield interesting results.

In all future experiments dealing with the measurement of photosynthesis (CO₂ uptake) and respiration (CO₂ output) attempts should be made to decrease variability between replications.
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