THESIS

THE EFFECTS OF CARBON DIOXIDE ON CARNATION GROWTH

Submitted by

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To my family, with whom I can now become reacquainted, my deepest gratitude.

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Chapter I

INTRODUCTION

In the past five years, much progress has been made in the control of greenhouse environment. With the advent of automation for heating and air conditioning, temperatures can now be controlled within a few degrees Fahrenheit throughout the year. Nutritional requirements can be more easily and economically maintained with fertilizer injection systems now available. Optimum moisture levels are also more evenly maintained where automatic watering systems are utilized. Light has been enhanced to some degree by various types of greenhouse construction. The near optimum relationships of the above factors in the environment complex have no doubt led to increased production and quality. It is quite possible that further increases in plant growth may be obtained by atmospheric fertilization with carbon dioxide, thus bringing into equipoise the environmental complex.

Early investigators have indicated that carbon dioxide assimilation is greatest at high light intensities. Optimum temperature has been found to vary with light intensity, and optimum light intensity has been found to vary with the water supply available to plants. Blackman, according to Meyer and Anderson (26) has postulated his "principle of limiting factors", which infers that the speed of the plant growth process is dependent on a number of separate factors, the rate of which is limited by the factor in the least supply.

Several investigators (2, 6, 9, 13, 32, 37, 43) have increased the carbon dioxide concentration of the atmosphere surrounding plants with positive results of increased plant growth. Other investigators (17, 23, 38) have reported no increase in dry matter production from carbon dioxide fertilization.

Carbon dioxide is one of the least considered factors in plant growth by most researchers, while some realize its very definite importance to the environmental complex. The atmosphere is usually considered to contain 300 parts per million of carbon dioxide by volume. Lundegardh (25) states that this concentration may often limit optimum plant growth.

Chapter II

REVIEW OF LITERATURE

Since the environmental complex of plants is composed of several factors, it is almost impossible to discuss one factor without considering the others. This discussion will take into consideration the effects of varying concentrations of carbon dioxide and their relationship to other factors in the complex.

Light and carbon dioxide

For many years scientists have realized that carbon dioxide assimilation is most dependent upon light. Plants have been shown to vary in their light requirements, which is the major factor governing carbon dioxide assimilation, thus they are often classified on the basis of light saturation. Shade plants are generally saturated at 400 to 900 foot candles while high light plants are saturated at 3000 to 5000 foot candles (3, 24, 26).

The assimilation rate of Nasturtium palustre was doubled by Lundegardh (25) when he increased the light intensity on the plant to three times its former value. Kramer and Decker (22) indicated that carbon dioxide assimilation by loblolly pine, eastern red oak and white oak reached its maximum at one-third or less full sun and showed insignificant decreases at higher light intensities. With controlled temperature at 30.1° C and a .05 per cent carbon dioxide concentration, Singh and Lal (36) recorded a doubling of assimilation rates when leaves of mature sugar cane were increased in illumination from 90 candle power to 1875 candle power.

Several investigators infer that even though light saturation is reached, carbon dioxide is often limiting due to the fact the physical processes of its absorption commonly determines the rate of carbon dioxide assimilation (14, 24, 25). Verduin and Loomis (41) found that the light saturation value for fully exposed maize leaves was approximately 2500 foot candles or one-fourth full sunlight. Light intensities above 4000 foot candles caused a decrease in carbon dioxide assimilation. Working with wheat, Hoover (20) reported that plants grown in a 1200 ppm concentration of carbon dioxide reached complete saturation at 947 foot candles. On the other hand, plants grown in a 820 ppm concentration reached saturation at 100 foot candles. Upon completion of this investigation, he concluded that maximum carbon dioxide assimilation is linearly proportional to light up to 1000 foot candles.

Plants, whether grown in the field or greenhouse, often shade one another. The effects of various light intensities caused by alfalfa plants shading one another was evinced by Thomas and Hill (40). Plants 48 inches tall assimilated two times more than plants 6 to 8 inches tall and the weight of the leaves was 3.6 times as great.

To a degree, certain physical reactions take place in plants due to minor changes in environment. A physical reaction of leaves caused by carbon dioxide as well as light was demonstrated by Scarth and Shaw (34). They showed that a small reduction in carbon dioxide concentration caused the stomata to open at 50 foot candles and to open even wider at 400 foot candles.

Even though light levels affect carbon dioxide assimilation, Went (42) concluded that maximum assimilation of carbon dioxide and effectiveness of light is at dusk (17:00 to 18:00 - December) and before sunrise (06:00 to 07:00).

Temperature and carbon dioxide

Temperature also has a definite relationship to carbon dioxide assimilation. Plants may be classified according to their temperature sensitivity and its effect on assimilation rates. Under low light and high carbon dioxide concentrations, Bonner (3) states that assimilation rates will not increase appreciably with an increase in temperature, but assimilation in high light and low carbon dioxide concentrations can be greatly increased by increases in temperature.

In general, carbon dioxide assimilation can take place in a wide range of temperatures. It has been reported that some conifers assimilate carbon dioxide at temperatures as low as -35° C, while semi-desert and tropical species can withstand temperatures up to 55° C (26). Ewart (1896), according to Post (30), states that warm temperature plants cease assimilation at temperatures near freezing and tropical plants stop assimilating carbon dioxide at temperatures around 40° F.

The relationship between temperature and the rate of carbon dioxide assimilation is rather complex and is further complicated by the fact that the relationship may vary to a greater degree according to the light intensity present. This complexity can best be discussed by presenting results of various investigators such as Decker (12). He found that apparent photosynthesis of loblolly pine at 4500 foot candles was nearly twice as high at 30° C than at 40° C. Verduin and Loomis (41) reported that carbon dioxide assimilation decreased at temperatures less than 25° C and decreased more seriously with temperature increases.

With a constant carbon dioxide level (.05 per cent) and light at 1875 candle power, Singh and Lal (36) varied carbon dioxide assimilation of mature sugar cane leaves by varying temperature.

Temperature °C	Real assimilation mg. per 100 sq. cm. per hr.
23.0	2.30
30.1	3.03
34.0	3.20
39.0	3.05

By varying one environmental factor, the optimum for the remaining factors may be changed. Lundegardh (25), under constant light, added carbon dioxide to the atmosphere thus causing a shift in the optimum temperature of assimilation from 20° to 31° C for potatoes, 19° to 36° C for sugar cane and 30° to 36° C for beans.

Water and carbon dioxide

A deficiency of water as a raw material is not commonly considered a limiting factor in its relationship to carbon dioxide assimilation, although a reduction in the water content of the leaves usually causes a decrease in their ability to assimilate carbon dioxide. Meyer and Anderson (26) feel that there are two possible ways this effect is exerted: (1) a reduction in the diffusive capacity of the stomates because of a decrease in the water content of the leaves, and (2) reduction in hydration of the protoplasm. According to Verduin and Loomis (41) the carbon dioxide assimilation rate may be decreased, not only by stomatal closure due to wilting, but by many other internal changes.

Schneider and Childers (35) investigated the effects on small apple trees when soils were gradually dried. They placed the trees in chambers with temperatures of 80°, 90° and 100° F. Gradual drying of the soil reduced assimilation in the 100° F chamber within three days. The 90° chamber also showed a decrease in assimilation the third day, but the 80° F chamber did not decrease carbon dioxide assimilation until the fifth day. Before wilting there were marked reductions in carbon dioxide assimilation and transpiration accompanied by an increase in respiration. In one case there was a 55 per cent decrease in assimilation, 65 per cent decrease in transpiration and a 62 per cent increase in respiration. Upon wilting, there was an 87 per cent decrease in carbon dioxide assimilation and transpiration.

Work by Thomas and Hill (40) also indicates that assimilation decreases with wilting. Alfalfa plants which were starting to wilt in dry soil assimilated carbon dioxide much slower than plants grown in heavily irrigated plots. Reductions in carbon dioxide assimilation were also noted by Dastur (10) following a decrease in the water content of leaves.

Chapman and Loomis (7) observed that wilted leaves of potato assimilated approximately one-half as much carbon dioxide as non-wilted leaves. They also found that wilted plants upon watering would resume their rate of assimilation proportionately to the duration they were wilted.

There are some indications that increased humidity surrounding the plants may also decrease assimilation. Bolas and Henderson (1) feel that high humidity within closed compartments such as growth chambers and possibly greenhouses might be detrimental when experiments on plant growth are being conducted.

Nutrients and carbon dioxide

The nutrients available to plants are not generally considered a part of the environmental complex, but some research indicates a correlation between nutrient levels and carbon dioxide assimilation.

Sugar beets grown in sand culture produced somewhat larger roots and smaller tops in lower nutrient concentrations. When the principal nutrients were increased five to tenfold in both levels, there was no appreciable increase in carbon dioxide assimilation. When the atmosphere of both nutrient levels was fertilized with carbon dioxide, the plants grown in the high nutrient level produced a much greater amount of dry matter. Under lower carbon dioxide levels the dry matter differences were not as great (40).

In 1946, Thomas and Hill (40) treated tomatoes with increased carbon dioxide concentrations from 9:00 AM until 3:00 to 6:00 PM daily for two weeks. Many necrotic areas developed on the leaves in plots of low nutrient level, but less necrosis was observed on leaves of plants grown in higher nutrient concentrations. The lesion size increased rapidly until the treatment was stopped, then the plants grew new leaves and in time appeared normal. It was also indicated that healthy plants respond well to increased carbon dioxide concentrations, while sulfur deficient and chlorotic plants are unable to utilize the additional gas.

The main benefit of fertilizer additions to plant media is nutritional. Fertilizer also has a beneficial effect on the various bacteria in the medium. Lundegardh (25) conducted investigations to show the effects of manure and manure-inorganic fertilizer combinations on bacteria. He found that the bacterial activity was stimulated and greater amounts of carbon dioxide were evolved for plant use with the manure-inorganic fertilizer combinations.

Carbon dioxide concentrations

Atmospheric levels.--The atmospheric content of carbon dioxide varies from 200 ppm to 400 ppm. This is partly due to the seasonal temperature changes causing increases or decreases in photosynthesis, respiration and decay. Climatic conditions such as high and low pressure areas, air movements from over the ocean and storm fronts all tend to influence the carbon dioxide content of the air. Generally, the carbon dioxide content of the atmosphere is considered to average about 300 ppm by volume (8, 24, 25, 26).

Pushner (31), in 1892, investigated the carbon dioxide content of the atmosphere in seven areas around Munich, Germany. He found higher carbon dioxide during the day than at night in the city; the suburbs had higher winter levels than summer; and the higher he went in the mountains, the lower the carbon dioxide level. This investigation showed the effects of industrial areas, topography, and heating with coal.

Research in the United States has indicated that the average carbon dioxide concentration has increased to at least 330 ppm. Various aerial flights have shown carbon dioxide concentrations to be fairly uniform up to approximately forty-five miles (18).

The concentration of carbon dioxide in the layer of atmosphere over vegetation varies in wide limits (25), with some of the largest variations reported over field crops. During periodic high rates of photosynthesis, carbon dioxide reductions of 25 to 50 per cent have been noted during the day and smaller variations during the night, or at various seasons (8, 41).

Closed systems.--The carbon dioxide content of closed systems such as control chambers, small transparent bags or even greenhouses, can vary much more than the concentration in the earth's atmosphere.

Gabrielson (15) using elder leaves (*Sambucus nigra* L.) in closed containers reported that the carbon dioxide concentration surrounding the leaf dropped to 90 ppm within two hours. Using portable compartments in an alfalfa field, Thomas and Hill (40) observed several different carbon dioxide levels during a six-hour period. In an unrenewed atmosphere, carbon dioxide levels ranged from 130 ppm at noon and 5:00 PM to approximately 88 ppm at 3:30 PM. An indication of the range of carbon dioxide concentrations in greenhouse atmospheres was presented by Heinicke and Hoffman (19). Small apple trees grown in a closed greenhouse produced carbon dioxide variations from 200 ppm on bright sunny mornings and up to 10,370 ppm at night. Owen (27) found that carbon dioxide was distributed fairly evenly throughout glasshouse atmospheres and was not stratified.

Concentration limits for plant growth.--Various researchers have indicated a fairly definite range of carbon dioxide concentrations tolerated by most plants. Brown and Escombe (5) obtained negative results when closed compartments were fertilized with carbon dioxide. The concentrations varied from three to one hundred times normal and were administered for twelve hours. Carbon dioxide concentrations as high as 1000 ppm were injurious and the control plants were always more vigorous.

Arnon, according to Steward (39), found that most plants will synthesize sugars faster when the carbon dioxide concentration of the air is increased. He further recorded that some plants will assimilate carbon dioxide much faster with concentrations up to 1 per cent.

Photosynthesis on a short time basis can be increased up to ten times normal with increased carbon dioxide concentrations. Over long periods of time, these concentrations become toxic, or other factors become limiting (24). Generally, it is felt that normal carbon dioxide concentrations (300 ppm) are limiting, and that plant growth is far from optimum (24, 25).

The lower limits of carbon dioxide are also of importance. Investigations by Gabrielson with elder leaves suggest that the photosynthetic process necessitates a concentration of 90 ppm carbon dioxide surrounding the assimilation centers. Below this level no photosynthesis takes place (15, 16).

Carbon dioxide preparations.--During the many years of carbon dioxide research, there has always been a need for a simple and economical method of preparing carbon dioxide gas. The most important factor in adding carbon dioxide is to be sure that it is pure (29). Bomer and Rintelen (4) obtained carbon dioxide by burning coke and then purifying and cooling it before application. In another investigation they burned charcoal to obtain carbon dioxide. Dry ice is another method of enriching the atmosphere, but could prove costly. Purification of flue gases would be an ideal source for increasing carbon dioxide in greenhouses (13, 30). Cummings and Jones (9) dissolved sodium bicarbonate in water and added sulfuric acid to produce pure carbon dioxide.

Additions of manure or other organic matter produce carbon dioxide and increase the concentrations in the atmosphere (25). Commercially, various gas extraction methods are also used to produce relatively pure carbon dioxide. Chapman and Loomis (7) used commercial tanks of carbon dioxide, purifying it before it was used.

Air movement is another inexpensive method of enriching the plant atmosphere. The carbon dioxide uptake depends on the concentration gradient of carbon dioxide from air to leaf. Concentrations near the leaf can be increased by moving fresh air across the plants (11, 42).

Increased carbon dioxide concentrations.--Increases in carbon dioxide above the normal amount found in the atmosphere have produced beneficial results in almost all cases. Bomer and Rintelen (4) added carbon dioxide to field plots by burning coke and distributed it by natural winds. They reported that broad leafed plants such as cabbage, beet, and lupine responded better than narrow leafed plants like cereals. Cabbage seemed to improve in quality and beets increased in dry material, while oats tended to lodge. Additions of carbon dioxide on potatoes also gave an increased yield under field conditions. The average weight of tubers formed increased from 140 to 330 grams with carbon dioxide additions (21). Other field studies indicated that yields varying from 1 to 3 times normal were harvested from plots treated with additional carbon dioxide (33). The most extensive work has been done with tomatoes. Some investigators found that by increasing carbon dioxide they could increase tomato yields from 20 to 35 per cent (2, 13, 21, 28, 40). Riedel (33) reported an increase of 175 per cent in tomato yields from plants in a greenhouse with carbon dioxide introduced through perforated pipes. Some investigators have reported that additions of carbon dioxide on tomatoes increased yields, but the increase was not profitable (37, 43).

After enriching greenhouse atmospheres with carbon dioxide, several researchers observed increased yields of various vegetables. Treated cucumber plants increased from 16 to 235 per cent in yield, while spinach, potatoes, and barley increased over 100 per cent above the controls (21, 28, 33). The dry weight of bean seed showed increases from 32 to 204 per cent over the check, while pod weights were 75 to 143 per cent higher. Total dry matter of pea plants was 18 to 117 per cent greater than the control with seed yield 167 to 291 per cent greater. Compared to untreated conditions, the number of leaves on treated lettuce and swiss chard increased approximately 10 per cent. Darker and crisper leaves were observed on lettuce. The average gain in weight of strawberries was 80 per cent while the increase in the number of plants was 55 per cent. Ried (32) using a carbon dioxide concentration of 1 per cent produced increases in fresh and dry weight of squash as compared to lower yields at .02 per cent concentrations. He also observed a larger root system and more strengthening tissue.

Increases in carbon dioxide concentrations have shown varied results on flowering plants. Marked responses on nasturtium plants were observed by Cummings and Jones (9). The gross weight was greater, more flowers bloomed and blooming began earlier than in untreated plots. Using leaves of <u>Helianthus annus</u>, Brown and Escombe (6) observed that assimilation, in all cases, was greater in the higher concentrations of carbon dioxide. However, they also reported negative results when seven types of plants were treated with increased carbon dioxide Plants including fuchsia, kalanchöe, begonia, and impatiens were placed in both a control chamber and one enriched with carbon dioxide. The check contained ordinary air and the treated was 1147 ppm. In all cases the check plants appeared to be in better condition than the treated plants.

Summary

In practically all cases where the carbon dioxide concentration was increased, in field or greenhouse, beneficial results have been obtained. The results were measured as increased yield of grain, fruit, flowers or amount of dry matter produced.

It is evident that many investigators were unable to accurately measure the concentrations of carbon dioxide which they used. Thus, in many cases, the carbon dioxide concentrations used to obtain increased growth were unknown.

Carbon dioxide has a definite relationship to the environmental complex. It may become limiting or be in excess due to a change in one or all of the other factors in the complex.

Chapter III

METHODS AND MATERIALS

Installation of a carbon dioxide measuring system

Analyzer.--For this investigation a Beckman model LB 15A infrared gas analyzer was installed to insure accurate measurements of the carbon dioxide content in the atmosphere surrounding growing plants. The instrument, which consists of an analyzer and an amplifier, contained a cell capable of analyzing carbon dioxide concentrations ranging from 0 to 600 ppm. Operation is based on the absorption of infrared radiations of approximately 4.23μ wavelength. Absorption varies in proportion to the amount of carbon dioxide in the air being sampled. The instrument is accurate to within 1 per cent of full scale (Figure 1).

Since the instrument was designed for continuous use, the analyzer was never turned off except for minor repairs during the time of the investigation. Approximately once each week the analyzer was recalibrated with a 315 ppm standard gas. This procedure insured accurate measurements in all phases of the investigation.

Figure 1.--Carbon dioxide analyzing system; a. analyzer, b. amplifier, c. pumping station, d. selector valve, e. recorder.

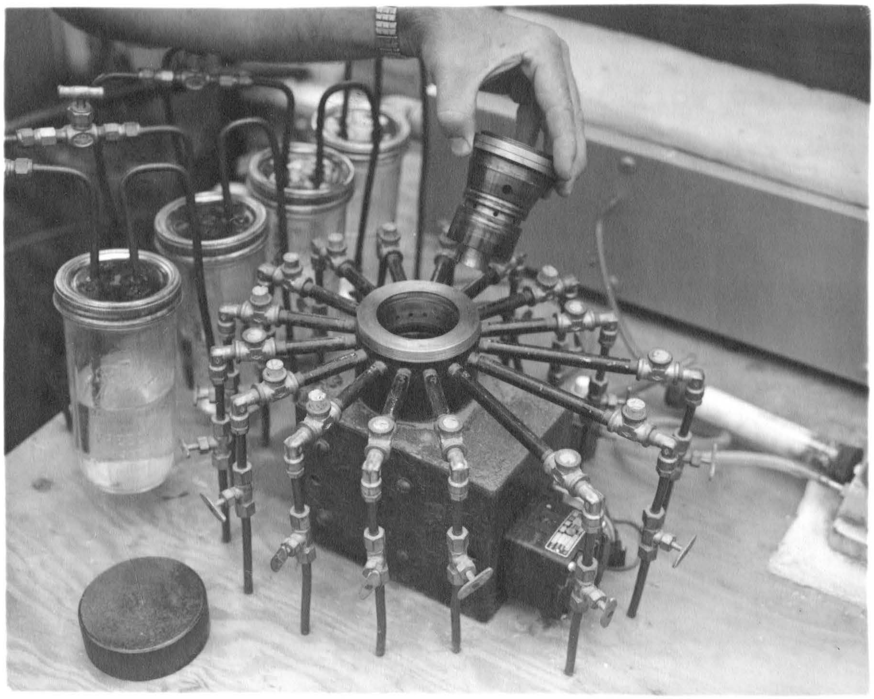


Figure 2.--Multiple port selector valve.

Selector valve.--Maximum utilization of the infrared analyzer was achieved by installing a multiple port selector valve (Figure 2). The valve assembly contained a 1/20 hp Bodine motor which was geared to 1 rpm. The motor was then connected to a Boston reducing gear unit, which gave a drive speed of two revolutions per hour. The valve assembly contained 16 ports and the revolving cone allowed air samples to be taken from each port for approximately 100 seconds every half hour. Each port was connected to a 1/4 inch O.D. copper tube which conveyed the air samples from the sampling areas.

Air pumping station.--A model 2, dyna pump was used to pull the air through the sampling tubes and selector valve, forcing the sample through a cotton filter into the analyzer. The rate of flow through the sampling tubes was 0.9 to 1.10 liters per minute, depending on the length of the tube.

Recorder.--The infrared gas analyzer was connected to an Esterline-Angus recorder which continuously recorded the carbon dioxide concentrations.

Studies of normal carbon dioxide concentrations found in the greenhouse.

Two sampling tubes from the analyzer system were placed in the greenhouse range. One lead in the carnation section was placed at flower bud height and a second was placed in a rose house among the heaviest vegetation. Air samples were taken continuously each half hour throughout a period of 24 months.

Meteorological data were obtained from records at the research greenhouses as well as the Colorado State University weather station. This data was used to show the correlation between carbon dioxide concentrations in the greenhouse and outside weather conditions. The data included measurements of solar energy and atmospheric carbon dioxide levels from the research greenhouse, and daily mean temperature, humidity, and barometric pressures from the weather station.

Construction of chambers for atmospheric fertilization with carbon dioxide

Four chambers, each containing 520 cubic feet of space, were constructed on a 35 ft. by 15 ft. area inside a greenhouse section. The complete set of chambers was aligned from east to west and the digits 1, 2, 3, 4 were assigned (Figure 3). The wooden framework consisted of a 3/4 inch plywood floor laid on 2 inch by 4 inch joists with the remaining shell made of 2 inch by 2 inch material. Wire netting placed on the top provided additional support for the clear polyvinyl

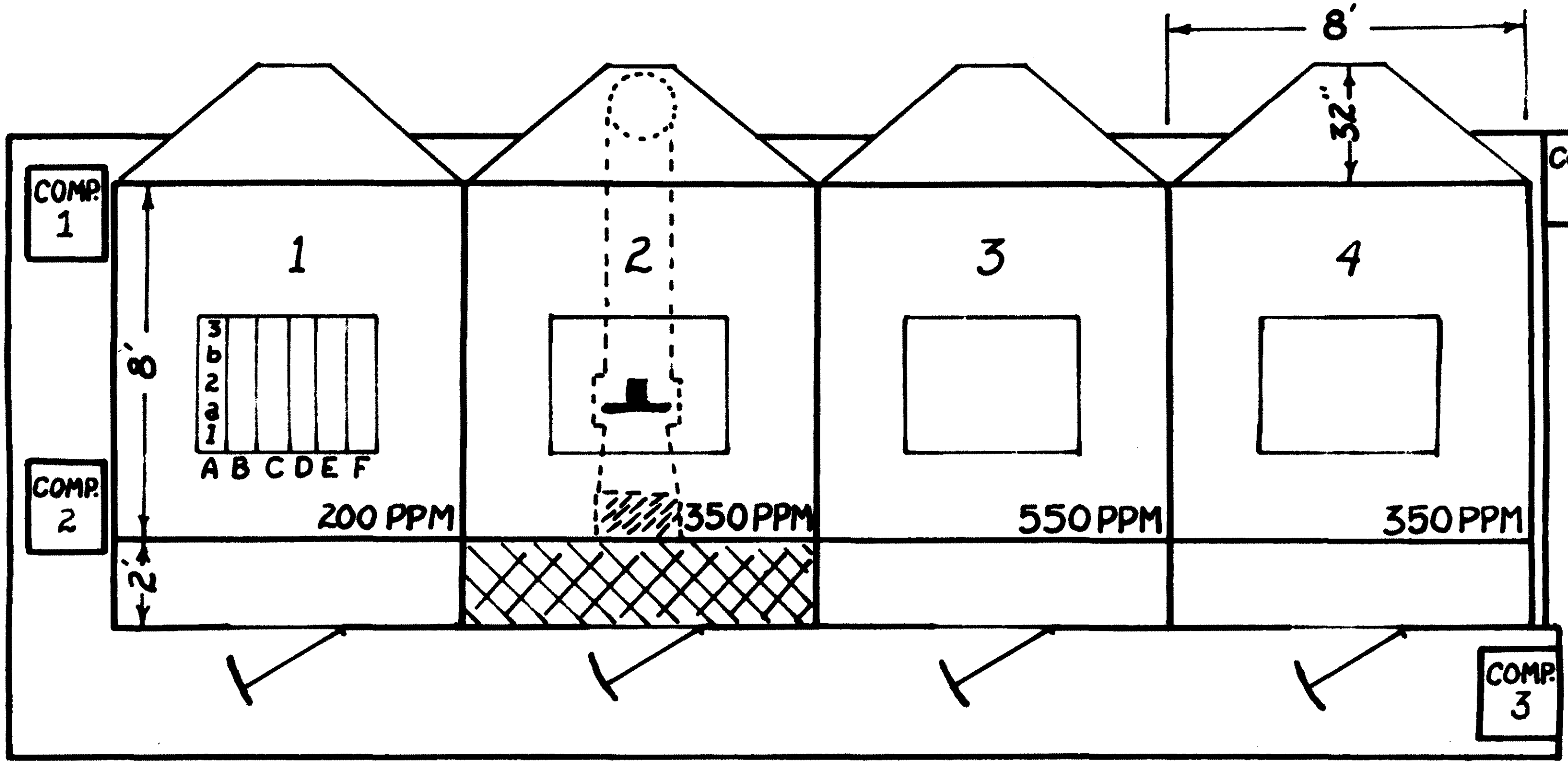


Figure 3.--Floor plan of carbon dioxide chambers; chamber 1, planting system; chamber 2, duct system.

plastic which was used to inclose each chamber. The chambers were constructed so that they were nearly air tight.

Cooling system.--Each chamber contained a duct system for recirculating and cooling air. The recirculating system consisted of a return air manifold on the rear of each chamber, which collected the air and conducted it through an 18 inch round duct, across the evaporative coil and into a plenum. The plenum, containing louvers, distributed the air into the main chamber area (Figures 3 and 4).

The air was circulated by a unit consisting of a 1/4 hp. motor and 20 inch cast alluminum fan with three blades capable of moving free air at the rate of 4400 CFM. In this installation, the air change in the chamber was approximately 2200 CFM and produced an air flow of 130 FPM over the plants.

The cooling system consisted of a two-hp. compressor and a two-ton evaporative coil charged with freon refrigerant. Temperature could be maintained as low as 53° F on the brightest days.

Carbon dioxide injection system.--The carbon dioxide for this investigation was obtained from a dry ice convertor which was installed in a remote part of the greenhouse range. A 1/4 inch O.D. copper tube

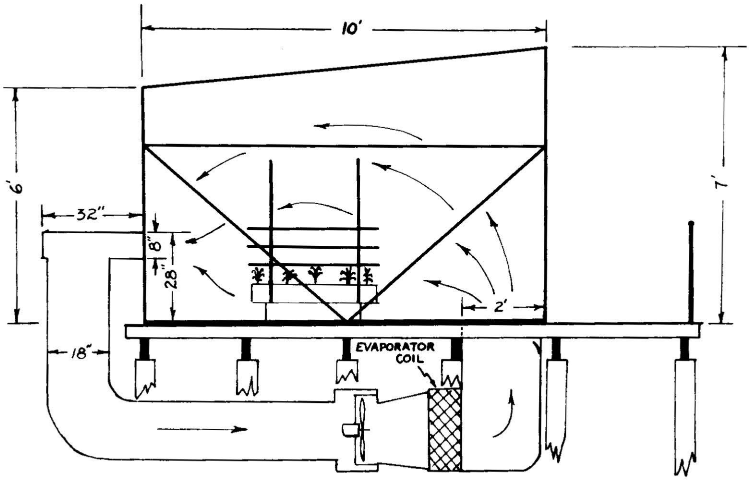


Figure 4.--Side view of carbon dioxide chamber.

Figure 5.--Colorado State University carbon dioxide chambers.

transported the carbon dioxide from the convertor to a central pressure regulator and then into a manifold where four separate flow meter systems, consisting of jars of water, distributed the gas to the ducts of the individual chambers. The concentration of carbon dioxide in each chamber was controlled by observing the recorder and manually regulating the rate of carbon dioxide bubbling through the jars of water. When the proper concentrations were obtained the pressure regulator was used to evenly increase or decrease the carbon dioxide flow during variable light periods (Figure 6).

Plant environment within the chamber

Temperature.--Each chamber was maintained at a 65° F temperature throughout daylight hours. During the night the cooling system was turned off, doors opened and the temperature allowed to fall to approximately 52° F, the temperature maintained in the greenhouse surrounding the chambers.

Light.--Light levels were dependent upon climatic influences, thus solar energy was one of the factors that could not be controlled. On bright sunny days the light levels were equal to approximately 80 per cent of the light outside the greenhouse range. On

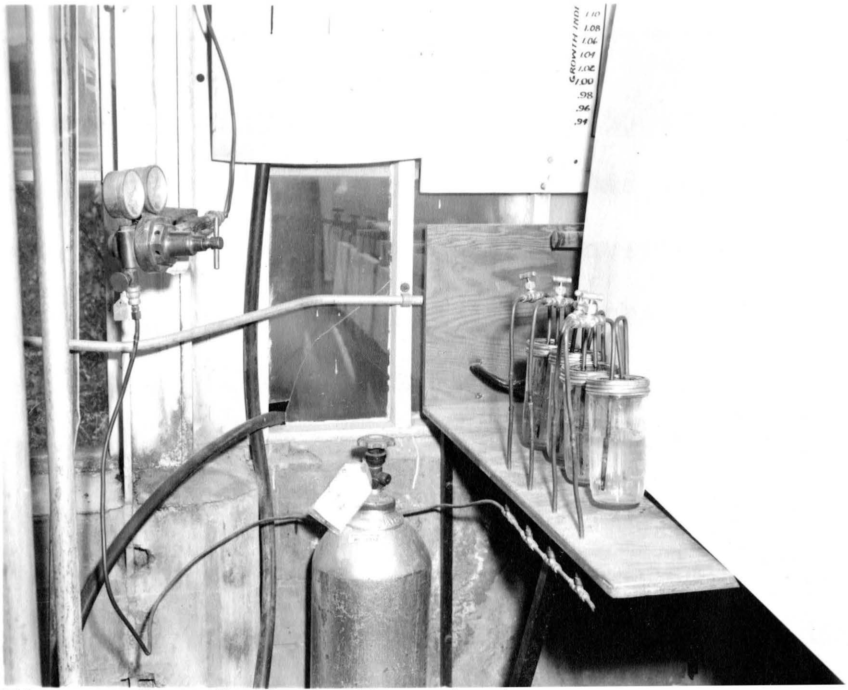
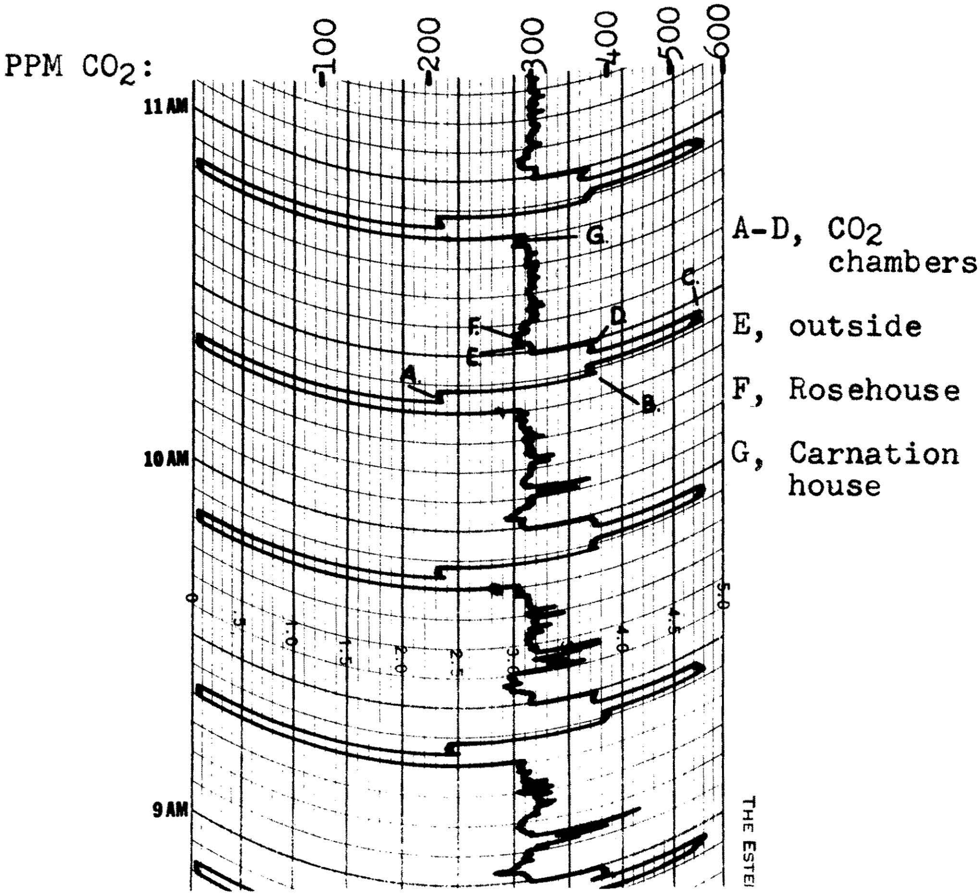


Figure 6.--Carbon dioxide injection system.

Figure 7.--Chart section from carbon dioxide recorder.



cloudy days the light level was only 55 to 60 per cent of the outside light. Each chamber had relatively equal amounts of light during the entire investigation.

Humidity.--Humidity in the chamber varied with the age of the plants. Six months after planting, the relative humidity during the day averaged 43 per cent in all chambers. After the plants were one year old the relative humidity increased to approximately 67 per cent. When the doors were opened after dark, the humidity equalized with the surrounding greenhouse.

Carbon dioxide levels.--The carbon dioxide concentrations maintained in this investigation were based upon preliminary work conducted following the completion of the control chamber construction. The following concentrations were manually controlled as closely as possibly: chamber 1, 200 ppm; chamber 2, 350 ppm; chamber 3, 550 ppm; and chamber 4, 350 ppm, a check on chamber 2. With the exception of small variations due to periodic cloud formations, the above levels were maintained proportionally during daylight hours (Figure 7). The carbon dioxide levels were brought into equilibrium with the greenhouse surrounding the chambers at night when the doors were opened. This level varied from 350 to 450 ppm depending on the amount and size of the vegetation present.

Growing media.--Within each chamber there were six fiberglass lined boxes designated as A, B, C, D, E, and F (Figure 3). Each box was 36 by 8 by 6 inches and contained a volcanic scoria media. Volcanic scoria, which is a completely inert material, allowed perfect control of the plant nutrient requirements while limiting excess amounts of evolved carbon dioxide. The boxes were steamed and care was taken not to recontaminate them during planting.

Watering.--Watering intervals were determined by the condition of the plants. When the plants in any one chamber showed the first signs of wilting all chambers were watered.

Nutrition.--Preliminary work indicated that plants grown in higher carbon dioxide concentrations required increased nutrients. Plants in all chambers were fertilized with an automatic fertilizer injection system each time they were watered. The following nutrient concentrations were applied at each watering: Nitrogen 187 ppm; Potassium 210 ppm; Phosphorous 150 ppm; Magnesium 18 ppm; Iron 3 ppm; and Borax 1-1/2 ppm. Other minor elements were available in the tap water.

Experiment

Each box within the four chambers was planted to five rooted cuttings of the carnation variety Red Gayety on May 28, 1960 (Figure 3). They were designated as 1, a, 2, b, and 3. These cuttings were taken from Colorado State University's foundation stock. After planting, an air sampling lead from the analyzer was placed above the plants so that the desired carbon dioxide level of the air passing over the plants could be measured and maintained. All plants were pinched once within 23 to 28 days after planting.

To establish a trend of plant response to the various carbon dioxide concentrations, plant "a" was removed from each box on July 30, 1960 and analyzed. Plants "b" were harvested September 10, 1960 and analyzed. The remaining three plants in all boxes (1, 2, 3) were grown for further records (Figure 3).

Measurements

The following measurements were used to evaluate the effects of atmospheric fertilization of carbon dioxide on carnation growth:

The yield of flowers harvested between September 7, 1960 and the termination date, June 2, 1961, was recorded.

Lateral growths were removed and all flowers were weighed to the nearest gram immediately after they were cut.

Stem length was measured in inches from the top of the blossom to the end of the cut stem.

All the flowers produced from September 7, 1960 through April 24, 1961 were dried for three days at 180° F and weighed on a torsion balance. Percentage of dry matter was then calculated.

A weight per inch of stem was calculated for the flowers cut from September 7, 1960 to April 24, 1961.

The internodes between the first and second as well as the fourth and fifth pairs of leaves below the calyx were measured from February 21, 1961 through May 1, 1961.

Cut flower life was measured from May 5, 1961 through June 2, 1961. Immediately after harvest all flower stems were cut to 18 inches in length and placed in tap water to which 100 ppm chlorine was added. The flowers were then placed in a compartment at a temperature of 70° F ± 1° and a relative humidity of approximately 65 per cent. When a blossom lost its "crispness" to the touch and began to wither, it was removed and one day subtracted from the actual number of days it was in the keeping room. A mean was computed for each sample.

Rate of crop return was estimated by tagging the remaining lateral growths left on the stems after each flower was cut.

Three 25-gram samples of young vegetative breaks were taken from all four chambers for sugar analysis during the second week of May. Chromatographic methods and techniques developed by the American Crystal Sugar Company were utilized to estimate the sucrose and fructose sugar content of the samples.

Chapter IV

RESULTS

The first section of the results shows relations between carbon dioxide concentrations found in the greenhouse and outside meteorological conditions. The second section covers the influence of controlled atmospheric fertilization of carbon dioxide on carnations grown in chambers.

Carbon dioxide concentrations

Atmospheric levels.--The outside carbon dioxide levels in Figures 8 and 9 show that atmospheric carbon dioxide concentrations vary from hour to hour during a given day as well as from day to day. The peak periods on both days were possibly caused by changes in wind direction, automobile traffic, or the operation of the boiler at the research greenhouses. Average carbon dioxide concentrations during daylight have varied from 207 ppm to 362 ppm during the investigation.

Meteorological influences.--Figure 10 indicates the relationship between solar energy, mean temperature and carbon dioxide outside the greenhouse to

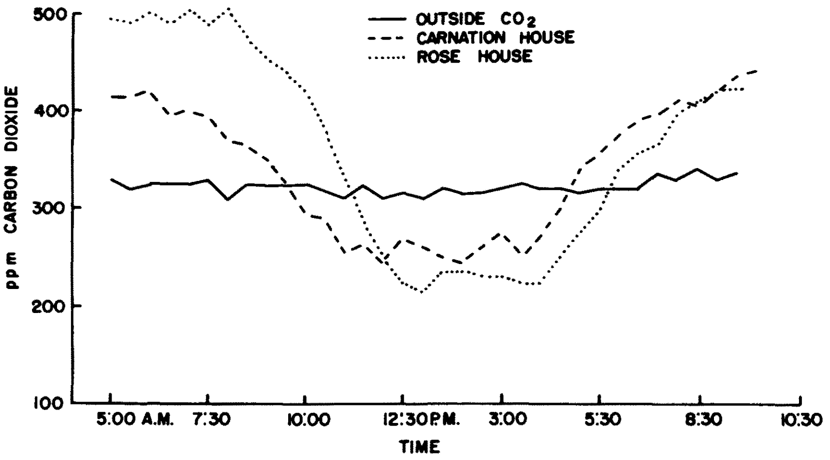


Figure 8.--Hourly carbon dioxide levels in carnation and rose greenhousea, and outside atmosphere on February 10, 1960, with 127 gm cal/cm^2 of light, and a mean temperature of 29.4° F.

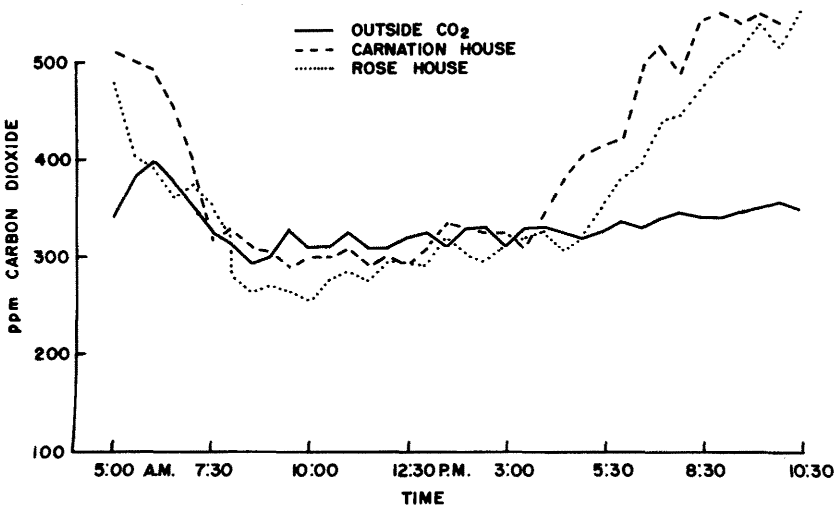


Figure 9.--Hourly carbon dioxide levels in carnation and rose greenhouses, and outside atmosphere on October 2, 1960, with 394 gm cal/cm^2 of light, and a mean temperature of 54.0° F.

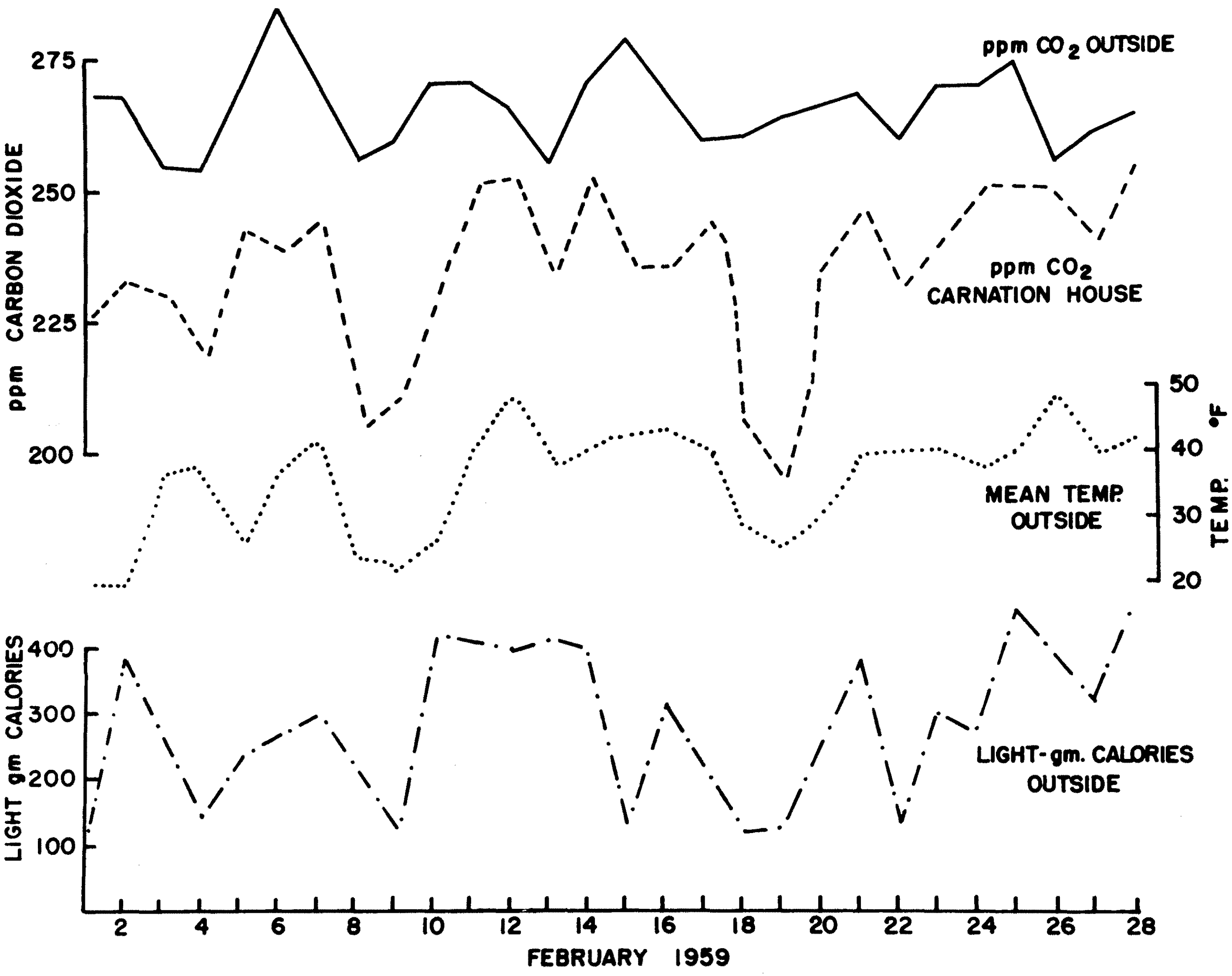


Figure 10.--Correlation between carbon dioxide levels in a carnation greenhouse and meteorological influences.

the carbon dioxide concentrations in a greenhouse containing flowering carnation plants.

February 8 was a day of relatively low light and a mean temperature below 30° F. Radiant energy was insufficient to cause the fan ventilating system to function. Even though the light was low, photosynthesis continued and the carbon dioxide level in the house decreased and remained below the concentration outside the greenhouse.

On February 12 light and temperature were high and the carbon dioxide level in the greenhouse approached the outside level. In this case the heat load was sufficient to start automatic ventilating, pulling fresh air into the house and raising the carbon dioxide concentration around the plants.

Effects of low light in rose and carnation houses.--Carbon dioxide levels in a carnation house vary somewhat from those in a rose house. Figure 8 illustrates their relationship on February 10, 1960, with a total of 127 gram calories/cm^2 of solar energy and an outside mean temperature of 29.4° F.

It is evident that the rise in the carbon dioxide level in the carnation house at 11:30 AM was due to the operation of the fan ventilating system for a short period of time. Even though there was very little direct sun on this date the fans functioned again at 12:30 PM and from 2:00 PM to 3:00 PM. From this time on, probably respiration surpassed carbon dioxide assimilation.

The rose house, which has top vents, was not ventilated until 1:00 PM. The degree of opening was enough to allow an adequate amount of outside air to enter and raise the carbon dioxide level. Since the outside temperature was below 30° F and the required temperature in the rose house was the main consideration, the vent could not be opened too wide. From 1:30 PM until 4:00 PM the carbon dioxide level remained fairly constant, increasing at 4:00 PM when respiration apparently exceeded assimilation.

Effects of high light in rose and carnation houses.--Figure 9 shows the effects of higher solar energy in the same carnation and rose houses on October 2, 1960. The total amount of solar energy was 394 gram calories/cm^2 and the mean outside temperature 54° F.

The fan ventilating system in the carnation house started functioning about 8:00 AM and continued to run until 12:30 PM. At this time heavy cloud formations started developing, causing the fans to stop and carbon dioxide assimilation to decrease. By 2:00 PM the heavy cloud formation had passed and assimilation gradually increased until 3:30 PM, when respiration evidently surpassed carbon dioxide assimilation.

The rose house vents were opened at 8:00 AM allowing carbon dioxide to remain relatively constant until 10:00 AM. At this time the vents were opened wider and the carbon dioxide level approached that of the outside atmosphere. The cloud formation at 12:30 PM caused a slight decrease in carbon dioxide assimilation followed by a greater increase than that observed in the carnation house. This condition is no doubt related to the difference in leaf area and growth rates of the two plants.

Influences of increased carbon dioxide concentrations

Young plants.--Rooted cuttings of the carnation variety Red Gayety were planted May 28, 1960, and grown for 9 and 15 weeks before harvesting for fresh and dry weights. The reaction of these young plants to increased carbon dioxide concentrations is presented in Table 1. An increase in production of dry matter and in percentage of dry matter was indicated when carbon dioxide concentration was increased from 200 to 550 ppm. The percentage of dry matter was higher and showed larger differences as carbon dioxide levels increased, for the September harvest date than six weeks earlier.

Table 1.--SUMMARY OF FRESH AND DRY WEIGHTS AND PERCENTAGE OF DRY MATTER FROM YOUNG RED GAYETY CARNATION PLANTS GROWN AT DIFFERENT CARBON DIOXIDE LEVELS.

	PPM Carbon dioxide concentrations			
	200	350	350	550
Nine weeks after planting				
Mean fresh wt. (grams)	65.5	69.6	79.0	80.3
Mean dry wt. (grams)	9.7	11.0	13.9	13.5
Per cent dry matter	14.7	15.8	17.5	16.8
Fifteen weeks after planting				
Mean fresh wt.	208.0	222.5	218.0	242.0
Mean dry wt.	38.9	46.7	45.1	55.3
Per cent dry matter	18.7	20.9	20.7	22.8

Producing plants.--The effects of increased carbon dioxide on producing plants are summarized in Figure 11, and in Tables 2 and 3.

The accumulative yield by monthly periods (Table 2) indicates a definite relationship to increases in carbon dioxide. The 200 ppm level continuously produced less flowers than any other chamber. The production of the 350 and 550 ppm levels remained similar until the end of February. From this point on, the 550 ppm level showed greater differences in yield. There was a slight variation in percentage of malformed flowers as the carbon dioxide levels were increased.

Table 2.--EFFECTS OF INCREASED CARBON DIOXIDE ON YIELD OF RED GAYETY CARNATIONS.

	PPM Carbon dioxide concentrations			
	200	350	350	550
Accumulative yield for months ending:				
September 30, 1960	16	35	44	43
October 31, 1960	73	83	82	83
November 30, 1960	91	94	91	93
December 31, 1960	105	129	139	151
January 31, 1961	153	201	224	236
February 28, 1961	218	272	296	302
March 31, 1961	274	330	346	368
April 30, 1961	324	401	390	436
May 31, 1961	378	490	477	517
Total yield through June 2	381	494	482	521
Per cent malformed flowers	3.94	5.46	7.05	5.57
Speed of crop return				
Mid-point of first crop (1960)	Oct. 17	Oct. 6	Oct. 3	Oct. 3
Mid-point of second crop (1961)	Mar. 2	Feb. 21	Feb. 11	Feb. 16

By tagging the remaining laterals, as the first crop was cut, production mid-points of first and second crops could be established. While there was virtually no difference between the mid-points of either crop grown in the 350 and 550 ppm carbon dioxide levels, the 200 ppm level was approximately two weeks behind the other two levels in both the first and second crops.

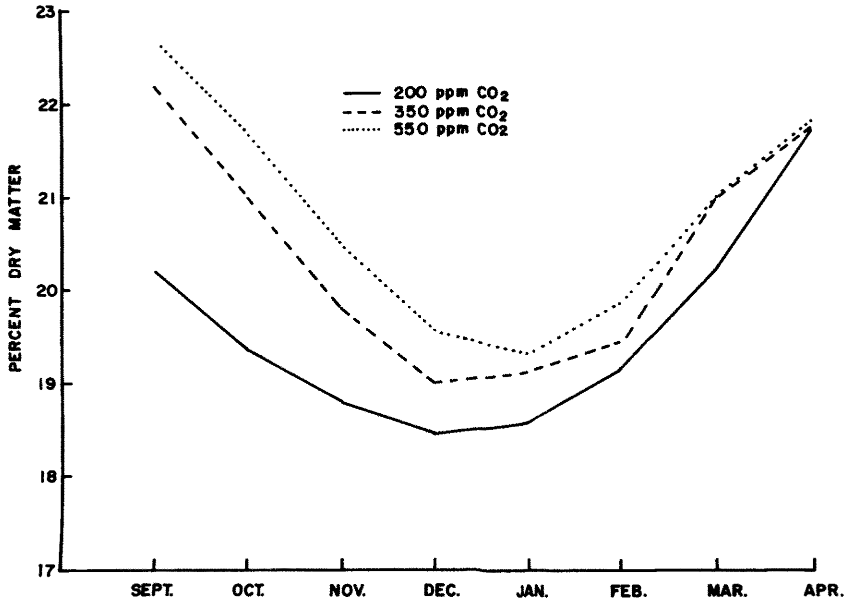


Figure 11.--Monthly percentage of dry matter from flowers produced in three levels of carbon dioxide.

The effects of the three levels of carbon dioxide on several physical measurements of the cut flowers are summarized in Table 3. While the differences in stem length were small, the relationship was inverse. Flower stems produced in the 200 ppm level were consistently longer than those produced by 350 and 550 ppm.

The fresh and dry weights of the flowers were approximately the same in all carbon dioxide levels. Flowers produced with 200 ppm of carbon dioxide had greater fresh and dry weight during the first five months. During the last three months mean fresh and dry weights were greater in 350 and 550 ppm levels.

A graph of the monthly percentage of dry matter from the flowers produced in the three levels of carbon dioxide is shown in Figure 11. The curves show typical reduced dry matter percentages in mid-winter and consistent differences between the levels. The dry matter percentage over the 8-month period averaged about one per cent greater for 550 ppm when compared to 200 ppm, with 350 ppm being intermediate (Table 3).

The second and fifth internodes were measured on flowers cut between February 21, and May 1. Measurements taken at the second internode correlated closely with the total length of the flower (Table 3). When carbon dioxide increased the internode length decreased. Measurements of the fifth internode produced opposite results. As carbon dioxide increased the internode increased. Thus, length lost in one internode was gained in another. The average length of the second plus the fifth internodes was similar in all carbon dioxide concentrations.

Table 3.--SUMMARY OF THE EFFECTS OF INCREASED CARBON DIOXIDE CONCENTRATIONS ON SOME PHYSICAL MEASUREMENTS OF CARNATION CUT FLOWERS.

	PPM Carbon dioxide concentrations			
	200	350	350	550
Mean length of flowers in inches. Sept. 7, 1960 to April 24, 1961.	27.8	26.0	26.1	25.6
Mean fresh weight of flowers in grams. Sept. 7, 1960 to April 24, 1961.	31.2	30.8	30.4	31.0
Per cent dry matter of flowers. Sept. 7, 1960 to April 24, 1961.	19.7	20.5	20.3	20.7
Internode length of flowers in centimeters. Feb. 21 to May 1.				
Second internode	3.7	3.0	3.0	2.7
Fifth internode	10.4	11.0	11.2	11.5
Total	14.1	14.0	14.2	14.2
Keeping quality in days. May 5 to June 2.				
Cut every second day	10.2	10.2	10.5	10.0
Cut every third day	10.1	10.0	10.6	10.3

Cut flower life was measured in a controlled room from May 5, to June 2. The differences due to carbon dioxide concentrations were so small that they are insignificant. Furthermore, there were no differences in keeping life of flowers cut on two or three-day intervals from the various carbon dioxide concentrations.

The amounts of sucrose and fructose in vegetative growths taken from each carbon dioxide concentration were measured chromatographically. The amounts of these sugars appeared to be the same in the 200, 350 and 550 ppm concentrations.

Chapter V

DISCUSSION

Most researchers working with increased concentrations of carbon dioxide on plants have found that there is a definite increase in fruit or flower production, total dry matter and time of flowering (9, 21, 28, 33, 37, 43). This investigation showed similar effects on carnations.

It has also been noted (20, 24, 25, 36) that decreases in light, temperature, and carbon dioxide concentrations below 300 ppm retard carbon dioxide assimilation, thus the per cent dry matter.

By correlating the above factors in the environmental complex with the results of this investigation, there is probably a range in per cent dry matter required by a carnation plant in order to be reproductive.

The most outstanding results of this investigation were the effects of carbon dioxide concentration on carnation production and rate of crop return. The plants grown in the 200 ppm level were apparently using most of the available carbon dioxide for carbohydrates to develop flowers and less for vegetative growth. This would account for the lower total production and lengthened interval between crops. The plants grown in the 350 and 550 ppm carbon dioxide concentrations had sufficient carbohydrates available for rapid flower production and heavy vegetative growth which correlates with the increased total production and shorter time interval between crops. Therefore, under constant light values and constant temperature, lower carbon dioxide concentrations in the environmental complex will cause plants to be slower in gaining the required amount of dry matter to complete flower development.

The results also indicated that there were actually no differences between the quality of flowers produced in the 200 ppm concentration and those produced in the 350 ppm or 550 ppm levels. Since the plant environment within the chambers did not change abruptly during the investigation, the results in keeping quality must have been due to the uniform light, humidity, and temperature conditions existing from hour to hour and day to day. It is conceivable at this point that the flowers in all concentrations were in the same stage of development. Even though the ones from the 200 ppm carbon dioxide level may have taken 10 days to two weeks longer to reach maturity.

Carbon dioxide levels in the greenhouse are greatly influenced by outside climatic conditions. Figures 8 and 9 show a definite relationship between outside temperature, solar energy and carbon dioxide concentrations in the greenhouse. In commercial carnation ranges, the delay in flowering has been attributed to periods of low light due to cloudy weather. A close study of Figure 10 and the results from the carbon dioxide fertilization investigation indicates that low carbon dioxide concentrations can also be limiting to crop production. Higher yields could be obtained by better control of the carbon dioxide level throughout the periods of low light. Carbon dioxide levels equal to or higher than outside concentrations could be maintained by more efficient use of the fan ventilating system (Figure 9), or additions of carbon dioxide.

Suggestions for further study

The results of this investigation have created a deeper interest in the relationship of carbon dioxide to the rest of the environmental complex. Thus the author feels that the following investigations should be conducted:

Determine the optimum temperatures required for growing plants in higher carbon dioxide concentrations.

Investigate the effects of various light levels with a constant carbon dioxide level and optimum temperatures.

Investigate the relationship between relative humidity and carbon dioxide assimilation.

Investigate the rate of air flow needed in the greenhouse to maintain a narrow carbon dioxide gradient between the plant and air.

Investigate the effects of soil respiration on the carbon dioxide concentrations existing in the greenhouse.

Investigate the effects of increased carbon dioxide concentrations on production of cuttings in increase blocks.

Investigate the influences of increased carbon dioxide on the rooting of cuttings and their subsequent recovery following propagation.

Chapter VI

SUMMARY

A carbon dioxide analyzing system consisting of a Beckman infrared analyzer and amplifier, a recorder, and a multiple port selector valve was installed in the research greenhouses. It was used to record continuously carbon dioxide concentrations throughout the greenhouse range and help maintain established levels of carbon dioxide in controlled chambers.

Carbon dioxide concentrations in carnation and rose greenhouses dropped below 225 ppm on days of cold cloudy weather when there was no ventilation. Ventilating on warmer days increased the carbon dioxide concentration to near that of outside atmospheric levels.

Four chambers of polyvinyl plastic were cooled by refrigeration and the air continuously recirculated. Each chamber had a constant temperature of 65° F and an air flow of 130 FPM across the plants during daylight hours. At night the temperature dropped to approximately 52° F when the doors were opened and the recirculating air system turned off. Light levels were dependent upon climatic influences. Carbon dioxide concentrations were controlled as closely as possible during daylight hours at 200, 350, and 550 ppm.

The following responses were observed on Red Gayety carnations as carbon dioxide concentrations increased:

Higher yields,

A shorter time interval between crops harvested in the 350 and 550 ppm levels than in the 200 ppm concentration,

Decreased length of stems,

Approximately equal fresh and dry weights,

Increased percentage of dry matter,

Shorter second internodes and longer fifth internodes,

Similar amounts of sucrose and fructose, and

Similar keeping quality.

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Abstract of Thesis

THE EFFECTS OF CARBON DIOXIDE ON CARNATION GROWTH

In the past five years, much progress has been made in the control of greenhouse environment. With the advent of automation for heating and air conditioning, fertilizer injection systems, automatic watering systems and increased light due to various types of greenhouse construction, near optimum relationships have resulted within the environmental complex and have led to increased production and quality. It is quite possible that further increases in plant growth may be obtained by atmospheric fertilization with carbon dioxide, thus bringing into equipoise the environmental complex.

Carbon dioxide is one of the least considered factors in plant growth by most researchers, although some realize its very definite importance to the environmental complex. Several investigators have increased the carbon dioxide concentration of the atmosphere surrounding plants with positive results of increased plant growth. Other investigators have reported no increase in dry matter production from carbon dioxide fertilization.

A carbon dioxide analyzing system consisting of a Beckman infrared analyzer and amplifier, a recorder, and a multiple port selector valve was installed in the research

greenhouses. It was used to record continuously carbon dioxide concentrations throughout the greenhouse range and help maintain established levels of carbon dioxide in controlled chambers.

Carbon dioxide concentrations in carnation and rose greenhouses dropped below 225 ppm on days of cold cloudy weather when there was no ventilation. Ventilating on warmer days increased the carbon dioxide concentration to near that of outside atmospheric levels.

Four chambers of polyvinyl plastic were cooled by refrigeration and the air continuously recirculated. Each chamber had a constant temperature of 65° F and an air flow of 130 FPM across the plants during daylight hours. At night the temperature dropped to approximately 52° F when the doors were opened and the recirculating air system turned off. Light levels were dependent upon climatic influences. Carbon dioxide concentrations were controlled as closely as possible during daylight hours at 200, 350, and 550 ppm.

Rooted cuttings of the carnation variety Red Gayety were planted in the chambers on May 28, 1960 and grown until the termination date, June 2, 1961. The following responses were observed as carbon dioxide concentrations increased:

a. The yields in the 550 ppm were 38 per cent and in the 350 ppm, 30 per cent more than the yield in the 200 ppm concentration.

b. The first and second crops in the 350 and 550 ppm levels flowered 2 weeks ahead of the 200 ppm level.

c. The average stem length in the 550 ppm level was 2 inches shorter and in the 350 ppm level, 1 inch shorter than the stems produced in the 200 ppm level.

d. Approximately equal fresh and dry weights were produced in all levels.

e. The percentage of dry matter increased approximately 0.5 per cent in the 350 ppm level and 1 per cent in the 550 level over the 200 ppm concentration.

f. The second internode decreased and the fifth increased in length as carbon dioxide concentrations increased.

g. There were similar amounts of sucrose and fructose in young vegetative shoots harvested in all 3 concentrations.

h. Flowers harvested from all 3 carbon dioxide concentrations had a keeping life of approximately 10 days.

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