THESIS

CO_2 PROFILES IN THE FIELD AND RESPONSE TO ENRICHED ATMOSPHERES USING STRAWBERRY

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INTRODUCTION

Carbon dioxide availability in many C-3 crop canopies has been found to limit photosynthetic processes under field conditions at current atmospheric concentrations (330 to 345 uL L^{-1}). Research conducted in enclosed environments under low irradiance conditions and under full sunlight, indicate that supplementation of CO_2 concentrations within a crop canopy has the potential for yield enhancement under field conditions. However, development of an efficient method for wide scale CO_2 enrichment of field crops has proven elusive due to excessive loss of added gas to the bulk atmosphere. The objective of this study was to investigate a method of plant canopy enrichment in the open field.

The efficiency of CO_2 enrichment of a crop canopy may depend on the type of gas conveyance and rate of application. Two forms of CO_2 conveyance, CO_2 in gaseous form and CO_2 mixed in water (carbonated water), were evaluated in a field study to test this hypothesis. Carbonated water and three rates of CO_2 gas application were compared for their effectiveness and efficiency in increasing the CO_2 concentration within a strawberry plant canopy. Both water and gas were delivered to the base of strawberry plants via bi-wall drip irrigation tubing laid on top of individual beds extending the entire length of the bed. Previous experimentation by Tarter (1983) demonstrated that a continuous mulch around the base of a plant functioned to delay immediate gas dispersion during ground level application of CO_2 to individual lettuce beds. To test the effect of this delay on CO_2 concentrations within the canopy, CO_2 gas and carbonated water were delivered to unmulched strawberry beds and beds covered with a non-degradable agricultural mulch. The drip tubes were covered by the mulch; the mulch used was a 6-mil black polyethylene film.

Substantial increases in CO_2 concentrations have been measured at the base of plant canopies during ground level CO_2 enrichment, however measurements at higher levels in the canopy reveal a rapid loss of added gas. Dense canopies provide some protection against CO_2 dissipation, and some evidence indicates that more CO_2 added from a ground source can be maintained within low growing plant canopies. Strawberry plant were chosen in this experiment for their low growing dense growth habit and C-3 photosynthetic mechanism. Also, the high cash value of strawberry yield makes these plants a particularly feasible candidate for CO_2 enrichment.

The effect of elevated atmospheric CO_2 concentrations on strawberry plants was evaluated in growth chambers. Vegetative and reproductive parameters were measured during and after growth under CO_2 enrichment. The objective of this second experiment was to evaluate response of strawberry to CO_2 enrichment in controlled environments. Growth chambers were used to maintain constant CO_2 concentrations during an invariable light period (16 hrs) over the course of nine weeks. A day-neutral cultivar was used for its periodic fruiting cycle that is unaffected by day-length. It was assumed that any response to CO_2 enrichment in the low irradiance of the growth chamber (1/13 full sunlight PPFD; Wong, 1985) would also be observed in field conditions where the incident radiation is much higher, provided that adequate nutrition and water are supplied to the plants.

LITERATURE REVIEW

Effects of Rising CO_2 on Climate and Productivity

Carbon release from fossil fuel consumption, devegetation practices, and many industrial processes during the past century has resulted in substantial increases in global CO_2 concentrations (Callender, 1958; Gates, 1983; Rosenberg, 1981; Stuiver, 1978). Current global atmospheric CO_2 concentrations are reported in the range of 330 to 345 uL L^{-1} (Allen, 1979; Detwiler and Hall, 1988; Trabalka et al., 1986). These values are estimated to be 15 to 25% higher than the atmospheric concentrations existing before the 1800's (Callender, 1958; Neftel et al., 1985; Wittwer, 1980), and current records show that concentrations are still increasing. From long term atmospheric testing at the Mauna Loa Observatory in Hawaii, Keeling et al. (1976) found an increase of 0.8 uL L^{-1} CO_2 per year from 1957 to 1971, and atmospheric modellers have predicted greater rates of increase into the 21st centrury even with assumptions of increased combustion efficiency (Dahlman, 1985; Siegenthaler and Oeschger, 1978; Stuiver, 1978).

Prediction of future global CO_2 concentrations range considerably, and depend on estimated energy use growth rates, assumptions concerning combustion efficiency, changes in vegetation masses, and predicted capacities for oceans to sequester CO_2 (Detwiler and Hall, 1988; Gaastra, 1959; Siegenthaler and Oeschger, 1978; Trabalka et al., 1986). At the conservative end, Siegenthahler and Oeschger (1978) estimate that

CO_2 levels will increase by 2.4 uL L^{-1} per year which, after equilibrium time is considered, will result in a doubling of pre-industrial CO_2 levels as late as the year 2480. In contrast, Baes et al. (1976) predicted a doubling of pre-industrial levels around the year 2025, peaking at about 1300 uL L^{-1}. At the extreme, Keeling et al. (1982) predicted global CO_2 levels to peak in the range of 7 to 8 times the assumed 1860 value of 295 uL L^{-1}. In reviewing much of the literature prior to 1986, Trabalka et al. (1986), found CO_2 concentrations predictions ranging from 500 uL L^{-1} to 1500 uL L^{-1} by the year 2080 depending on rate of fossil fuel consumption and carbon exchange between the atmosphere and the biosphere. Although, the outlooks vary, it is generally accepted that CO_2 levels will rise with the current rate of carbon release from industrial processes.

Environmental and ecological changes are inevitable responses to the most conservative estimates of future CO_2 concentrations (Detwiler and Hall, 1988; Menabe and Wetherald, 1975; Wittwer, 1986). Specifically, the effects of rising CO_2 levels are predicted to have impacts on agriculture through changes in world climate and plant productivity (Dahlman, 1985; Gaastra, 1959, Gates, 1983; Waggoner, 1984; Wittwer, 1980; Zelitch, 1982).

The CO_2 concentration in the global atmosphere plays an integral role in the dynamics of heat exchange between the earth's surface, the upper atmosphere, and outer space. Carbon dioxide allows the wavelenths of light from solar radiation to pass through but is largely opaque to wavelengths in the thermal bands. The solar energy that is radiated from the earth as heat is absorbed by CO_2 and other gases in the atmosphere. This heat is in turn radiated back to the earth's surface causing surface heating in addition to the initial heating from direct solar incidence. The secondary heating attributed to these atmospheric gases is popularly known as the "greenhouse effect", and it is generally accepted that the present rate of global atmospheric CO_2 concentration increase will intensify the heating associated with this phenomenon. Such addtional heating can cause increases in the earth's surface temperatures when the heat build-up exceeds global heat capacity (Allen, 1979, Kimball and Idso, 1983, Menabe and Wetherald, 1975, 1975, Wittwer, 1980). With the most extreme estimates of CO_2 increases and accompanying heat accumulation, earth temperatures are predicted to rise enough to change meterological cycles that could result in significant shifts in agricultural production regions (Waggoner, 1984; Wittwer, 1980; Zelitch, 1982).

Although temperature increases are universally predicted, there is a whole spectrum of predictions concerning the extent of these increases. In 1896 Arrhenius was the first to do extensive calculations in this area, and he estimated that an increase as large as 8 K could result from a doubling of the CO_2 content of the global atmosphere (from 300 to 600 uL L^{-1}) (Kimball and Idso, 1983). Later predictions from more refined mechanistic models are much smaller for the same atmospheric CO_2 increase (Dahlman, 1985). Menabe and Wetherald (1975) employed a 3-dimensional circulation model to predict a 2 to 3 K rise in earth surface temperature in response to CO_2 doubling. By 1980, the consensus in temperature increase predictions was in the range of 2 to 4 K (Wittwer, 1980). However, two separate studies, one published in 1979 (Newell and Dopplick, 1979), the other in 1980 (Idso, 1980), produced a common estimate of a temperature increase less than or equal to 0.25 K at twice the current CO_2 concentration. The models from these studies incorporated two new factors, one to account for the radiation perturbation that would accompany a doubling of atmospheric CO_2, and the other to account for effects of seasonal and humidity changes on the rate of thermal radiation from the earth's surface.

Since no climatic changes over the past century have been conclusively linked to increases in global CO_2, more recent less drastic predictions seem to reflect real world evidence much better than the extreme forcasts of the older models (Waggoner, 1984; Wittwer, 1980; Zelitch, 1982). For the most part, climatologists are beginning to moderate predictions of large scale climate changes, and they do not now anticipate the massively destructive shifts in agricultural production as they did when the problem was first confronted (Cooper, 1978). Currently proposed increases in earth surface temperature will most likely result in decreased rainfall, alteration in length of growing seasons, and more variability in temperature and percipitaion cycles (Allen, 1979; Kimball and Idso, 1983; Waggoner, 1984; Wittwer, 1980).

For some time, plant researchers have been focusing on the potential for greater crop yields under atmospheric CO_2 concentration higher than current global levels. Predicted plant responses to raised CO_2 concentrations generated from enrichment studies include increases in net photosynthesis and whole plant dry weight, accelerated flower and fruit production, increases in fruit number and size, increases in water use efficiency, and changes in carbohydrate partitioning (Allen, 1979; Baker and Enoch, 1983; Cure and Acock, 1986; Dahlman, 1985; Kimball, 1983; Kimball and Idso, 1983; Pearcy and Bjorkman, 1983; Reynolds and Acock, 1985; Rosenberg, 1981). Much of the recent work has been in response to a call for research by the U.S. Department of Energy to investigate the effect of increasing global CO_2 concentrations and predicted climatic change on plant growth and agricultural productivity (United States Department of Energy, 1984).

In a comprehensive review of CO_2 enrichment studies on 37 horticultural species, B.A. Kimball (1983) determined from 430 observations that a CO_2 concentration twice the current global level (about 660 uL L^{-1}) would produce a 33% increase in overall agricultural yield. In a more recent survey, Cure and Acock (1986) predicted that a doubling of global CO_2 concentration would result in an average yield increase of 41%. In comparing response of C-3 and C-4 crops, Cure and Acock determined that C-3 plants would contribute more to increases in agricultural yield than C-4 plants. From an evaluation of eight C-3 crops and two C-4 agronomic crops, they concluded that both C-3 and C-4 crops would contribute to the estimated 23% decrease in transpiration with a doubling of global CO_2 levels. In another review, Rosenberg (1981) predicted that most of the productivity increase in response to rising global CO_2 levels will be contributed by C-3 plants as opposed to C-4 plants. Rosenberg emphasized the benefits of reduced transpiration and photorespiration in increasing overall agricultural yield.

The majority of the first enrichment studies were short-term. Newer long-term enrichment projects indicate possible inhibition of photosynthesis reactions and increased senescence in plants acclimated to higher than present CO_2 levels (Omer and Horvath, 1983; Peet, 1986; Pearcy and Bjorkman, 1983, , 1984; Sasek et al., 1985). Such evidence is beginning to indicate more complex plant responses to predicted future CO_2 levels than was initially anticipated. Subsequently, there is a need to conduct long-term enrichment experiments under field conditions to more accurately assess the potential effects of global CO_2 increases.

Plant Response to CO_2 Enrichment

The basic process governing plant productivity is net photosynthesis, and CO_2 is a principle substrate in this process (Kimball, 1983; Pearcy and Bjorkman, 1983; Zelitch, 1982). Subsequently, increased productivity under CO_2 enrichment is primarily affected by a net increase in carbon assimilation. On the short-term, photosynthesis of C-3 plants has been shown to linearly increase with increases in CO_2 concentrations from 200 to 800 uL L^{-1} in the plant environment (Allen, 1979; Bierhuizen and Slayter, 1964; Pearcy and Bjorkman, 1983; Rosenberg, 1981). However, plant photosynthetic response to carbon dioxide is also dependent upon the level of the two other factors necessary for photosynthesis, irradiance and water. The response is then modified either directly or indirectly by a variety of environmental factors alone and interactively. Furthermore, photosynthetic response to elevated levels of CO_2 is complicated by plant species. It is generally accepted among plant physiologists and biochemists that present ambient CO_2 levels are not sufficient to saturate C-3 photosynthesis. Increased atmospheric CO_2 produces effects even when the supply of other resources are suboptimal to photosynthesis and growth (Bonner, 1962; Gifford, 1979; Hopen and Ries, 1962; Hurd, 1968; Radin and Ackerson, 1981; Wittwer, 1970).

Irradiance Levels and CO_2 Enrichment

Radiation in the range of 400 to 700 nm (photosynthetic photon flux density - PPFD) fuels the electron transport process in the photosynthetic mechanism. Variation PPFD intensity has direct effects on net CO_2 uptake (Bonner, 1962; Bierhuizen and Slayter, 1964; Brun and Cooper, 1967; Dietz, 1986; Eng et al., 1985; Hesketh and Moss, 1963; Macdowall, 1983; Moss et al., 1961, Sionit et al., 1982; Von Caemmerer and Farquhar, 1981). However, the interaction between irradiance and CO_2 is greater in C-3 plants than C-4 plants, because the Kranz anatomy facilitates more efficient CO_2 uptake in C-4 plants (Dietz, 1986; Ehleringer, 1979; Ehleringer and Bjorkman, 1977; Sionit et al., 1981).

Photosynthetic enhancement in C-3 plants under elevated CO_2 has been found to be significantly increased by supplemental radiation (Eng et al., 1985; Kendall et al., 1985; Macdowall, 1983; Wong et al., 1985). Furthermore, Egli et al. (1970) found that whole soybean plants grown in above ambient CO_2 concentrations (up to 1000 uL L^{-1}) were not light saturated under field irradiance conditions in July. These findings indicate that photosynthetic mechanisms are neither saturated by irradiance levels nor CO_2 concentrations under field conditions. Irradiances less than one-fifth full sunlight have been found to limit photosynthesis under CO_2 enrichment (Gaastra, 1959; Pearcy and Bjorkman, 1983). Brun and Cooper (1967) found virtually no photosynthetic increase in soybean leaflets exposed to 2910 lux (according to Hanan, 1984, about 3% maximum illumination at sea level) when CO_2 concentrations were raised from 200 to 1000 uL L^{-1}, but photosynthesis jumped 10 fold when leaflets in 1000 uL L^{-1} CO_2 were exposed to 75,000 lux (75% of maximum illumination at sea level).

In a more recent study, Dietz (1986) evaluated percent limitation of photosynthesis by broad spectrum fluence rates and CO_2 in individual leaves of two C-3 plants. In this study, the author found that at a low fluence rate (12.5 $W\ m^{-2}$), photosynthesis in spinach plants exposed to 500 to 1500 $uL\ L^{-1}$ CO_2 was limited by approximately 90 to 100% by fluence rate, and photosynthesis of plants exposed to 330 to 500 $uL\ L^{-1}$ CO_2 under the same low fluence rates showed a 75 to 90% limitation by fluence rate. At 400 $W\ m^{-2}$, the highest fluence rate tested, and 1500 $uL\ L^{-1}$ CO_2, photosynthesis of a C-3 plant was limited to a greater extent by CO_2 concentration (67%) than by fluence rate (33%). Additionally, Dietz found that photosynthesis of sunflower plants exposed to full sunlight was 35% limited by light and 65% limited by CO_2. From these findings and results from a shade adapted species and a C-4 species, Dietz concluded that photosynthesis in C-3 plants adapted to full sunlight are more limited by CO_2 than irradiance.

Other authors have found CO_2 to be more limiting than irradiance to the growth of C-3 crop species (Bonner, 1962, Kendall et al., 1985; Kramer. 1981; Krizek et al., 1974; Zelitch, 1982). Hesketh et al. (1984), quantified the relationship between light (radiation in the visible spectrum) and CO_2 usage for several C-3 species; they found a four-fold increase in plant response to an added increment of CO_2 as compared to an added increment of illumination. Macdowall (1972) determined that CO_2 enrichment stimulated growth of 'Marquis' wheat by increasing the efficiency of PPFD use, which indicates that CO_2 was the limiting factor in the growth response.

Perhaps the most convincing evidence in support of CO_2 as the predominant limiting factor in photosynthesis is that significant increases in growth and photosynthesis have been recorded in C-3 plants during CO_2 enrichment at irradiances much below those of natural sunlight (Bierhuizen and Slayter, 1964; Hurd, 1968; Hopen and Ries, 1962; Macdowall, 1983). Under low irradiances, it is most likely that raised CO_2 levels are sufficient to prevent a carbon drain by suppressing photorespiration, rather than enhancing gross CO_2 uptake (Ehleringer and Bjorkman, 1977; Ehleringer, 1979; Jolliffe and Tregunna, 1968).

Transpiration, Water Stress and CO_2 Enrichment

Transpiration and CO_2 uptake rates are inherently linked to CO_2 concentrations surrounding a plant and within intercellular spaces of a leaf because these factors control the supply of and demand for CO_2 (Farquhar and Sharkey, 1982). High CO_2 concentration increases leaf resistance to passage of water vapor and CO_2 by its regulatory effect on stomatal aperture (Raschke, 1975). Stomatal resistance, however, has been found to limit transpiration to a greater extent than carbon uptake (Farquhar and Sharkey, 1982). This appears to be the explanation for the findings of improved water use efficiency (WUE) under conditions of CO_2 enrichment. Water use efficiency is the ratio of CO_2 assimilation to the amount of water lost in transpiration, and WUE is often expressed as the amount of net gain in biomass for the amount of water lost over a given period of time (Wittwer, 1986).

Water use efficiency increases have been recorded in several species in response to CO_2 enrichment. These increases have been attributed primarily to reduced transpiration in some cases and increased CO_2 assimilation in others (Gifford, 1979; Kimball and Idso, 1983; Moss et al., 1961; Pearcy and Bjorkman, 1983; Rogers et al., 1984;

Valle et al., 1985a). Valle et al. (1985a) found that WUE of soybean leaflets at 660 uL L^{-1} was about twice that of leaflets under 330 uL L^{-1} CO_2. The authors attributed this to an increase in CER (carbon exchange rate) or net photosynthesis rather than a decrease in transpiration. However, other researchers have measured reductions in transpiration and/or leaf conductance in response to CO_2 enrichment (Akita and Moss, 1972; Moss et al., 1961; Pallas, 1965; Sionit et al, 1984; Tolbert, 1983, Wong 1985). For example, Jones et al. (1985a) recorded a 1.6-fold increase in canopy resistance to transpiration accompanied by about the same increase in CER when soybean plants were enriched in the field. Pallas (1965) reported a 68% reduction in transpiration of two C-4 plants (corn and sorghum) in response to 400 to 500 uL L^{-1} CO_2 and reductions from 21 to 53% in various C-3 plants. Generally reductions in transpiration recorded in C-4 plants are not accompanied by substantial increases in CER whereas, CER are usually greatly enhanced in C-3 plants. Consequently, greater increases in water use efficiency is more often found in C-3 plants than C-4 plants under CO_2 enrichment (Bazzaz and Carlson, 1984; Pearcy and Bjorkman, 1983).

A particularly beneficial aspect of CO_2 enrichment is the maintenance of higher photosynthesis and productivity levels of plants under water stress (Bazzaz and Carlson, 1984; Gifford, 1979; Huber et al., 1984; Pearcy and Bjorkman, 1983; Rogers et al, 1984; Sionit and Patterson, 1985; Valle et al., 1985). Sionit et al. (1980) found that CO_2 enriched wheat plants (1000 uL L^{-1} CO_2) yielded no less under water stress than unstressed wheat plants at ambient CO_2 concentrations. On the other hand, Gifford (1979) found that a reduction in water supplied to wheat plants resulted in smaller yield increases during CO_2

enrichment than when adequate water was supplied to the plants during CO_2 enrichment. However, water stressed plants exposed to CO_2 enrichment yielded more grain than water stressed plants exposed to ambient concentrations. A similar response was recorded in a natural plant community, in which C-3 plant biomass increased as CO_2 concentrations were raised from 300 to 1200 uL L^{-1} despite low soil water potentials (Bazzaz and Carlson, 1984). Tolley and Strain (1985) found that water stress was delayed in pine seedlings enriched with 1000 uL L^{-1} by reduction of stomatal conductance, and as a result seedlings exposed to a drying cycle photosynthesized at a higher rate during the cycle than unenriched controls. Such evidence indicates that CO_2 enrichment has some capacity to compensate for the lack of water availability and the effects of water stress.

Lower leaf water potentials have been found during CO_2 enrichment due to reduced transpiration (Rogers et al., 1984). It has been suggested that this occurrence may indirectly influence photosynthesis by decreasing leaf rolling and other stress responses when water availability is low (Kimball, 1983; Pearcy and Bjorkman, 1983). Additionally it has been proposed that increased CER associated with CO_2 enrichment can lead to higher carbohydrate concentrations and reduced osmotic potentials also resulting in lower leaf water potentials (Berkowitz and Gibbs, 1983; Ehleringer and Cook, 1984; Pearcy and Bjorkman, 1983; Rogers et al., 1984). Researchers also suggest that CO_2 enrichment could increase soil water use by stimulating root growth and subsequently water uptake (Acock and Pasternak, 1986; Baker and Enoch, 1983; Kimball, 1986; Wittwer, 1970).

Carbon dioxide enrichment can reduce the effects of low water availability by influencing stomatal aperture, but water stress inhibits some photosynthetic mechanisms that are unrelated to stomatal aperture and subsequently not affected by CO_2 enrichment (Berkowitz and Gibbs, 1983; Farquhar and Sharkey, 1982; Hanson and Hitz, 1982). In addition, stomata are more sensitive to closure in response to elevated CO_2 when the plant is under water stress (Radin and Ackerson, 1981). However, under conditions of suboptimal soil water availability, CO_2 enrichment reduces transpiration slowing the decrease in plant water potential and delaying the onset of stress response (Allen, 1979; Hanson and Hitz, 1982; Kimball and Idso, 1983; Sionit and Patterson, 1985; Wray and Strain, 1986).

Temperature and CO_2 Enrichment

Temperature is another factor that modifies the photosynthetic response to elevated CO_2 concentrations (Jollife and Tregunna, 1968; Pearcy and Bjorkman, 1983; Sharpe, 1983; Valle et al., 1985; Von Caemmerer and Farquhar, 1981). Leaf temperature both affects and is effected by stomatal resistance, and therefore also influences transpiration rate and WUE (Hanson and Hitz, 1982; Idso et al., 1987; Kimball, 1986; Pearcy Bjorkman, 1983; Raschke, 1975; Valle et al., 1985). Stomatal response to leaf temperature and CO_2 varies among species and environmental conditions, and both decreases and increases in stomatal aperture and transpiration have been observed under CO_2 enrichment in response to increasing leaf temperatures (Hallgren et al., 1982; Keys et al., 1973; Ku and Hunt, 1977).

Jones et al. (1984) measured a decrease in WUE within a soybean canopy in response to a controlled air temperature elevation from 28 to 35 C. despite CO_2 enrichment. This was attributed to an increase in transpiration rather than a depression of photosynthesis. Raschke (1975) reported in a review that the response of CO_2 assimilation to temperature was directly related to stomatal aperture such that at temperature optima for photosynthesis stomata are completely opened. Raschke further determined that when temperatures are optimum for photosynthesis, stomata are less susceptible to closure under high CO_2 concentrations. Findings by Sionit et al. (1984) support this; these authors recorded a smaller reduction in soybean stomatal conductance of CO_2 enriched plants than those grown at ambient concentrations when atmospheric temperature was increased from 20 C to 35 C.

Temperature regulation of stomatal conductivity has been found to be secondary to the regulatory effect of temperature on activity of ribulose bisphosphate carboxylase oxygenase, the enzyme that controls rates of photosynthesis and photorespiration (Pearcy and Bjorkman, 1983). Temperature, therefore directly influences the net uptake of CO_2 and thereby influences plant yield responses to CO_2 enrichment (Calvert and Slack, 1975; Idso, 1980; Krizek et al., 1974; Ku and Hunt, 1977; Zelitch, 1982). Net photosynthesis of C-3 plants is particularly sensitive to the interaction of temperature and CO_2 concentration due to the occurrence of photorespiration (Ehleringer and Bjorkman, 1977; Ehleringer, 1979; Jolliffe and Tregunna, 1968).

The benefit of CO_2 enrichment to C-3 plant species is generally greater at higher than optimum temperatures than at temperatures lower than optima for photosynthesis. Higher than optimum temperatures increase the O_2/CO_2 ratio in the chloroplasts. This results in a loss of CO_2 fixation due to greater O_2 fixation by ribulose bisphosphate carboxylase oxygenase in the photorespiration process. Carbon dioxide enrichment decreases the rate of O_2 fixation by increasing the amount of CO_2 available for fixation by ribulose bisphosphate carboxylase oxygenase (Salisbury and Ross, 1985). Additionally, it is unlikely that CO_2 enrichment would increase gross photosynthetic uptake significantly at temperatures much higher or lower than optimum, so any increase in net photosynthesis in such conditions would probably be due to decreases in photorespiratory loss of CO_2 fixation (Jolliffe and Tregunna, 1968; Pearcy and Bjorkman, 1983; Sharpe, 1983).

Calvert (1972) found that tomato plants yielded more fruit under the highest day/night temperatures tested (22 C/ 20 C) when the greenhouse atmosphere was enriched with CO_2. Krizek et al. (1974) determined that temperature was the greatest limiting factor in lettuce seedling growth, and the dry weight of vegetable seedlings grown at 2000 uL L^{-1} increased the most at the highest treatment temperatures (30 C day/24 C night). Carbon dioxide enrichment can compensate for the loss of carbon through photorespiration at higher temperatures, but little to no interaction has been discovered between CO_2 enrichment and low temperatures (Pearcy and Bjorkman, 1983).

Different Responses of C-4 and C-3 Plants to CO_2 Enrichment

Biochemical and morphological differences cause C-3 and C-4 plants to respond differently to CO_2 enrichment (Akita and Moss, 1972; Allen, 1979; Bazzaz and Carlson, 1984; Ehleringer and Bjorkman, 1977; Ehleringer, 1979; Kramer, 1981; Patterson and Flint, 1980; Patterson et al., 1984; Zelitch, 1982). Carbon dioxide enrichment generally results in larger net gains in carbon fixation and biomass production in C-3 plants than C-4 plants (Bazzaz and Carlson, 1984; Idso, 1980, Kimball and Idso, 1983; Kramer, 1981; Marc and Gifford, 1983; Patterson and Flint, 1980; Wittwer and Robb, 1963; Wong, 1979). Much of this difference may be attributed to the compartmentalization of CO_2 uptake facilitated by the Kranz anatomy in C-4 plants that is not present in C-3 plants. Photosynthetic processes are carried out in the bundle sheath cells, whereas mechanisms to provide CO_2 for these processes function in the mesophyll cells. Carbon dioxide is constantly being shunted via organic acids from the mesophyll cells to the bundle sheath cells. This process functions to maintain a large enough concentration difference between the intercellular spaces of the mesophyll cells and outside atmosphere to insure a steady influx of CO_2 under ambient atmospheric CO_2 concentrations. This influx has been found to provide enough CO_2 for saturation of ribulose bisphosphate carboxylase in the bundle sheath cells when ambient CO_2 concentrations are within the range of average levels. Consequently, CO_2 is almost totally eliminated as a limiting factor in C-4 photosynthesis under ambient CO_2 concentrations. Without this compartmentalization, the amount of CO_2 available to ribulose bisphosphate carboxylase oxygenase in C-3 plants is not high enough to prevent fixation of O_2 in the photorespiratory process and the corresponding loss of CO_2 fixation (Salisbury and Ross, 1985). Higher CO_2 levels during enrichment increase the CO_2 available for fixation, reducing photorespiration in C-3 plants and subsequently enhancing net photosynthesis. In contrast, ambient CO_2 concentrations are high enough to prevent photorespiratory loss of CO_2 fixation in C-4 plants, such that net photosynthesis is not affected by CO_2 enrichment (Ehleringer and Bjorkman, 1977; Jolliffe and Tregunna, 1968; Tolbert, 1983).

Wong (1979) recorded a two-fold increase in dry weight of cotton, a C-3 plant in response to 660 uL L^{-1} CO_2 for 40 days as compared to a 20% increase in corn, a C-4 plant. Patterson et al. (1984) found a similar response of two C-4 and two C-3 plants grown under 600 and 1000 uL L^{-1} for 45 days. The two C-3 plants, soybean and velvet leaf showed an average increase in dry weight of 71% and 42% respectively to CO_2 enrichment, while corn, one of the C-4 plants, showed a slight decrease for both 1000 and 600 uL L^{-1}. The other C-4 plant, itchgrass, a weed, showed a significant increase in dry weight of about 49% at 600 uL L^{-1} CO_2 but no further increases at 1000 uL L^{-1} CO_2. Patterson et al. (1984) concluded that increases in global CO_2 levels should cause C-3 plants to be more competitive for resources than C-4 plants. Other authors found that C-4 plant photosynthetic rates were saturated at CO_2 concentrations only slightly above ambient level, and they determined that C-4 photosynthesis was minimally affected by CO_2 enrichment (Moss et al., 1961; Sionit et al., 1982;). Bazzaz and Carlson (1984) found that CO_2 enrichment of a native plant community stimulated the growth of C-3 species more than that of the C-4 species in the community. However, C-4 species were found to be more competitive for nutrients and light than C-3 species exposed to ambient CO_2 concentrations and low soil moisture. Generally, C-4 plants benefit from reduced transpiration and water loss in response to CO_2 enrichment, with very little net gain in carbon uptake, whereas, the benefit to C-3 plants is increase in net photosynthesis with concomitant decreases in transpiration (Akita and

Moss, 1972; Allen, 1979; Cure and Acock, 1986; Sionit and Patterson, 1985).

The stomata of C-4 plants have been found to be more prone to closure under high CO_2 than C-3 plants explaining the lower level of transpiration in C-4 plants (Akita and Moss, 1972; Dubbe et al., 1978; Goudriaan and van Laar, 1978; Kramer, 1981). In addition, C-4 plants were found to close their stomata faster than C-3 plants in response to rising CO_2 concentrations. Akita and Moss (1972) concluded that the greater stomatal sensitivity to CO_2 facilitates better water control in C-4 plants than C-3 plants. Morison and Gifford (1983) found no evidence that stomata of C-4 plants were more sensitive to CO_2 in the atmosphere around a leaf than stomata of C-3 plants. They instead attributed the different stomatal responses to changes in intercellular CO_2 resulting from different rates of CO_2 assimilation. Despite their different conclusions concerning stomatal mechanism, both Morison and Gifford and Akita and Moss attributed their findings of greater WUE in C-3 species under CO_2 enrichment primarily to net photosynthetic enhancement.

Translocation and Stage Specific Effects of CO_2 Enrichment

Overall increases in net photosynthesis have been well documented for C-3 plants exposed to short-term CO_2 enrichment (Allen, 1979; Kimball, 1983; Kramer, 1981; Pearcy and Bjorkman, 1983; Rosenberg, 1981; Waggoner, 1984; Zelitch, 1982). However, plant response to long-term or continual enrichment is complicated by fluctuations in environmental conditions and availability of growth requirements which can alter photosynthetic rates. Furthermore, permanent growth responses can be complicated by changes in allocation of assimilated carbon and variation in the demand for these assimilates over the course of the plant's development (Baker and Enoch, 1983; Jones et al., 1985; Mauney et al., 1979; Wong, 1979). Carbon dioxide enrichment has been found to cause accumulation of starch in the chloroplasts when assimilate demands are low resulting in feedback inhibition of photosynthetic mechanisms and subsequent reductions in net gain of photosynthate (Peet et al., 1986; , 1984; Sasek et al., 1985; Tolbert, 1983). The chances of enrichment affecting such inhibition is higher during long-term CO_2 enrichment. Some effects of CO_2 enrichment over entire growth cycles are acceleration in whole plant senescence, alteration in reproductive development and changes in fruit number and size (Baker and Enoch, 1983; Bhattacharya et al., 1985; Hesketh and Hellmers, 1973; Marc and Gifford, 1983; Omer and Horvath; 1983). Researchers are just beginning to explore stage specific responses to CO_2 enrichment, and they are finding the existence of critical periods for certain CO_2 enrichment responses (Baker and Enoch, 1983; Baysdorfer and Bassham, 1985; Bhattacharya et al., 1985).

Carbon dioxide enrichment contributes to development rate, size, and yield of non-photosynthetic plant organs by increasing photosynthate supply. However, the transfer of the photosynthate to these organs is controlled by many factors and it is not necessarily directly related to CO_2 assimilation rate or supply of photosynthate (Baker and Enoch, 1983; Gent, 1984). Ho (1977) showed a positive relationship between increases in CO_2 concentration and translocation in tomato plants. Gent (1984) discovered the same relationship during CO_2 enrichment of tomato plants. Increases in total non-structural carbohydrate in whole tomato plants were strongly correlated to increases in translocation and relative growth rate (RGR). On the other hand, Huber et. al. (1984, 1984a) found no increase in translocatable sucrose, only an accumulation of starch in soybean plants, and subsequently no change in assimilate export in response to long-term CO_2 enrichment.

Several researchers have found an accumulation of starch in association with decreased photosynthesis rates under high CO_2 concentrations (Gent, 1984; Huber et al., 1984; Peet et al., 1986; Thomas et al., 1975). When the starch is converted to sucrose or other soluble sugars the feedback inhibition has been found to be relieved by export of accumulated photosynthate (Baker and Enoch, 1983; Huber et al, 1984; Jones et al., 1985). This generally happens when there is a demand for the exported assimilate in the form of rapidly growing vegetative organs or newly formed reproductive sinks (Sasek et al., 1985). Baysdorfer and Bassham (1985) concluded that the lack of photosynthate demand or sink strength limited photosynthetic response and dry matter accumulation in mature alfalfa plants exposed to high CO_2 concentrations. However, the greater response from seedlings was attributed to the greater demand for assimilates from the rapidly growing leaves and stems.

Clough et al. (1981) found that photosynthetic rates of high sink soybean plants (21 pods) was consistently higher than those of low sink plants (six pods) under long-term exposure to CO_2 enrichment (32 days at 1000 uL L^{-1} CO_2). Havelka et al. (1984) recorded a rapid depletion of carbohydrates accumulated during 22 days of CO_2 enrichment (1200 uL L^{-1}) at the onset of flowering in soybeans, indicating a delay in translocation until a sink was developed. These authors, however, did not find a lowering of net photosynthesis with increased carbohydrate accumulation.

Mauney et al. (1979) attributed the lack of significant decreases in cotton leaf photosynthesis with starch accumulation under high CO_2 to compensation of the inhibitory effects of starch accumulation by the increased supply of CO_2.

Several authors have observed that both net photosynthesis and dry weight accumulation decreases under prolonged exposure of plants to high levels of CO_2 enrichment; this is often referred to as CO_2 acclimation (Aoki and Yabuki, 1977; Baysdorfer and Bassham, 1985; Clough et al., 1981; Hickleton and Jolliffe, 1978; Peet et al., 1986; Porter and Grodzinski, 1984; Rogers et al., 1984a; Sasek et al., 1985; Tolbert, 1983). Despite the occurrence of CO_2 acclimation and feedback inhibition, there is a large body of literature that documents significant increases in yields and net photosynthesis of seed, leaf, and root C-3 crops in response to CO_2 enrichment lasting 15 days to entire growth periods. For example researchers have recorded whole plant dry weight increases in soybeans (Clough et al., 1981; Cooper and Brun, 1967; Egli et al., 1970; Finn and Brun, 1982; Hardman and Brun, 1971; Rogers et al., 1984a; Sionit et al, 1982), wheat (Havelka et al., 1984; Macdowall, 1972; Neales and Nicholls, 1978; Sionit et al., 1981), in lettuce (Krizek et al., 1974; Wittwer and Robb, 1963), radish, potato (Collins, 1976), and sugar beet (Sionit et al., 1982).

Greater reproductive yields have been recorded in wheat due to increases in grain number (Gifford, 1979; Havelka et al., 1984a; Sionit et al., 1981) and due to increase in grain size (Kendall et al., 1985). In soybean yield increases were due to increases in seed number (Hardmann and Brun, 1971; Havelka et al., 1984; Rogers et al., 1984a), in cotton due to increase in lint per plant (Mauney et al., 1979), in cucumber due to increases in fruit number (Enoch et al., 1976; Peet, 1986), in strawberry due to increase in number and fruit size (Enoch et al., 1976), and in tomato due to number of fruit (Calvert, 1972; Calvert and Slack, 1975; Kimball and Mitchell, 1979; Kretchman and Howlett, 1970; Wittwer and Robb, 1963).

Additionally, increases in net photosynthesis of soybean (Egli et al., 1970; Havelka et al., 1984; Hesketh et al., 1984; Huber et al., 1984; Jones et al., 1985; Rogers et al., 1984a; Sionit et al., 1982; Sionit et al., 1984; Valle et al., 1985), wheat (Macdowall, 1972; Neales and Nicholls, 1978), and cotton (Bierhuizen and Slayter, 1964; Harper et al., 1973) have been found in response to CO_2 concentrations from 500 to 1200 uL L^{-1} both in field and controlled environments. Reversal of CO_2 acclimation has been found to occur when plants developed a high demand for assimilates (Baysdorfer and Bassham, 1985; Havelka et al., 1984; Valle et al., 1985), perhaps explaining the occurrences of net growth increases when plants are exposed to CO_2 enrichment throughout the entire growth period of the plant.

Application of high CO_2 at critical times can enhance vegetative growth, change time of flowering and fruit set, increase number of flowers and viable fruit, and alter partitioning and translocation of photosynthate causing enlargement of each fruit (Hesketh et al., 1973; Kramer, 1981; Marc and Gifford, 1983). The critical times are usually during periods of high assimilate demand such as just after emergence, or at early stages of fruit set and growth when net photosynthesis is less limited by sink capacity (Baysdorfer and Bassham, 1985; Clough et al., 1981; Marc and Gifford, 1983; Tolbert, 1983). Vegetative growth is generally favored when CO_2 enrichment is started at the seedling stage

(Calvert and Slack, 1975; Krizek et al, 1974; Mauney et al., 1979; Sionit et al., 1982). Thomas et. al. (1975) showed that the relative growth rate (RGR) of tobacco seedlings grown under 400 and 1000 uL L^{-1} CO_2 was roughly three times greater than that of mature plants exposed to the two concentrations after transplanting. Rogers et al. (1984a) obtained similar results for soybeans in which RGR was increased over the enrichment interval from five days to two weeks after seeding, but enrichment after two weeks caused no further increase in RGR. Neales and Nicholls (1978) recorded an increase in RGR and net assimilation rate (NAR) in wheat seedlings only up to 10 days after seed germination, and Peet (1986) found that 1000 uL L^{-1} CO_2 did not increase RGR, leaf area, or total biomass in cucumber beyond the first 16 days after seeding. Sionit et. al. (1982) found greater increases in the growth parameters of soybean, sugar beet, radish, and corn when they were enriched at an early stage and the leaves were rapidly growing. Older leaves photosynthesize much less efficiently, resulting in decreases in NAR and increases in leaf thickness (Baker and Enoch, 1983; Hurd, 1968; Mauney et al., 1979; Neales and Nicholls, 1978; Rogers et al., 1984a; Patterson and Flint, 1982; Thomas et al., 1975).

Reproductive growth and development is known to be affected by continuous CO_2 enrichment (Baker and Enoch, 1983, Calvert and Slack, 1975; Kramer, 1981; Tolbert, 1983). The critical enrichment period for advancement of flowering was found to be very specific for wheat, and sunflower (Marc and Gifford, 1983). Flowering was advanced in sunflower when CO_2 was applied from 10 to 7 days before floral initiation, and in wheat within 10 days before formation of double ridges. Any other period of enrichment delayed the rate of primordial differentiation of inflorescence in wheat but had no effect in sunflower. Therefore, continuous CO_2 enrichment over the entire growth period can actually inhibit reproductive development.

Flower bud initiation and anthesis was delayed in soybeans (Rogers et al., 1984), corn, sunflower, cotton, and sorghum (Hesketh and Hellmers, 1973) by CO_2 enrichment over the entire growth period. However, Cooper and Brun (1967) found no change in floral initiation of soybean exposed to whole season enrichment, nor did Thomas et. al. in tobacco (1975). Acceleration of flowering has been recorded in response to whole season enrichment also. Omer and Horvath (1983) showed that both floral initiation and plant senescence of three winter annuals was advanced by up to 15 days when 700 to 2100 uL L^{-1} CO_2 was applied. Cowpeas initiated flowers 10 to 12 days earlier in enriched treatments (675 to 1000 uL L^{-1} over entire growth period) as compared to unenriched controls (Bhattacharya et al., 1985). Enoch et al. (1976) found that strawberry plants of the short-day (a Junebearer) cultivar Tioga enriched at 3000 uL L^{-1} CO_2 flowered about two weeks earlier than unenriched plants. They recorded a trend towards shorter fruit development times and increased early fruit yields. Several authors have recorded a similar advancement in early flower production and first truss yields in tomatoes (Calvert, 1972; Calvert and Slack; 1975, Hickelton and Jolliffe, 1978; Krizek, 1974). The different reproductive responses to either stage specific or entire season CO_2 enrichment may be explained in part by Kramer's (1981) hypothesis that indeterminate plants respond more to CO_2 enrichment than do determinate plants, so responses may vary according to species.

Critical periods of CO_2 enrichment have also been defined for enhancement of fruit set and yield with CO_2 often having the greatest effect on fruit yield when fruit are developing and assimilate demand is high (Baysdorfer and Bassham, 1985; Clough et al., 1981; Kramer, 1981). Kendall et al. (1985) found that grain yields in wheat were only affected by enrichment after anthesis when the heads were beginning to develop. Findings by Ackerson et al. (1984), Egli et al. (1970), and Hardman and Brun (1971) showed consistently that CO_2 enrichment was most effective in increasing soybean seed yield during pod filling. Havelka et al. (1984), however, maintained that rapid depletions of stored leaf carbohydrate and sharp increases in photosynthesis rate in soybean plants indicated that the period of flower bud initiation was the critical period for enhancement of seed yield by CO_2 enrichment. Furthermore, Cock and Yoshida (1973) found that there were two critical periods of CO_2 enrichment influencing rice grain yield. Enrichment before flowering was found to increase grain yield by increasing the number of grains produced by the rice plants. Enrichment after flowering, during grain fill, increased yield by increasing numbers of grain as well as increasing percentage of filled ears and weight of each grain. Plant assimilate demand was found to be the integral factor in rice grain yield increase in response to CO_2 enrichment, but this study indicated that interaction between reproductive development and partitioning of assimilates gained from CO_2 enrichment could be quite complex.

The importance of photosynthate demand was emphasized by Sasek et al. (1985) when he concluded that the development of strong sink strengths could override photosynthetic inhibitions that occur under long-term enrichment. Clough et al. (1981) found that decreasing reproductive sink strength, by removal of soybean pods just after pod set, caused an increase in starch accumulation by vegetative tissue and subsequent reduction of photosynthesis and seed yield. It was concluded from this experiment that CO_2 enrichment is most effective when developing storage tissue provides a sink to prevent photosynthetic inhibition due to starch accumulation in the leaves. The literature supports a positive relationship between sink strength and CO_2 enrichment effectiveness (Baysdorfer and Bassham, 1985; Cock and Yoshida, 1973; Huber et al., 1984; Valle et al., 1985), but there is controversy concerning the developmental stage of greatest assimilate demand. Valle et al. (1985) found that soybean plants utilized elevated levels of CO_2 more efficiently during anthesis, and Ackerson et al. (1984) verified the findings of other authors (Egli et al., 1970, Hardman and Brun, 1971) that CO_2 enrichment is most effective in increasing soybean seed yield when photosynthesis rates are high during grain fill.

The evidence supporting the seed development stage as the critical CO_2 enrichment period for seed yield enhancement is less ambiguous and more common than that in support of the flowering stage. However, this issue has not been adequately resolved. In an AAAS symposium concerning the response of plants to CO_2, Baker and Enoch (1983) emphasized the need for more research to elucidate the effects of permanent global CO_2 enrichment on plant development and productivity.

Greenhouse CO_2 Enrichment

Carbon dioxide enrichment is an economic reality in the greenhouse industry with significant yield increases verified for a variety of horticultural crops in response to increased CO_2 levels in the greenhouse atmosphere (Allen, 1979; Calvert and Slack, 1975; Goldsberry and Holley, 1962; Kimball, 1983; Wittwer and Robb, 1963; Wittwer, 1986). European growers started commercial use of CO_2 enrichment in greenhouses as early as 1931, but it wasn't until the 1960's that the economic benefits of carbon dioxide enrichment were widely accepted (Allen, 1979; Wittwer, 1984). Goldsberry and Holley established the benefits of CO_2 enrichment of flower crops in 1962; they showed significant increases in early flower production, flower size, stem length, flower quality and yield. Wittwer and Robb (1963) conducted the first comprehensive CO_2 enrichment study on food crops, which started a rash of enrichment research on greenhouse grown fruits and vegetables as well as on flowers and foliage plants.

Greenhouse CO_2 levels can drop substantially below outside ambient levels even during ventilation when CO_2 is replenished from the incoming air supply (Goldsberry and Holley, 1962; Hickleton and Jolliffe, 1978; Kimball and Mitchell, 1979; Kimball, 1986; Slack and Hand, 1985). Wittwer and Robb (1963) found CO_2 concentrations as low as 170 uL L^{-1} on a clear cold day in February when the ventilators were closed.

The advantage of CO_2 enrichment is obvious in a closed off greenhouse during a bright day, but loss of added CO_2 to the outside air significantly reduces the profitability of enrichment during ventilation (Kimball and Mitchell, 1979; Slack and Hand, 1985). For this reason, greenhouse enrichment is usually conducted in winter and only in the morning and late afternoon hours during summer when ventilation is unnecessary (Enoch et al., 1976; Kimball and Mitchell, 1979).

In the late 1970's and early 1980's concern for the rising atmospheric CO_2 levels, stimulated a new wave of greenhouse enrichment experiments focused on globally important agronomic crops and natural ecosystems (Allen, 1979; Bazzaz and Carlson, 1984; Kimball and Idso, 1983; Patterson and Flint, 1980; Wittwer, 1986). Much of this change was influenced by the research plan established by the United States Department of Energy (U.S. DOE) to evaluate the impact of rising atmospheric CO_2 concentrations. This plan called for estimation of crop and ecosystem response to CO_2 concentrations twice as high as current levels (Dahlman, 1985).

Several reviews have been published that summarize the results of the many experiments conducted with greenhouse grown crops since 1962 (Allen, 1979; Baker and Enoch, 1983; Cure and Acock, 1986; Kimball, 1983; Rosenberg, 1981; Wittwer, 1986). A wide variety of commercially grown greenhouse crops as well as several field crops have been tested in these reviews. Enrichment concentrations in these studies ranged from just over ambient to 4000 uL L^{-1} CO_2. However, by 1970 it was concluded that concentrations from 1000 to 2000 uL L^{-1} were the most effective and economical for greenhouse enrichment (Kretchman and Howlett, 1970; Wittwer, 1970). Consequently, most greenhouse enrichment research is conducted with CO_2 concentrations of 1000 or lower (Kimball, 1986). The use of concentrations in the 600 to 700 uL L^{-1} started in 1978 as a response to the U.S. DOE research plan (Dahlman, 1985).

Two early research projects that firmly established the yield benefits and feasibility of greenhouse CO_2 enrichment were conducted by

Hopen and Ries in 1962 and Wittwer and Robb in 1963. Prior to this, researchers concentrated on the short-term effects of CO_2 enrichment on photosynthesis and transpiration to establish CO_2 response curves under various environmental conditions (Chapman et al., 1954; Gaastra , 1959; Thomas and Hill, 1949). Hopen and Ries (1962) established the concept of mutual compensation between irradiance and CO_2 on plant growth. It was found that the growth response to high CO_2 increased with increasing irradiance. However, these authors found positive responses under illumination as low as 3500 lux, showing that CO_2 enrichment could produce positive yield responses under the suboptimal irradiances often found in greenhouses. Wittwer and Robb (1963) conducted a thorough assessment of the effects of entire season CO_2 enrichment on several varieties of lettuce, cucumber, and tomato grown in a greenhouse. They showed that reproductive development was advanced, and that fruit yield and quality substantially increased in all cucumber and tomato varieties exposed to the high CO_2 treatment (800 to 1200 $uL\ L^{-1}$). Maturity was accelerated in lettuce with marked increases in head size. By 1970 Wittwer reported that the evidence collected was more than sufficient to prove the effectiveness of greenhouse enrichment.

The focus of enrichment research has now been shifted to experimentation under precisely controlled environments with specific levels of CO_2 and interacting plant growth factors. Various morphological, physiological, and biochemical plant responses to CO_2 enriched atmospheres are being evaluated under such controlled conditions. The data generated is being used to develop optimization models for CO_2 enrichment and to more adequately understand the mechanisms involved in the photosynthetic response to CO_2 concentration (Dahlman, 1985; Gates, 1983; Pallas, 1970; Pearcy and Bjorkman, 1983; Reynolds and Acock, 1985; Enoch and Baker, 1983; Tolbert, 1983).

Field CO_2 Enrichment

Carbon dioxide enrichment has much potential for enhancing yield and general plant vigor in field grown crops because water availability is often limited and incident radiation is minimally obstructed in the field. In addition, the increased availability of CO_2 can counteract the deleterious effects of reduced stomatal aperture and increased maintenance respiration due to high levels of salinity often encountered in field soils (Schwarz and Gale, 1984). Researchers have reported increases in photosynthetic rate and overall yield (Allen et al., 1974; Cock and Yoshida, 1973; Copper and Brun, 1967; Hardman and Brun, 1971; Harper et al., 1973; Havelka et al., 1984, 1984a; Hesketh et al., 1984; Huber et al., 1984, 1984a; Moss et al., 1961; Rogers et al, 1984a; Sionit, 1984; Valle et al., 1985, 1985a) and reductions in transpiration resulting in increased water use efficiency (Moss et al., 1961; Rogers et al., 1984; Sionit, 1985) in response to enrichment under field conditions. Most of these studies were carried out in open topped chambers placed in the field and the techniques used could not be applied to wide scale field enrichment. However, some research has been preformed using methods of direct CO_2 release into field crop canopies (Allen et al., 1971; Allen et al., 1974; Harper et al., 1973; Kretchman and Howlett. 1970; Takami and Van Bavel, 1975, 1975a).

The main limitation on CO_2 enrichment of field air by direct gas release is that imposed by rapid gaseous exchange with the bulk atmosphere. As a result, many researchers have declared wide scale field enrichment to be inefficient and costly under most meteorological and micrometeorological conditions (Allen et al., 1974; Kimball, 1983; Kretchman and Howlett, 1970; Krizek et al., 1974; Montieth et al., 1964). However, some of these researchers drew their conclusions from research with corn canopies. Harper et al. (1973), Takami and Van Bavel (1975a) and Allen et al. (1971) showed that a denser growing C-3 crop canopy was more responsive to field enrichment than was a corn canopy. This can be attributed not only to the greater photosynthetic recovery rate by C-3 plants of CO_2 at enriched concentrations but also to a greater capacity for entrapment of released gas near the photosynthetically active areas of the canopy by lower growing plants. Chang (1968) attributed this greater entrapment capacity by low dense canopied crops to the reduced eddy diffusivities closer to the ground.

Allen et al.(1974) determined that enrichment of a corn canopy was not feasible with a single line source; they found little enrichment benefit 15 meters down wind from single line CO_2 applications as high as 583 kg ha^{-1} hr^{-1} in a corn canopy. They determined that the majority of the added gas was loss to vertical mixing and that dilution from horizontal flow also prevented CO_2 accumulation in the canopy. On the other hand, Harper et al. (1973) found that CO_2 concentrations as high as 450 to 500 uL L^{-1} could be attained at 3/4 plant height (65 cm) in a cotton canopy when 222.6 kg CO_2 ha^{-1} hr^{-1} was applied from a single source via a multiple line ground release system instead of from a single line. The increased availability of CO_2 from this enrichment method was found to result in an average increase of 26% in net photosynthesis and as much as 33% recovery of the added CO_2 by photosynthetic mechanisms of the canopy. Part of the difference between the findings of Harper et al.

and Allen et al. may be attributed to the different wind speed conditions encountered during enrichment in each experiment; wind speeds higher than 2 m s^{-1} were not measured above the cotton canopy, whereas wind speeds as high as 4.8 m s^{-1} were recorded above the corn canopy. Relatively small increases in wind have been found to severely reduce the enrichment effectiveness of added CO_2 gas. Takami and Van Bavel (1975) predicted that recovery of added CO_2 by a Sorghum canopy would be approximately halved by wind speeds increases from 1.0 to 3.0 m s^{-1}. Maximum efficiency of released CO_2 occurs at high irradiances when leaf area and light penetration is maximum (Allen, 1971), and when the atmosphere around the plant is most stable during periods of low wind velocity (below 3.0 m s^{-1}) and minimum canopy to air temperature gradients (Chang, 1968; Harper et al., 1973; Takami and Van Bavel, 1975). Using a simulation model, Allen et al. (1971) predicted an 81% increase in uptake efficiency (increased CO_2 assimilation divided by total added CO_2) of a theoretical C-3 crop during field enrichment with a decrease in wind speed from 6.0 to 1.0 m s^{-1}. The highest enrichment efficiency (10.1) was predicted for a 50 cm high canopy with a leaf area index of 10 and a nearly vertical leaf orientation (80^0 from horizontal) during wind speeds of 1.0 cm s^{-1}.

Pallas (1970) suggested that the efficiency of field enrichment could be greatly improved with CO_2 stagnation systems that minimize the turbulent loss of applied CO_2 from the crop microenvironment. As early as 1963, Sheldrake suggested that continuous black plastic mulch may serve as a barrier trapping CO_2 evolved from soil respiration and funneling it out into the crop canopy through the hole made for the plant. In this way the CO_2 directed into the plant canopy could benefit the crop by increasing the supply of CO_2 for photosynthesis instead of being dispersed in the air above the canopy.

Using drip tube released CO_2 as an enrichment source, Tarter (1983) measured a significant increase in the CO_2 concentration within a dense lettuce canopy when a continuous poly-coated paper mulch was used as a barrier to decrease CO_2 loss. Mulch was particularly suitable as a barrier, because the CO_2 was released from ground level. The mulch was placed directly over the tubes providing an immediate obstruction to gas dispersal after release from the drip tube. Additionally, mulch is economical and frequently used for its advantages to crop growth including weed control, moisture retention, and soil warming (Honma et al., 1959; Hopen and Oekber, 1975).

Nakayama and Bucks (1980) tested a CO_2 enrichment method in which gas was mixed with water and delivered to the root zone through buried drip tubing. These authors measured significant increases in soil CO_2 concentrations around the roots in the application zone of cantaloupe, potato, and wheat crops after 0.5 hours of carbonated water release. This resulted in a significant 20% increase in wheat yield and slight yield increases in both cantaloupe and potato. The yield increases were attributed to a greater availability of micronutrients such as iron, phosphorous, and zinc as well as possible increases in soil water conductance in response to the temporary decreases in soil pH. However, these authors suggested that yield increases could have also been attributed to enhanced CO_2 evolution from the soil resulting from the measured increases in soil CO_2 concentration. On the other hand, Mauney and Hendrix (1988) attributed carbon exchange rate increases in pot-cultured cotton plants irrigated with CO_2 saturated water only to increases in zinc and manganese availability, because none of the labeled carbon from the water appeared in lint samples from the cotton plants.

Carbonated water may be a better source than free gas for aerial enrichment in the field, because CO_2 is retained in water and released over a longer period of time. Subsequently, carbonated water may serve as a longer lasting source of CO_2, perhaps reducing the amount of added gas dispersed into the bulk atmosphere.

Promotion of rooting in woody plant propagation has been recorded when CO_2 mixed in water was delivered directly via mist to the leaves on the cuttings (French and Lin, 1984; Lin and Molnar, 1981; Molnar and Cummings, 1968). French and Lin (1984) attributed increased rooting in English holley cuttings to photosynthesis enhancement by CO_2 delivered in the mist water, as supplementary lighting augmented the rooting response to the carbonated mist. The positive results from such experimentation with carbonated water warrants further research to test the potential of carbonated water as a source for field CO_2 enrichment.

The use of carbonated water in field enrichment may be further justified in species that can benefit from CO_2 + HCO_3^- taken up from the soil solution through roots. However, there is conflicting evidence concerning whether adding CO_2 to the root atmosphere inhibits or stimulates root and/or shoot growth. Arteca et al. (1979) found that the addition of 45% CO_2 and 21% O_2 by volume in an aeration stream to potato roots grown in a nutrient solution culture enhanced both shoot and root growth as well as tuberization. Stolwijk and Thimann (1957), however, found that the growth of Pisum sativum, Vicia Faba, Phaseolus vulgaris, and Helianthus annuus roots were completely inhibited by aeration of the nutrient solution culture with 6.5% CO_2 by volume. On the other hand, Avena sativa and Hordeum vulgare roots were unaffected. Furthermore, aeration of the solution culture with CO_2 concentrations slightly higher than 1% by volume resulted in measurable inhibition of Pisum sativum root growth. The results of this experiment lead the authors to conclude that CO_2 levels in most soils were supra-optimal for plant growth, since roots were found to take up very little added CO_2. However, Baron and Gorski (1986) demonstrated that aeration of a root atmosphere in soil with 15% CO_2 and 21% O_2 by volume significantly increased eggplant dry matter production with no limitation of root growth when CO_2 was applied from mid April to mid May. Since these researchers prevented gas diffusion from the soil to the external atmosphere by sealing the soil surface, the increase in yield could be attributed directly to root uptake and translocation. Part of the differences observed among these three experiments could be attributed to species difference and different proportions of CO_2/HCO_3 in the soil solution as affected by pH (Geisler, 1962).

The different responses observed by Arteca et al. (1979) and Stolwijk and Thimann (1957) to CO_2 concentrations in a root culture aeration stream may be attributed to the different durations of root exposure to the CO_2. Arteca et al. (1979) aerated their potato root media for 12 hours, whereas the roots of the four species tested by Stolwijk and Thimann (1957) were aerated for 10-13 days. Geisler (1962) asserts that influence of CO_2 on root growth is cumulative, therefore, continuous soil CO_2 concentrations greater than 1% by volume may be detrimental to root growth depending on the species. On the other hand, Geisler found that one hour bursts of pure CO_2 injection into aerated water cultures of Pisum sativum accelerated root growth with no detrimental effects recorded. This indicates that short irrigations with carbonated (CO_2 saturated) water may be beneficial to root growth provided CO_2 does not stay in the soil solution too long. However, since Baron and Gorski aerated the eggplant soil atmosphere with O_2 and elevated CO_2 for 23 days, long term CO_2 enrichment of the soil atmosphere with gaseous CO_2 may be more effective than enrichment with CO_2 mixed in water.

Leonard and Pinckard (1946) found that cotton tap root elongation was not inhibited by aeration of solution root media with concentrations as high as 30% CO_2 by volume applied for 24 hours. Although, 10% was found to be optimal for root growth. This optimization was found only when the O_2 concentration in the air stream was held at 21% by volume. Root growth in response to 10% CO_2 by volume progressively declined with decreasing O_2. Low O_2 levels were found to suppress cotton tap root growth particularly under high CO_2 concentrations. Grable and Danielson (1965) found that aeration of soil media with 20% CO_2 by volume was inhibitory to corn root growth only when O_2 was reduced from 21 to 10%. Consequently, O_2 availability in soil solution may be a mitigating factor in the inhibitory affect of CO_2 concentration. Since O_2 concentrations were not reported, part of the root growth inhibition recorded by Stolwijk and Thimann (1957) may have been due to sub-optimal oxygen concentrations in the aeration stream. On the basis of the evidence presented here, it would seem prudent to use CO_2 mixed with air or pure O_2 for soil enrichment, rather than enriching with pure CO_2 gas.

In conducting ^{14}C studies, researchers showed that roots of several species (barley, potato, pea, alfalfa, soybean, sunflower, oat, cotton, snap bean) can take-up and fix CO_2 into various organic acids and sugars independent of photosynthetic mechanisms in the leaves (Arteca et al., 1979; Arteca and Pooviah, 1982; Graf and Aronoff, 1955; Jacobson, 1954). Arteca and Pooviah (1982) found that most of the CO_2 applied to the roots was transported to shoots as malic acid, small amounts of other organic acids and amino acids synthesized in the roots from the CO_2, but that some was transported directly as CO_2. These authors suggested that the free CO_2 and CO_2 from decarboxylation of the malic acid could be fixed by ribulose bisphosphate carboxylase oxygenase in the leaves. Furthermore, Baron and Gorski (1986) and Schaeffer (1988) found labelled photosynthetic products in the leaves after ^{14}C was applied to roots of eggplant and spring wheat respectively. Grable and Danielson (1965) recorded growth increases in both roots and shoots of soybeans when the soil was CO_2 enriched. These studies indicate some sort of transport mechanism that delivers carbon to the leaves where it can be assimilated. However, for the most part enrichment of the root zone has favored root growth over shoot growth indicating that most of the CO_2 taken-up by roots is not translocated and photosynthetically assimilated but instead fixed within the roots (Arteca et al., 1979; Geisler, 1962; Leonard and Pinckard, 1946).

In summary, carbon dioxide enrichment has been shown to increases overall plant productivity, particularly in C-3 plants numerous times under several different environmental conditions. Other effects of CO_2 enrichment reported in this review are reductions in stomatal aperture, increases in water use efficiency, acceleration of plant development and reproduction, changes in translocation and photosynthate partitioning, stimulation and inhibition of root growth, and also both stimulation and inhibition of photosynthesis. Most of these effects were determined under controlled environmental conditions in enclosed structures, but some positive responses were found in dense canopied crops under atmospheric field enrichment.

Continued research is needed to devise methods of field enrichment that effectively reduce CO_2 exchange with the bulk atmosphere. Development of an effective system for field enrichment will enable plant researchers to more adequately predict the effects of anticipated future CO_2 levels on the biosphere. On a more practical level, such systems could be used in crop production to increase yield and conserve water.

The purpose of this research was to compare the effectiveness of carbonated water and gaseous CO_2 application for field enrichment of strawberry plants, and to test an enrichment method that incorporates continuous black polyethylene mulch and drip tubing in a system similar to those used in commercial production.

MATERIALS AND METHODS

Field Experiment

Carbon dioxide concentrations were measured in a strawberry plant canopy to evaluate the enrichment capacity of CO_2 gas and carbonated water application in the field. Three rates of CO_2 gas application 360, 630, and 900 kg ha^{-1} h^{-1} and 420 kg ha^{-1} h^{-1} carried in carbonated water were compared under field conditions. The 420 kg ha^{-1} h^{-1} rate was the estimated amount of CO_2 carried in the carbonated water after release from the pressurized delivery system.

Using methods presented by Takami and Van Bavel (1975), Tarter (1983) calculated that an application of 360 kg CO_2 ha^{-1} h^{-1} from a ground source should produce a concentration of 1000 uL L^{-1} at the base of dense canopied low growing plants. The two higher gas application rates were chosen for comparison and to evaluate the effectiveness and efficiency of increasing CO_2 application. Carbonated water was included in the experiment to assess a delivery medium that retains CO_2 after application to the plant environment.

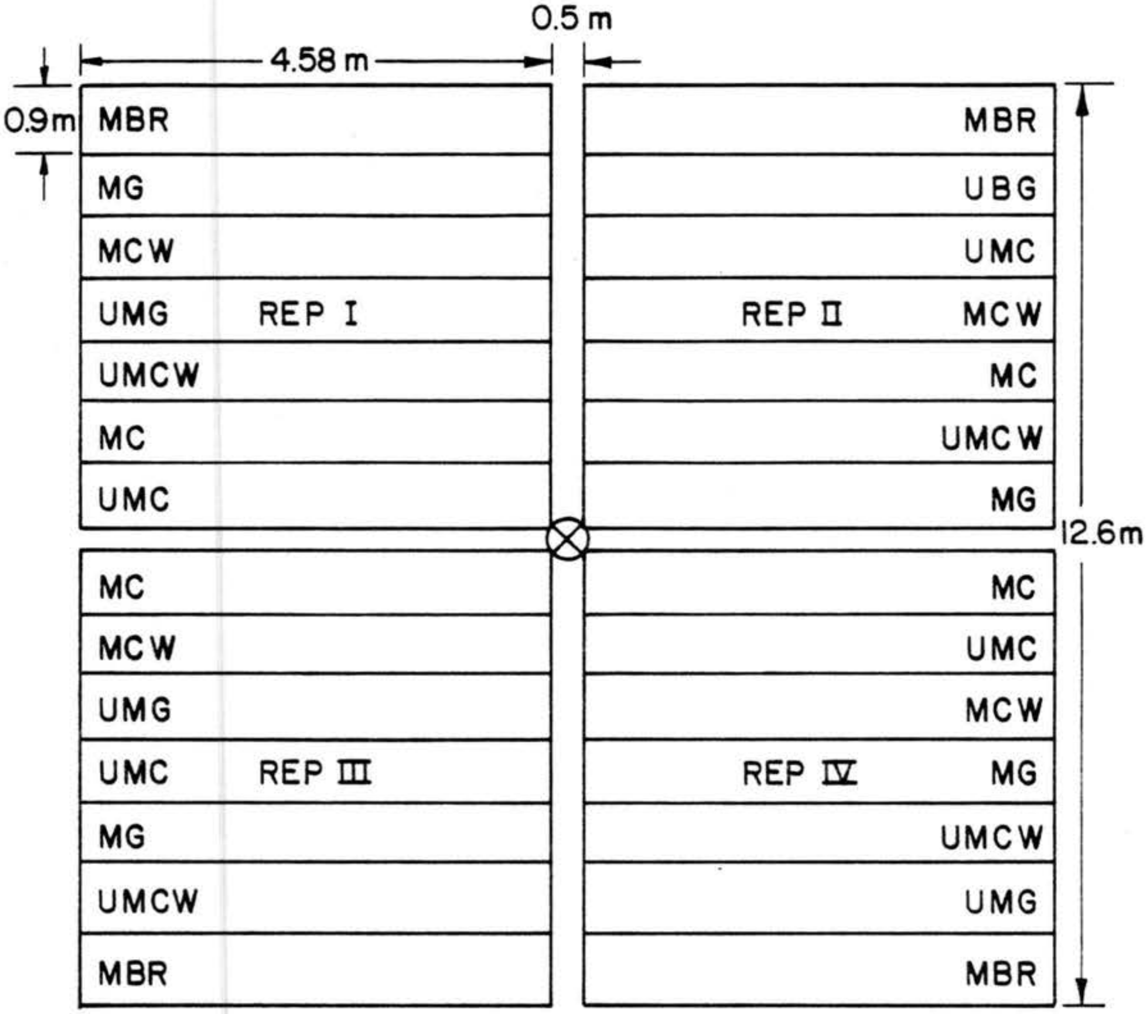
The three gas application rates and carbonated water were delivered via bi-wall drip irrigation tubing laid on top of slightly raised strawberry beds. Carbon dioxide gas and carbonated water were delivered underneath a continuous polyethylene mulch covering or directly to the base of the plants in unmulched beds. Carbon dioxide concentration were measured at 1, 10, and 20 cm above the base of the strawberry plant canopies during CO_2 application to evaluate the vertical distribution of CO_2 added from a ground source. Twenty centimeters was the mean height of the plants, therefore, 10 cm was in the middle of the canopy, and 1 cm was at the base of the plants, close to the point of CO_2 release.

Planting Procedures and Field Design

Strawberry plants (Fragaria x ananassa Duch) of the day neutral cultivar Fern were planted at the Colorado State University Horticulture Research Center on May 7, 1985. The Center is located 13 km (8 miles) northeast of the Colorado State University Campus, and the strawberry experiment plot was surrounded by clean-cultivated areas and irrigated vegetable research plots.

Field preparations of the calcareous Nunn clay loam soil included incorporation of 79 kg ha^{-1} nitrogen and 160 kg ha^{-1} triple superphosphate. Two alternating rows of bare root strawberry transplants were planted on slightly raised 90 cm wide beds. The rows were planted 10 cm apart and the plants within the rows were also spaced at 10 cm. The entire experimental area was 115.4 m^2 with four blocked replications (field plot replications). Each field plot replication consisted of seven east west oriented beds 4.58 m long, containing 90 plants (Figure 1). Three randomly selected beds in each field plot replication, including all of the beds along the perimeter of the entire experimental area were mulched with strips of 6-mil black polyethylene film 1.0 m in width before planting. The mulch was anchored with soil at the sides of the selected beds and plant holes, 6.5 cm in diameter, were cut using a cardboard template to insure consistent spacing. Drip tubes delivering either CO_2 gas or carbonated water were randomly assigned to a mulched

Figure 1. Randomized complete block field design. Randomization of mulched (M) and unmulched (UM) beds recieving CO_2 application as gas (G) and carbonated water (CW) and border rows (BR) within four field plot replications. Pressurized CO_2 cylinder, ⊗. Strawberry field plot, 1986.


0.5 m
4.58 m
0.9m
12.6m
MBR
MG
MCW
UMG
REP I
UMCW
MC
UMC
MBR
UBG
UMC
REP II
MCW
MC
UMCW
MG
MC
MCW
UMG
UMC
REP III
MG
UMCW
MBR
MC
UMC
MCW
REP IV
MG
UMCW
UMG
MBR

and unmulched strawberry bed in each of the four field plot replications. One mulched and one unmulched bed not supplied with drip tubes for CO_2 application was also randomly distributed in the field plot replications. These were the control beds receiving no CO_2 application. The resulting field arrangement was a randomized complete block design with six treatment beds (Figure 1). The three gas application rates (360, 630, 900 kg CO_2 ha^{-1} h^{-1}) were administered by changing the gas flow through the drip tubes supplying the gas treatment beds (MG and UMG in Figure 1). Each rate was not applied to separate treatment beds, so simultaneous application was not performed.

Irrigation System

The plants were irrigated with a combination of drip tubing and overhead sprinklers during establishment in the 1985 season. In 1986, all irrigations were completed with a drip system designed to deliver water independently to the mulched and unmulched beds. The delivery of water was separated, because mulch decreases soil evaporation thus reducing irrigation requirements. Irrigation began on may 3, 1986.

Irrigation water was delivered in a single 12-mil bi-wall drip irrigation tube placed between the two rows of plants in each bed. The tubing was laid underneath the mulch or directly on the ground of the unmulched beds. The strawberry beds designated for carbonated water treatment were irrigated with uncarbonated water until carbonated water application was started on July 15, 1986. After that time all irrigation of designated beds was with carbonated water.

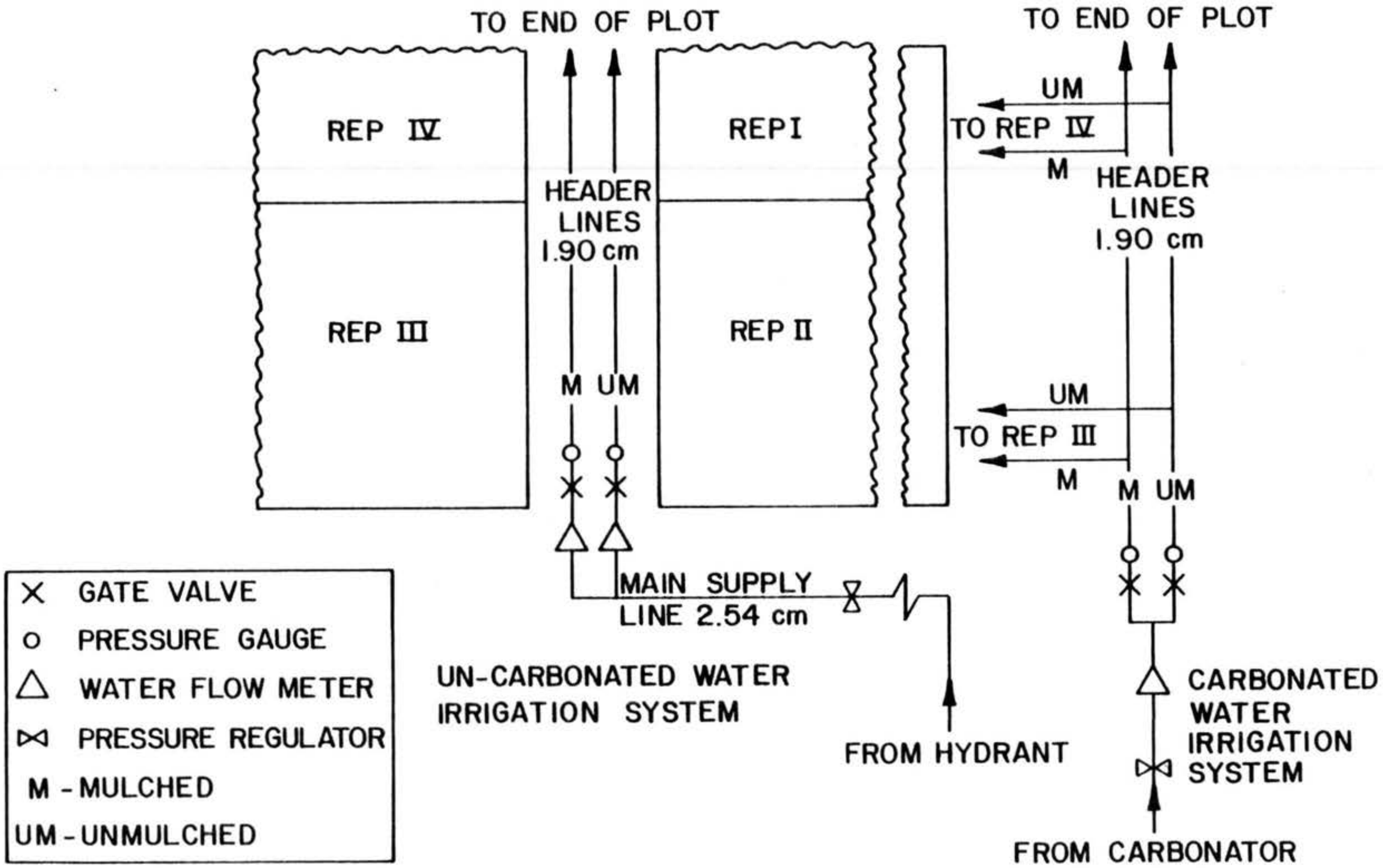
Irrigation with carbonated and uncarbonated water of mulched and unmulched beds was conducted on the same day. In order to compensate for the greater water requirements of the unmulched plants, they were irrigated for one hour longer than the plants in the mulched beds. Subsequently, irrigation of the unmulched plants started at 1000 h and ended at 1600 h, whereas irrigation of the mulched plants started at 1000 h and ended at 1500 h.

Two 12.6-m long polyethylene header lines 1.91 cm in diameter were placed along the alley way splitting the field plot into east and west sections. The mulched beds were supplied by one line and the unmulched beds by the other (Figure 2).

Tensiometers were used to schedule irrigations. The tips of the tensiometers were placed at 20 cm depths in all treatment beds of field plot replications II and IV. Irrigation water was applied when the average of the 6 tensiometers in the mulched treatments reached 0.03 MPa. Irrigation dates and water flow rates are presented in appendix Table 8.

The pressure for both header lines was regulated by a single 0 to 0.4134 MPa range drip irrigation pressure regulator placed in the main supply line, a 2.54-cm diameter polyethylene pipe. This was incorporated to maintain the water pressure within the 0.008 to 0.069 MPa required by the drip tubing. The resulting water pressure was monitored by a 0 to 0.2062 MPa pressure gauge placed in each of the header lines. Pressures were monitored periodically during irrigation to insure consistent delivery of both uncarbonated and carbonated water. In order to separately control the flow and pressure to the mulched and unmulched beds, each header incorporated a gate valve just down-stream from the flowmeters placed in the line to determine the amount of irrigation water applied (Figure 2).

Figure 2. Diagram of carbonated and uncarbonated water irrigation system. Separate water supply lines were used for irrigation of mulched and unmulched beds in the randomized complete block experimental design. Strawberry field experiment, 1986.


TO END OF PLOT
TO END OF PLOT
REP IV
REP I
UM
TO REP IV
M
HEADER LINES 1.90 cm
HEADER LINES 1.90 cm
REP III
REP II
M UM
UM
TO REP III
M
M UM
MAIN SUPPLY LINE 2.54 cm
UN-CARBONATED WATER IRRIGATION SYSTEM
FROM HYDRANT
CARBONATED WATER IRRIGATION SYSTEM
FROM CARBONATOR
× GATE VALVE
o PRESSURE GAUGE
△ WATER FLOW METER
⋈ PRESSURE REGULATOR
M - MULCHED
UM - UNMULCHED

Carbonated Water Irrigation System

Carbonated water was delivered to assigned treatment beds via drip tubes in the same manner as the uncarbonated irrigation water but the two delivery system were separate. Water for carbonation came from a separate hydrant such that flow and pressure in the line supplying the carbonator was not reduced when water was drawn for uncarbonated water irrigation.

Carbon dioxide gas was forced into tap water (pH 6.0) by a pressure differential created in a Cornelius VA13 Balanced Controlled Carbonator in a building near the experimental plot. The resulting carbonated water was considered to be saturated with CO_2. After carbonation, the water was delivered to two 1.91-cm diameter polyethylene header lines in the field via a 2.54-cm diameter polyethylene main supply line. The pressure and flow of both the water and CO_2 gas that supplied the carbonator was controlled to specified levels in the building. Carbon dioxide was supplied by a number two size (64 kg) CO_2 cylinder.

Two header lines running north and south on the east end of the plot separately supplied the drip tubing delivering carbonated water to mulched and unmulched beds. Consequently, carbonated water irrigation of mulched and unmulched beds could be controlled separately. The drip tubing in field plot replications I and II were supplied directly by the two header lines. However, four 1.91-cm diameter lateral lines extended from the header lines to supply the treatment beds in blocks III and IV (Figure 2). The pressure and flow to the header lines were regulated and measured with the same type of equipment and a similar design as that used in the uncarbonated water irrigation system.

Carbonated water pH was measured on July 15, August 14, and September 11 to determine the amount of CO_2 in the water after release from the drip tube. Three samples were taken from the end of the drip tube in each field plot replication. The pH was determined from one sample before another sample was taken to minimize loss of carbonated water from each sample. The pH measurements are presented in appendix Table 9. A linear regression equation relating pH to CO_2 concentration is presented in appendix Figure 14. The relationship between CO_2 concentration and carbonated water pH was established by titrating samples of carbonated water at several different pH levels to determine their CO_2 concentrations. Titrations were performed with 0.1 N sodium hydroxide using a method outlined in a wastewater analysis manual (American Public Health Association, 1985).

The pH of the carbonated water from the point of carbonation to the furthest distance from the carbonator at the end of the drip tubes in field plot replications III and IV (approximately 28 m) was consistent during each application period. Additionally, no substantial decrease in water pressure was recorded at the end of any of the lateral or header lines supplying carbonated water. This indicated that there was no significant loss of carbonation along the length of the drip tube during application. It was assumed, then, that the entire length of the bed (4.58 m) received the same amount of CO_2 from the carbonated water after release from the drip tube.

Since the pH of the carbonated water did not change along the drip tube, the pH of the water at the end of the drip tubing was used to determine the concentration of CO_2 in the carbonated water. The mean carbonated water pH from the end of the drip tubes supplying both mulched and unmulched beds was 4.0 from samples taken on three different dates from the four field plot replications (appendix Table 9). Using the regression equation in appendix Figure 14, the CO_2 concentration corresponding to a pH of 4.0 was estimated to be 1810 mg L^{-1} (.00181 kg L^{-1}). This concentration was used to derive the 420 kg ha^{-1} h^{-1} rate of CO_2 carried in the water as follows:

$$\text{kg ha}^{-1}\ \text{h}^{-1} = \frac{8.4\ \text{gal h}^{-1}\ \text{bed}^{-1} \times 3.785\ \text{L gal}^{-1} \times .00181\ \text{kg L}^{-1}}{0.000137\ \text{ha bed}^{-1}}$$

in which 8.4 gal h^{-1} bed^{-1} was the mean flow rate of carbonated water delivered to each mulched and unmulched bed (0.000137 ha per bed) from July 15 to September 19, 1986 (appendix Table 8). It should be noted that this calculation does not account for the amount of CO_2 lost from the carbonated water due to the drop in water pressure upon release from the drip tube. Consequently, it is not reflective of the actual rate gas released into the canopy. Neither is the calculated rate reflective of the loss of CO_2 from the carbonated water after release.

Carbon Dioxide Gas Application System

The three CO_2 gas application rates (360, 630, 900 kg CO_2 ha^{-1} h^{-1}) were delivered to the strawberry beds assigned for gas application at different times. The gas was delivered via the same 12-mil bi-wall drip irrigation tubing placed parallel to the irrigation tubing on the beds. The release system was based on a design by Tarter (1983) to simulate a multiple line source for application of gas at a constant rate. The drip tubing consisted of a 1.5-cm diameter main supply chamber and a 0.5-cm diameter dispersion chamber with 0.6-mm release holes every 0.3 m along the tube within the wall of the dispersion chamber. Application of each rate began at 1000 h and ended at approximately 1500 h, except where designated otherwise.

Carbon dioxide was supplied to drip tubes from a single number two size cylinder placed in the center of the experimental plot (Figure 1). Gas flow from the cylinder was supplied to eight drip tubes (one tube supplying mulched and unmulched beds in the four field plot replications) by a series of divided connections. Penn Pax Lok Tite brass gang valve assemblies with three outgoing valve ports and one connection port were used in the connections for gas regulation after initial regulation from the cylinder. Carbon dioxide was initially transported by a 1-cm I.D. Tygon tube divided into two 3-mm I.D. tubes by a Tygon Y-joint. Each of these lines supplied two gang valve assemblies connected in series, such that four assemblies were connected to the cylinder. The eight drip tubes were supplied by 6 m lengths of 6-mm I.D. tygon tubing each connected to a valve port on one of the four assemblies. Two of the three outgoing valve ports were used from each assembly, and each assembly supplied the mulched and unmulched beds in one field plot replication.

The 6 m long CO_2 supply tubes were coupled to the drip tubes with a glass connection tube inserted into a number one neoprene stopper which fit snugly into the main drip tube chamber at the leading end of the tubes. The gas flow supplied to all eight drip tubes was measured in the 1-cm I.D. tube leading directly from the CO_2 cylinder with a Gilmont number three 13 L min^{-1} capacity flow tube. All flows were monitored and adjusted just before sampling, as well as at the beginning of the application period. Fine adjustments were made with the gang valves to insure, as nearly as possible, consistent flow to all drip tubes

The gas flow to the drip tubes was measured in L min^{-1} with the Gilmont flow meter. The following conversion was used to determine the gas application for each of the three flows:

$$\mathrm{kg\ ha^{-1}\ h^{-1}} = \frac{\mathrm{L\ min^{-1}} \times 0.044\ \mathrm{kg\ mole^{-1}} \times 60\ \mathrm{min\ h^{-1}}}{0.001098\ \mathrm{ha} \times 26.73\ \mathrm{L\ mole^{-1}}}$$

in which 26.73 L mole^{-1} is the molar volume at the altitude of the experiment location (1524 meters above sea level) (Hanan, 1984) and 0.001098 ha is the area of the 8 treatment beds (8 x 4.5 m x 0.305 m x 0.0001 $\mathrm{m}^2\ \mathrm{ha}^{-1}$). The lowest flow rate, 360 kg $\mathrm{ha}^{-1}\ \mathrm{h}^{-1}$ was delivered at 4 L min^{-1} as measured with the Gilmont flow tube, 630 kg $\mathrm{ha}^{-1}\ \mathrm{h}^{-1}$ at 7 L min^{-1}, and the highest rate, 900 kg $\mathrm{ha}^{-1}\ \mathrm{h}^{-1}$ at 10 L min^{-1}.

Carbon Dioxide Sampling

Carbon dioxide concentrations were measured at the 10 cm sampling height above mulched and unmulched beds during gas application at three places along the length of the drip tube in each field plot replication. Samples were taken 50 cm from either end of the length of the drip tube and in the middle to determine consistency along the release line.

Air samples for CO_2 measurement were drawn into 10-ml B-D PlastiPak Luer-Lok syringes with 4 cm long 17 gauge hypodermic needles. The needles were removed and the syringes were plugged with neoprene stoppers and transported in a styrofoam cooler to the Department of Horticulture laboratories on the main CSU campus. Transport and analysis took up to 6 hrs after the samples were taken.

The CO_2 concentration in each air sample was analyzed with a Hewlett-Packard 5840A gas chromatograph. A 1.8 m long 32 mm O.D. stainless steel column packed with Poropak QS (Applied Science Laboratory) was used to separate the CO_2 portion of the samples from the other gases. The CO_2 was first converted to methane gas by a nickel catalyst methanator and the methane was then quantitatively detected by a Flame Ionization Detector (FID). The gas chromatograph was calibrated with 0.5-ml aliquots of six known CO_2 concentrations (301, 452, 602, 753, 904, and 1054 uL L^{-1}). The calibration curve is presented in appendix Figure 15. Nitrogen gas was mixed in different proportions with a 1506 uL L^{-1} calibration gas concentration (research grade - 99.998% pure) in a 50 ml glass syringe to obtain the six concentrations.

A graduated Hamilton 1.0 ml gas-tight syringe was used to extract samples from the plastipak collection syringes for analysis with the gas chromatograph. The air samples were drawn through the resealable neoprene stoppers placed on the syringes after sampling. Aliquots of 0.5 ml were drawn from the collection syringes used to sample the unenriched controls, and these samples were analyzed without dilution. However, 0.25-ml aliquots of dried N_2 gas were added to the 0.25-ml of the air sampled from treatment beds during CO_2 application to halve CO_2 concentration. This dilution procedure was performed since some of the measurements from the CO_2 application rates were found to exceed 1100 uL L^{-1} CO_2, the upper limit of the methanator. The diluted samples were analyzed and the measurements were multiplied by two to determine the concentration in the original 0.25-ml sample. This was not done with the control samples, because the dilution would have yielded concentrations too low for accurate detection by the FID.

Experimental Procedure

From Takami and Van Bavel (1975) and independent research, Tarter (1983) determined that ground source CO_2 enrichment becomes inefficient at wind speeds exceeding 3.0 to 3.5 m s^{-1} and irradiance values below 210 W m^{-2}, due to excessive gas dispersion and low recovery rates respectively. Consequently, the potentials of the four CO_2 application rates in the present experiment were evaluated for comparison when wind speeds were below 3.0 m s^{-1} and irradiances above 210 W m^{-2}. These factors were measured prior to the designated CO_2 application period. Wind speeds were measured 2.0 m above the ground with a 3-cup anemometer and analog readout registering in kilometers located 37 m northeast of the experimental plots. Irradiance measurements were obtained from an Epply Pyranometer located approximately 15 km southwest of the CSU Horticultural Research Center. Environmental conditions during dates of CO_2 application are presented in appendix Table 10.

Each CO_2 application rate was applied and sampled on one date in July, August, and September, 1986. Sampling dates were designated from wind speed measurements taken prior to the CO_2 application period, and application only occurred on those dates in which wind speed measurements were below 3.0 m s^{-1} between 900 and 1000 h Local Solar Time. The details of the sampling schedule are presented in Table 1. On each sampling date air samples were taken at the three sampling heights above mulched and unmulched treatment and control beds (no CO_2 application). The CO_2 concentrations in these air samples were used to detect any change in ambient concentration resulting from the differences due to sampling date. All air samples were taken at solar noon (1200 h) and the sampling procedure took about 75 minutes.

Table 1. Carbon dioxide sampling schedule. All samples were taken 1, 10, and 20 cm above mulched and unmulched beds from each of four field plot replications during application of CO_2 gas (G) or carbonated water (CW) on designated dates. Samples from unenriched controls (CTRL) were taken on each date. Strawberry field experiment, 1986.

CO_2 Application Rate

kg ha^{-1} h^{-1}

Sampling Date 1986	CTRL 0	G 360	CW 420	G 630	G 900	G 360	CW 420	G 630	G 900	CTRL 0
			Mulched				Unmulched			
July 8	X	X				X				X
12	X			X				X		X
15	X		X				X			X
17	X				X				X	X
Aug 10	X	X				X				X
11	X			X				X		X
14	X		X				X			X
17	X				X				X	X
Sept 11	X		X				X			X
12	X	X				X				X
14	X			X				X		X
17	X				X				X	X

The experimental design to compare the CO_2 concentrations measured during enrichment at wind speeds below 3.0 m s^{-1} was a three factor factorial. The three factors were CO_2 application rate at four levels, presence or absence of mulch, and three sampling heights. The resulting design was a four by three by two factorial.

Mid-canopy CO_2 concentrations were measured during application of each CO_2 rate to evaluate the effect of varying wind speed enrichment capacity over the course of a day. Four air samples were taken at hourly intervals between 1000 and 1500 h 10 cm above the mulched and unmulched beds in field plot replication III during CO_2 application. Each application rate was administered on a separate date in which wind speeds were below 3.0 m s^{-1} from 900 to 1000 h. Hourly wind speeds from 1000 to 1500 h were determined from wind runs between sampling times.

The effect of wind speeds exceeding 3.0 to 3.5 m s^{-1} on the vertical distribution of CO_2 was compared on August 1, 1986. The four rates were consecutively applied on this date and samples were taken at the 1, 10 and 20 cm sampling height above mulched and unmulched beds in field plot replication III during each application. Each CO_2 application was administered for approximately one hour starting at 800 h. Wind speeds were determined from the wind runs during each application period. Four air samples at each of the three heights were taken in immediate succession as close as possible to the middle of the application period.

Because CO_2 mixed with water is not immediately released into the atmosphere as is gas upon application, soil pH and canopy CO_2 concentrations were measured between carbonated water irrigations to detect any residual effects after irrigation. Soil pH was measured at two day intervals between July 15 and October 18, 1986. Seven carbonated water irrigations were applied over this period. Samples were taken at a 5 cm soil depth from the carbonated water treatment beds in each field plot replication. Soil was sampled 50 cm from both ends of the drip tube length and in the middle to detect any differences along the release line. No differences were found in the first sampling, so soil samples were taken only from the middle of the drip tube for the rest of the sampling dates. Carbon dioxide measurements were taken at the 10 cm sampling height every two days between carbonated water irrigations on August 22 and September 11, 1986.

Soil and water pH was measured with an Orion analog pH meter and 91-04-00 combination pH probe. Soil samples taken from the carbonated water treatment beds and control beds were mixed to paste consistency with irrigation water in the field just after irrigation. The same water used in irrigation was added to the samples taken between irrigations to attain paste consistency.

Experimental Design and Analysis

Preliminary analyses were conducted to determine whether the control measurements should be included in the analysis of CO_2 application rate responses at wind speeds below 3.0 m s^{-1}. They were also used to determine the different sampling dates need be considered as a source of variance in the application rate response measurements. The analyses are presented in appendix Tables 9-11.

The results of these analyses indicated that control measurements and sampling date differences were not important to the analysis of the application rate response. Consequently, the different sampling dates were treated as replications, and control measurements were not included in the analysis. The four field plot replications (spatial replication) and three sampling dates (temporal replication) comprised twelve replications in the analysis of CO_2 concentrations measured during application of the four rates under stable wind conditions.

A split-split plot design was used to analyze the effects of application rate, mulch, and sampling height during CO_2 application at wind speeds below 3.0 $m\ s^{-1}$. The four application rates (3 gas application rates and carbonated water) were treated as the main units, presence or absence of mulch as the subunits, and the three sampling heights as the sub-subunits. Greater precision was given to the sampling heights because all heights of a given application rate mulch combination were sampled at the same place, allowing for the least amount of variability due to error in the experiment. More error variability was associated with the mulch factor due to the greater time and distance between samples. Finally, the four application rates were assigned to the main units because of the different dates of application and the intrinsic variability in CO_2 application.

Forward stepwise regression procedures were used to generate multiple regression equations relating wind speed and CO_2 gas application rate to CO_2 concentration measured 10 cm above mulched and unmulched beds. Those variables contributing less than 0.01 to the R-squared value were not included in the equation. Response surfaces were generated from each equation and the orientation and slope of the surfaces were visually and quantitatively evaluated to compare the affect of wind speed on CO_2 concentrations in mulched and unmulched strawberry canopies during application of the three gas rates (360, 630, 900 kg CO_2 ha^{-1} h^{-1}). The value of mulching was visually assessed by comparing the position and orientation of the two response surfaces.

RESULTS AND DISCUSSION

Field Experiment

Carbon Dioxide Concentrations With Wind Speeds Below 3.0 m s^{-1}

The preliminary analyses presented in Tables 11, 12, and 13 of the appendix indicate that CO_2 concentrations measured during application of 360, 630, 900 kg CO_2 ha^{-1} h^{-1}, and carbonated water carrying 420 kg CO_2 ha^{-1} h^{-1} were significantly higher than ambient concentrations at all sampling heights above mulched and unmulched strawberry beds when wind speeds were below 3.0 m s^{-1}. Mean concentrations above control beds and above treatment beds during CO_2 application are presented in Tables 14 and 15 for each sampling date.

Tarter (1983) detected a much smaller enrichment at the top of an unmulched lettuce canopy (25 cm above the ground) during application of 360 kg CO_2 ha^{-1} h^{-1} than was recorded at the top of the strawberry plants in the present experiment. An increase of 75 uL L^{-1} over the mean ambient concentration (332 uL L^{-1}) was recorded above the strawberry canopy, which was about twice that recorded above the lettuce canopy. The differences in results from these experiments could be attributed to more effective entrapment of released CO_2 by the lower denser strawberry plant canopy, suggesting that enrichment of field grown strawberry plants with a ground source of CO_2 may be more feasible than enrichment of lettuce plants.

No significant differences were found between the CO_2 concentrations measured 50 cm from either end of the drip tube length and in the middle during application of any of the four CO_2 application rates tested in this experiment. Consequently, it was assumed that gas release along the length of the tube was uniform. Thus, measurements were taken only from the middle of the drip tube during CO_2 application to assess enrichment capacity of each application rate.

The analysis of the split split-plot design presented in Table 2 shows that the main effects due to CO_2 application rate, mulch, and sampling height, as well as the two and three-way interactions between these three factors were significant when CO_2 was applied during wind speeds below 3.0 m s^{-1}. Tukey's Honestly Significant Difference (HSD) procedure was used to separate the CO_2 means of all treatment combinations. These means and corresponding HSD values are presented in Table 3. Differences in mean CO_2 concentrations for each application rate are graphically illustrated in Figure 3. The means are plotted as concentration profiles to depict the vertical distribution of gas within the canopy.

Figure 3 illustrates the trend towards increasing dispersion of added CO_2 with increases in sampling height. Carbon dioxide concentrations were significantly lower at each higher sampling height during application of all four rates. This was expected because gas from a ground source is increasingly susceptible to the dispersive action of the bulk atmosphere as it moves vertically through the plant canopy (Allen et al., 1974; Takami and Van Bavel, 1975). With the exception of the carbonated water application rate (420 kg CO_2 ha^{-1} h^{-1}), Figure 3 demonstrates that the rate of vertical CO_2 loss became greater

Table 2. Analysis of CO_2 concentration (uL L^{-1}) response variance from four CO_2 application rates (360, 420, 630, 900 kg CO_2 ha^{-1} h^{-1}) at 1, 10, and 20 cm over mulched and unmulched strawberry beds, where four field plot replications and three sampling dates were considered 12 blocks. All concentrations were determined on days when wind speeds were below 3.0 m s^{-1} at the beginning of CO_2 application. Strawberry field experiment, 1986.

Source of Variance	df	SS	MS	F
Main Plot Error	33	151548.77	4592.39	
Block	11	43822.41	3983.86	0.867
CO_2 Application Rate	3	2857851.73	952617.20	207.43**
Subplot Error	44	118970.28	2703.87	
Mulch	1	1819743.90	1819743.90	673.01**
Mulch X CO_2	3	529044.45	176348.15	65.22**
Sub-subplot Error	176	199562.04	1133.88	
Sampling Height	2	5460308.30	2730154.15	2407.81**
Height X CO_2	6	7491553.10	124858.85	110.12**
Height X Mulch	2	429406.58	214703.29	189.35**
Height X Mulch X CO_2	6	196292.81	32715.47	28.86**

** Significance at $P<0.01$

Table 3. Mean CO_2 concentrations (uL L^{-1}) for main effects and interactions of CO_2 gas (G) application and carbonated water, the presence (Mu) and absence (Umu) of mulch, and sampling height. Each mean is from four field plot replications and three sampling dates (n=12). All measurements were taken during wind speeds below 3.0 m s^{-1} at the beginning of CO_2 application. Strawberry field experiment, 1986.

		CO_2 Application Rate kg ha^{-1} h^{-1}					
	Sampling height cm	G 360	CW 420	G 630	G 900	Height x Mulch[y]	Mulch[x]
		Rate x Mulch x Height[z]					
Mu	1	728.0	762.2	990.6	1325.3	675.5	
	10	589.7	622.4	762.7	895.5	540.0	548.6
	20	452.6	490.4	531.2	606.6	430.3	
Umu	1	565.3	695.0	678.5	849.9	531.6	
	10	476.4	561.3	546.6	656.7	454.3	460.0
	20	406.5	464.0	451.8	497.8	394.0	
						Height[t]	
Rate x Height[w]	1	646.7	728.6	834.5	1087.6	603.6	
	10	533.1	591.9	654.6	776.1	497.1	
	20	429.5	477.4	491.5	552.2	412.2	
Mulch x Rate[v]	Mu	590.1	625.1	761.5	942.5		
	Umu	482.7	573.5	558.9	668.1		
Rate[u]		536.4	599.3	660.2	805.3		

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[z] $HSD_{.01}$ = 56.5, between rate means for same or different mulch and height. $HSD_{.01}$ = 46.4, between mulch means for same rate and same or different height. $HSD_{.01}$ = 40.1, between height means for same rate and same mulch.

[y] $HSD_{.01}$ = 23.2, between mulch means for same height. $HSD_{.01}$ = 20.0, between height means for same mulch.

[x] $HSD_{.01}$ = 16.5, between mulch means.

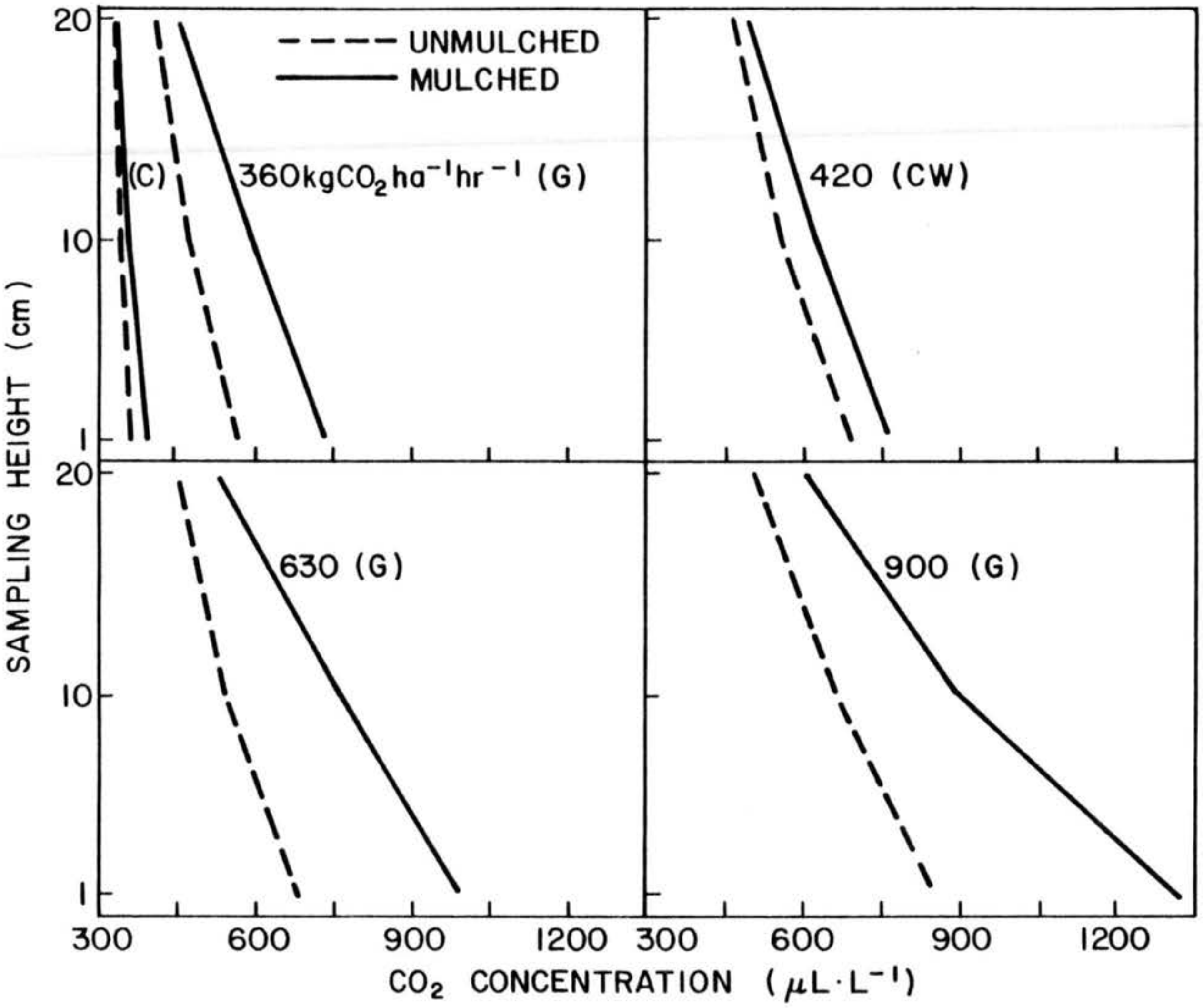
[w] $HSD_{.01}$ = 28.3, between height means for same rate. $HSD_{.01}$ = 44.51, between rate means for same height.

[v] $HSD_{.01}$ = 33.0, between mulch means for same rate. $HSD_{.01}$ = 44.4, between rate means for same mulch.

[u] $HSD_{.01}$ = 38.1, between rate means.

[t] $HSD_{.01}$ = 14.2, between height means.

Figure 3. Differences in CO_2 concentration means above mulched and unmulched beds at three sampling heights with no CO_2 enrichment (C) and with applications of CO_2 gas (G) and carbonated water (CW). Each application rate mean was from four field plot replications sampled on three dates July - September (n=12). The (C) means are from samples taken on 12 dates July - September. Wind speeds on the sampling dates were below 3.0 $m\ s^{-1}$ at the beginning of CO_2 application. Strawberry field experiment, 1986.


UNMULCHED
MULCHED
(C)
360 kg CO2 ha⁻¹ hr⁻¹ (G)
420 (CW)
630 (G)
900 (G)
SAMPLING HEIGHT (cm)
20
10
1
20
10
1
300
600
900
1200
300
600
900
1200
CO2 CONCENTRATION (μL·L⁻¹)

as application rate increased. However, in all cases CO_2 concentrations were higher than ambient levels (control profile) at the 20 cm height.

The mulch covering in this experiment was found to consistently enhance enrichment from all four of the CO_2 application rates. Figure 3 shows that CO_2 concentrations were the least increased in the presence of mulch during carbonated water application, however, this observed enhancement in the presence of mulch became greater as rate of gas application increased. The effect attributed to mulch declined with increasing sampling height during all four application rates. Despite this negative interaction between mulch and sampling height, only carbonated water did not yield significantly larger CO_2 concentrations at the highest sampling height (20 cm) above mulched beds as compared to unmulched beds (Table 3). Based on the means presented in Table 3, CO_2 concentration was 11, 18, and 22% higher 20 cm above mulch during application of 360, 630, and 900 kg CO_2 ha^{-1} h^{-1} respectively. In comparison, the increase attributed to mulch during carbonated water application was 6% at the 20 cm sampling height.

Tarter (1983) recorded a 33% enrichment enhancement just above a lettuce canopy in the presence of mulch during application of 360 kg CO_2 ha^{-1} h^{-1}. This was three times that recorded above the strawberry canopy in the present experiment. However, as stated previously, the CO_2 concentrations recorded by Tarter above a lettuce canopy during enrichment without mulch were substantially lower than those recorded during application of 360 kg CO_2 ha^{-1} h^{-1} to the strawberry plants here. The difference indicates that mulch interacts differently with different plant types. The lower growth habit of the strawberry plant canopy may have functioned to moderate the loss of CO_2 in the absence of mulch.

Nevertheless, the distinct enrichment enhancement due to mulch in both these experiments suggests that using a continuous mulch barrier during CO_2 gas application is a reliable method to increase the effectiveness of this treatment.

Enhancement of CO_2 concentrations recorded above a continuous mulch covering with or without external CO_2 application may be explained by a phenomenon observed by Sheldrake (1963) in mulched muskmelon. Sheldrake detected 1300 uL L^{-1} directly above the plant hole of a poly-coated mulch. He hypothesized that the mulch delayed dispersal of CO_2 from soil respiration by acting as a barrier to immediate loss of the evolved gas. The enrichment recorded above the mulch was attributed to channelling of the accumulated gas into a muskmelon canopy through the plant holes. Since CO_2 concentrations were significantly greater at all three heights above mulched beds than above unmulched beds during gas application, it appears that the mulch did increase vertical transport of the added gas in the present experiment. This vertical transport may have also been aided by concentration depletion at mid-canopy due to photosynthetic usage and horizontal loss of added CO_2 as suggested by Harper et al. (1973) and Allen et al. (1974).

It has been well established that photosynthetic use of added CO_2 increases with incident radiation (Gaastra, 1959). Due to self shading by leaves within a canopy, incident radiation is highest at the top of the canopy under field conditions. Thus photosynthetic demand is greatest at the top of the plant. Consequently, enrichment concentrations at the top of the strawberry canopy (20 cm sampling height) are considered most important and will be discussed in detail.

The 900 kg CO_2 ha^{-1} h^{-1} application rate yielded the highest CO_2 concentration at the 20 cm height over mulched and unmulched beds. A significant difference was detected between the CO_2 concentration means observed 20 cm above mulched beds during application of 360 and 900 kg CO_2 ha^{-1} h^{-1}. However, no significant difference was found at this height during application of 360 and 630 kg CO_2 ha^{-1} h^{-1}. Without mulch, concentrations resulting from application of 630 kg CO_2 ha^{-1} h^{-1} and carbonated water (420 kg CO_2 ha^{-1} h^{-1}) were not significantly different than those from the 900 kg CO_2 ha^{-1} h^{-1} rate at the 20 cm sampling height (Table 3). Therefore, in the absence of a continuous mulch, increasing the rate CO_2 gas application above 630 kg CO_2 ha^{-1} h^{-1} does not appear to be a feasible method for increasing CO_2 concentrations at the top of a strawberry canopy under stable wind conditions (wind speeds below 3.0 m s^{-1} at the beginning of CO_2). Additionally, the results indicate that without mulch, carbonated water could be substituted for gas application resulting in no loss of enrichment at the top of a strawberry canopy. No significant difference was detected between the means yielded by carbonated water and the two highest gas application rates without mulch at 20 cm (Table 3). However, CO_2 concentration means resulting from carbonated water application were significantly higher than those from 360 kg CO_2 ha^{-1} h^{-1} without mulch at the top of the canopy.

When CO_2 was delivered in the presence of a continuous mulch, significant gains in CO_2 enrichment at the top of the strawberry canopy were obtained by applying gas at 900 kg CO_2 ha^{-1} h^{-1}. The 630 kg CO_2 ha^{-1} h^{-1} rate was also statistically more effective than the 360 kg CO_2 ha^{-1} h^{-1} at the 20 cm height when applied underneath a mulch covering (Table 3). Carbonated water application did not yield statistically higher CO_2 concentrations than 360 kg CO_2 ha^{-1} h^{-1} and was not as effective as 900 kg CO_2 ha^{-1} h^{-1} at the 20 cm sampling height in the presence of mulch. In view of the results presented here, increasing CO_2 gas application from 630 to 900 kg ha^{-1} h^{-1} rate would result in an enrichment advantage only when applied in conjunction with a continuous mulch covering. On the other hand, enrichment of a strawberry canopy with carbonated water appears to be more feasible without mulch than with mulch. This is because mulch was not found to significantly increase the CO_2 concentration yielded by carbonated water at the top of the canopy where CO_2 was most available for photosynthetic utilization. Also, no significant enrichment advantage was recorded at the top of the canopy during carbonated water application when applied in conjunction with mulch, whereas without mulch carbonated water was more effective than 360 kg CO_2 ha^{-1} h^{-1} and as effective as the two higher gas application rates.

Referring to means and accompanying HSDs in Table 3, CO_2 enrichment with carbonated water at the 20 cm sampling height was only statistically less effective than the 900 kg CO_2 ha^{-1} h^{-1} rate when both were applied underneath mulch. Without mulch, the 900 kg CO_2 ha^{-1} h^{-1} was not statistically more effective than carbonated water. Application of carbonated water without mulch resulted in significantly greater CO_2 concentrations than the 360 kg CO_2 ha^{-1} h^{-1} rate at all sampling heights. Although CO_2 concentrations yielded by 360 kg CO_2 ha^{-1} h^{-1} were significantly increased by mulch, the increase was not large enough to offer a statistically significant enrichment advantage over carbonated water in the absence of mulch at any sampling height. Nevertheless, application of 360 kg CO_2 ha^{-1} h^{-1} to mulched beds was statistically as effective as increasing the rate of gas application to 900 kg CO_2 ha^{-1} h^{-1} without mulch.

In view of the results presented here, application of carbonated water appears to interact differently with mulch than does gas application. This is most clearly demonstrated by the relationship of the carbonated water concentration means and the 630 kg CO_2 ha^{-1} h^{-1} means with and without mulch. Although, the difference was not significant, the carbonated water means were higher than the 630 kg CO_2 ha^{-1} h^{-1} means without mulch, whereas the 630 kg CO_2 ha^{-1} h^{-1} means were higher than the carbonated water means with mulch. Water appeared to have substituted to a certain degree for mulch, and mulch did not seem to have as great a barrier effect against CO_2 dispersion during application of carbonated water as during direct gas application. Water may have acted as a barrier to immediate CO_2 dispersion after release of the carbonated water from the drip tube.

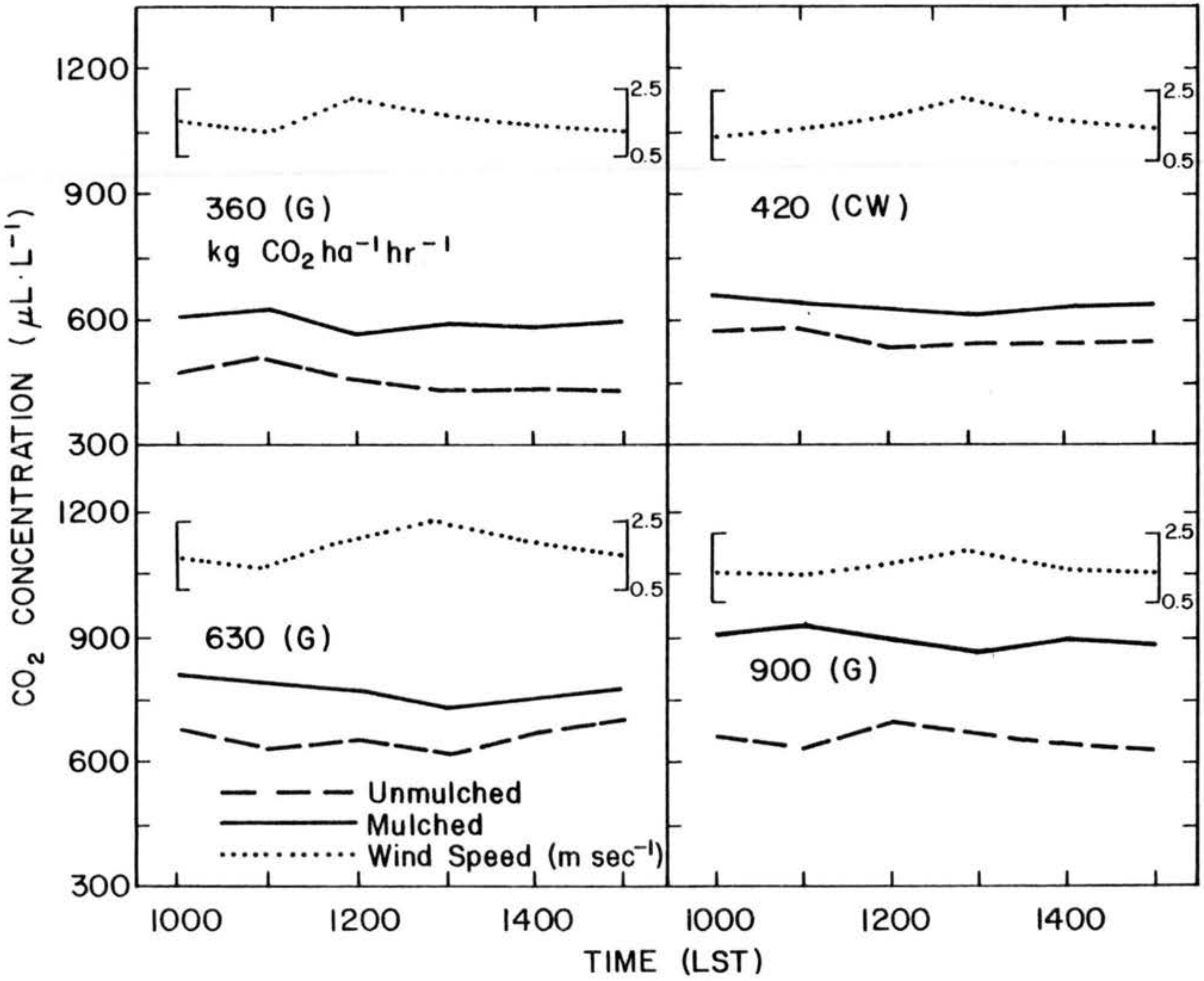
Like mulch, water could have functioned to slow the escape of CO_2 gas from the point of release allowing it to build up at the top of the canopy by the same sort of channelling hypothesized by Sheldrake explaining enrichment enhancement above mulch. Additionally, carbonated water may have provided a more constant source of CO_2 evolution, reducing the amount of total gas dispersed by the bulk atmosphere. The reasons for lack of additivity between the effects of water and mulch is not apparent. It would seem that mulch should have enhanced enrichment during carbonated water application to a greater extent than during gas application. Provided that carbonated water did supply a more constant source of CO_2 within the canopy, it seems likely that more CO_2 would have been available at any one time to accumulate under the mulch covering.

From the evidence presented in Table 3 and Figure 3, the use of mulch was not of great advantage during enrichment with carbonated water. However, a continuous mulch covering was necessary to attain the maximum enrichment advantage at the top of a strawberry canopy from application of CO_2 gas at the highest rate tested in the present experiment, 900 kg CO_2 ha^{-1} h^{-1}.

Carbon dioxide concentrations at the 10 cm sampling height for each hour of CO_2 application (1000 to 1500 h) are presented graphically in Figure 4. Each CO_2 rate was applied on a different date, and the dates were chosen to determine CO_2 concentration fluctuations during average hourly wind speeds below 3.0 m s^{-1}. None of the CO_2 concentrations measured dropped below the highest mean control measurements recorded in Table 16 of the appendix.

As expected, the lowest CO_2 concentration 426 uL L^{-1} was measured during application of 360 kg CO_2 ha^{-1} h^{-1} without mulch (Figure 4). However, the corresponding hourly wind speed, 1.7 m s^{-1} was not the highest measured during the day (Figure 4). Since wind speeds were from average wind runs, the recorded values may not reflect the dispersive wind factors at the instant of measurement. The concentration low measured here may be a result of a burst of wind or other factors not measured in this experiment. Conversely, as expected, the highest CO_2 concentration, 958 uL L^{-1} was measured during application of the 900 kg CO_2 kg ha^{-1} h^{-1} at the lowest hourly wind speed, 0.6 m s^{-1} during the day. For the most part, CO_2 concentrations fluctuated with wind speed, decreasing when wind speeds increased. This trend was also recorded in

Figure 4. Time course of CO_2 concentrations during applications of CO_2 gas (G) carbonated water (CW) with varying wind speeds. Each mean was from four samples taken 10 cm above mulched and unmulched beds during CO_2 application at designated rates from one field plot replications on one date in July or August (n=4). Wind speeds are from hourly wind run measurements. Strawberry field experiment, 1986.



CO$_2$ CONCENTRATION (μL · L^{-1})
1200
900
600
300
2.5
0.5
360 (G)
kg CO$_2$ ha^{-1} hr^{-1}
420 (CW)
630 (G)
900 (G)
Unmulched
Mulched
Wind Speed (m sec^{-1})
1000
1200
1400
TIME (LST)

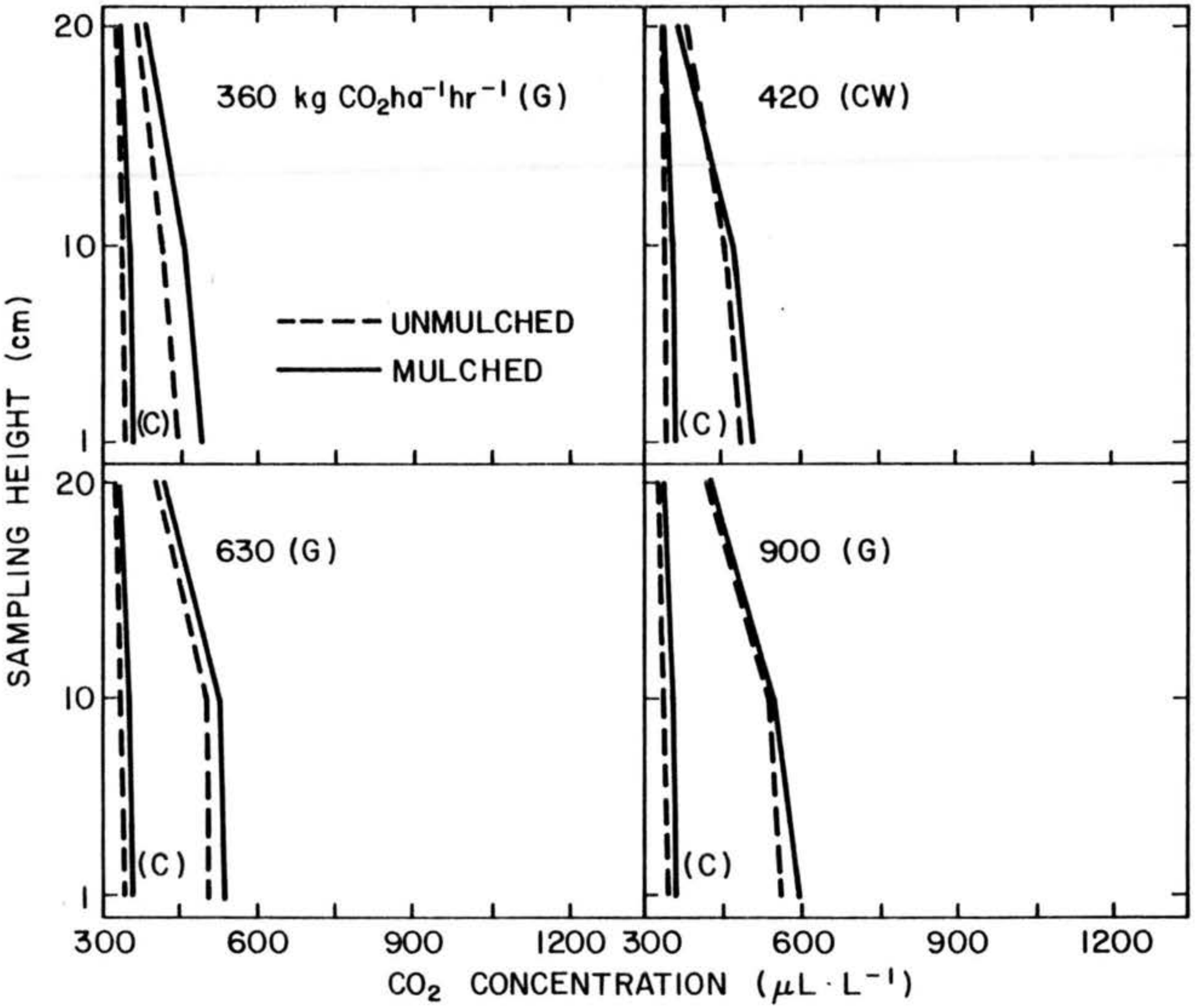
the fluctuations of ambient CO_2 near the top of a corn crop (Allen, 1971). In a later paper, Allen et al. (1974) found that added CO_2 was quickly lost from a corn canopy during unstable thermal conditions and high vertical and horizontal winds. Simultaneous measurements of wind and CO_2 made by these authors confirmed that CO_2 concentration fluctuations coincided with wind speed fluctuations with only a slight lag (less than a second).

Figure 4 also illustrates that CO_2 concentrations above unmulched beds fluctuated more over the course of the day with the changes in wind speed than did those above mulched beds. This implies that the mulch functioned to a slight degree as protection against loss of added CO_2 to wind dispersion. Consistent with findings discussed earlier, the difference between the concentrations above mulched and unmulched beds irrigated with carbonated water was smaller than that for the gas application rates.

Effect of Wind Speed and Application Rate on CO_2 Concentration

Carbon dioxide concentration profiles resulting from the four application rates during wind speeds exceeding 3.0 m s^{-1}, the prescribed threshold limit up to 4.5 m s^{-1} are presented in Figure 5. Concentrations in Figure 5 were substantially lower than the corresponding concentrations in Figure 3 in which wind speeds were below the 3.0 m s^{-1} at the beginning of the CO_2 release period. The higher winds caused concentration measurements to fluctuate enough to severely reduce enhancement of enrichment by mulch. However, except for carbonated water and 360 kg CO_2 ha^{-1} h^{-1} at the top of the canopy (20 cm sampling height), the concentrations from every application rate were higher than

Figure 5. Carbon dioxide concentration profiles during CO_2 gas (G) and carbonated water (CW) application at hourly wind speeds between 3.0 and 4.5 $m\ s^{-1}$. Each mean was from four samples taken during CO_2 application on August 1 (n=4). Strawberry field experiment, 1986.



360 kg $CO_2ha^{-1}hr^{-1}$ (G)
420 (CW)
630 (G)
900 (G)
UNMULCHED
MULCHED
(C)
SAMPLING HEIGHT (cm)
20
10
1
300
600
900
1200
CO_2 CONCENTRATION ($\mu L \cdot L^{-1}$)

those measured above mulched and unmulched beds with no enrichment (controls) during the same wind speed conditions.

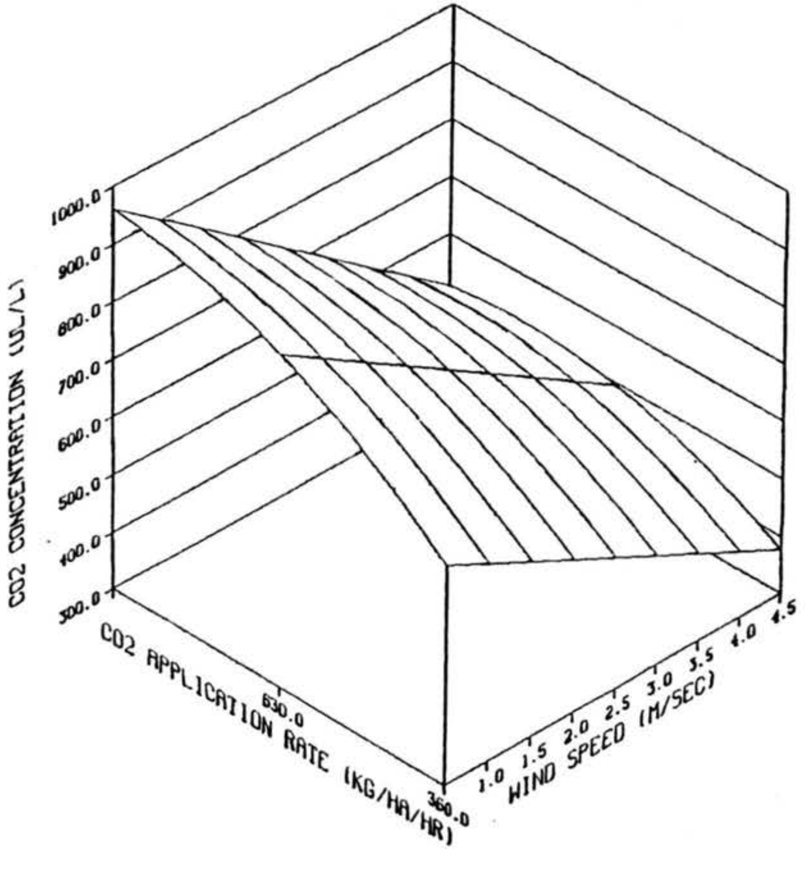
The trends in CO_2 enrichment response to application rates at different wind speeds suggest that the CO_2 concentrations in the strawberry plant canopy were predominantly a function of wind speed, application rate, and mulch. To test this hypothesis, CO_2 concentrations were regressed against corresponding rates of gas application (360, 630, and 900 kg CO_2 ha^{-1} h^{-1}) and wind speed during application (Figure 6). Response surfaces were generated from equations resulting from multiple regression procedures. Separate regressions were performed for concentrations measured in mulched and unmulched canopies to assess the effect of mulch. Each regression equation was derived from 30 observations. Samples from the 10 cm sampling height were used to generate the relationship, because this height was considered to be least affected by other environmental factors due to protection by the dense canopy vegetation (Harper et al., 1973). Concentrations from carbonated water applications were not used in the regression procedure as the actual amount of gas escaping from the water was unknown.

The high R-squared values of the two regressions (Figure 6) indicate that factors other than wind speed and application rate exert little influence on CO_2 concentration during CO_2 enrichment with gas. Consequently, interpretation of the two surfaces is considered to afford a high level of confidence in assessing the effects of these two factors and mulch on CO_2 concentration.

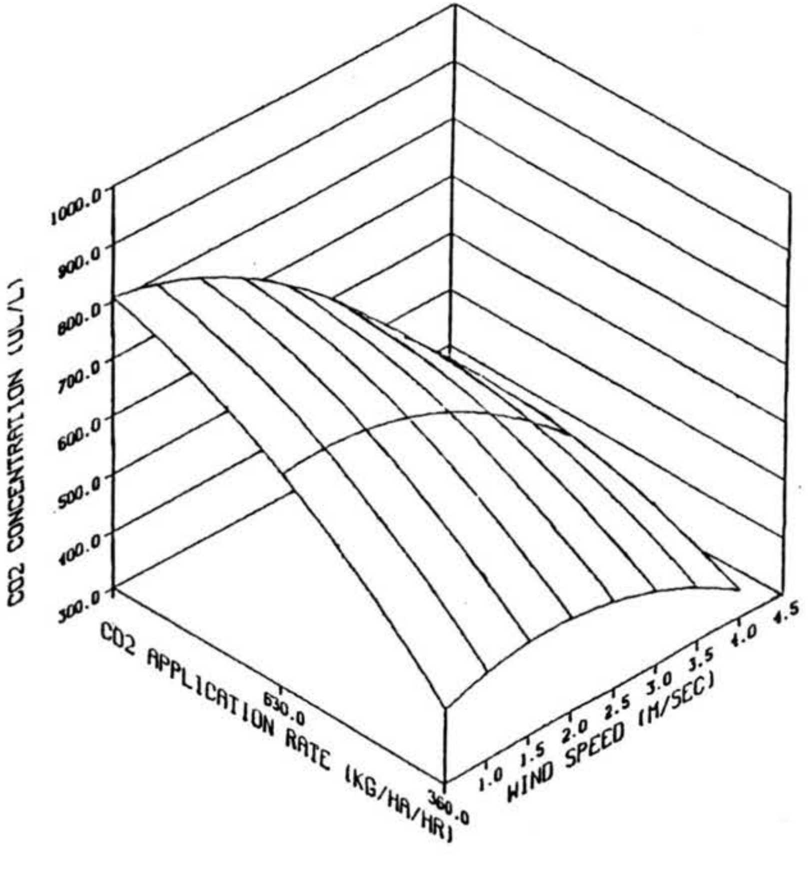
The CO_2 response surface associated with mulched beds exhibits a much higher trajectory than does the surface associated with unmulched beds, clearly showing enhanced enrichment by mulch at all wind speeds

Figure 6. Response surfaces relating hourly wind speeds and three CO_2 gas application rates to CO_2 concentration 10 cm above mulched and unmulched beds. Samples were taken during wind speeds ranging from 0.5 to 4.5 $m\ s^{-1}$ above and from 0.5 to 4.0 above unmulched beds. The adjusted R-squares of the second order polynomials are 0.97 and 0.92 respectively for the mulched and unmulched relationships. Each equation was derived from 30 observations. Strawberry field experiment, 1986.

MULCHED



UNMULCHED



(Figure 6). The upward trend in both surfaces from the 360 to the 900 kg ha^{-1} h^{-1} CO_2 application rates for all wind speeds demonstrates the overall increase in CO_2 concentration with increasing application rate. However, the change in the slope of the response along CO_2 application rate axis (y-axis) from upward to downward, indicates that the enrichment above both mulched and unmulched beds does not linearly increase with application rate. The curvature of both response surfaces along the application rate axis appears to be very similar across wind speeds below 3.0 m s^{-1}, indicating little interaction between mulch and wind speed at all application rates below 3.0 m s^{-1}.

Carbon dioxide applied to exposed or unmulched beds appeared to be more susceptible to wind dispersion than that applied underneath a mulch covering (Figure 6). Carbon dioxide concentration detected above unmulched beds were reduced to a greater extent by wind speeds higher than 3.0 m s^{-1} than those detected above mulched beds, particularly during application of 900 kg ha^{-1} h^{-1} CO_2. This is interpreted from the steeper decline and greater curvature in the response surface associated with unmulched beds along the wind speed axis (x-axis) at wind speeds above 3.0 m s^{-1}, and the relatively drastic drop in the CO_2 concentration response associated with unmulched beds at the highest wind speed and application rate. In contrast, such a drop was not predicted for concentrations above mulched beds. Overall, the rate of CO_2 concentration decline, with increasing wind speed for both mulched and unmulched beds, indicates that the positive effects of mulch and higher application rate, were increasingly diminished by higher wind speeds.

The downward curvature of both response surfaces from low to high wind speeds along the wind speed axis for each application rate depicts the decreasing influence of application rate with increasing wind speed (Figure 6). The greater downward trend in CO_2 concentration with increasing CO_2 application rate demonstrates that greater proportions of CO_2 were lost due to wind dispersion as application rate increased. This is further supported by the greater curvature in both surfaces between the 630 and 900 kg ha^{-1} h^{-1} CO_2 application rates at the highest wind speeds along the application rate axis compared to the same curvature between 360 and 630 on the application rate axis. Using a simulation model, Allen et al. (1971) predicted a similar trend. The predictions indicated that a slightly higher percentage of CO_2 would be lost from an application rate of 450 kg CO_2 ha^{-1} h^{-1} as compared to a rate of 225 CO_2 ha^{-1} h^{-1} when wind speeds increased from 1 to 6 m s^{-1}.

The regression equations and accompanying statistics for the response surfaces associated with the mulched and unmulched treatments are presented in appendix Table 16. The lack of a quadratic wind effect, in the model associated with the mulched beds, indicates that CO_2 concentrations in the canopy above mulched beds were less influenced by wind speed than those above unmulched beds. This is further evidence that mulch curbed the loss of CO_2 from the canopy due to dispersion by wind within ranges of wind speeds measured.

In solving for the regression equations presented in appendix Table 16, a 39 and 41% decrease in CO_2 concentration at 10 cm resulted from an application rate of 360 kg CO_2 ha^{-1} h^{-1} in the presence of mulch when wind speed increased from 0.5 to 4.0 m s^{-1}. Likewise in the absence of mulch, a 31 and 45% decrease in CO_2 concentration resulted from 360 and 900 kg CO_2 ha^{-1} h^{-1} application rates considering the same wind speed range. This indicates that more CO_2 was dispersed from the canopy due to increases in wind speed as gas application rate increased.

The interaction between the mulch and application rate factors was less clear. Since the percent concentration reduction due to dispersion by wind was larger in the presence of mulch than in the absence of mulch during application of 360 kg CO_2 ha^{-1} h^{-1}, mulch appeared to increase the dispersive loss of CO_2 yielded by this rate. On the other hand, the percent reduction was smaller during application of 900 kg CO_2 ha^{-1} h^{-1} to mulched beds, indicating that mulch functioned as a greater limitation to CO_2 loss by wind dispersion at the higher rate of gas application. Consequently, during wind speeds as high as 4.0 m s^{-1}, increasing mid-canopy enrichment by applying gas at a rate above 360 kg CO_2 ha^{-1} h^{-1} would be most effective in the presence of mulch.

In comparing the enrichment enhancement attributed to mulch during gas application at wind speeds below 3.0 m s^{-1} (calculated from data in Table 3) to that predicted during wind speeds above 3.0 m s^{-1} (calculated from regression equations in Table 16), mulch was found to be relatively more effective in decreasing CO_2 loss at the lower wind speeds. Concentrations yielded by 360, 630, and 900 kg CO_2 ha^{-1} h^{-1} at the 10 cm sampling height were increased by 24, 39, and 36% respectively when gas was applied to mulched beds during wind speeds below 3.0 m s^{-1}. In contrast, the increases due to mulch at the 10 cm height were predicted to be 20, 23, and 29% during application of the same rates.

Comparison of Application Rate Efficiencies

An efficiency ratio (ER) was derived for each application rate at the separate sampling heights by the following formula:

$$ER = \frac{\text{uL L}^{-1}\ CO_2\ \text{enriched} - \text{uL L}^{-1}\ CO_2\ \text{control}}{\text{kg ha}^{-1}\ \text{h}^{-1}\ CO_2\ \text{application rate}}$$

This ratio was created to normalize the CO_2 enrichment capacity of each application rate. By subtracting concentrations measured above unenriched beds (paired controls) from the concentrations measured above treatment beds during enrichment, any bias due to changes in ambient concentration were factored out. The ER is not a percentage of added CO_2 retained by the canopy, because the numerator is expressed in concentration units and the denominator in application rate units. Instead, this ratio is a measure of relative enrichment efficiency. Also ER is not to be confused with E, the efficiency of plant uptake derived by Allen et al. (1971). Efficiency ratios for CO_2 application during wind speeds above and below 3.0 m s^{-1} are presented in Table 4.

Efficiency ratios decreased with increasing sampling height for all application rates, and enrichment was most efficient at the base (1 cm sampling height) of the plants when CO_2 was applied under mulch under both wind conditions (Table 4). Under both wind speed conditions, the efficiency of gas application was higher at all sampling heights when enrichment was performed with mulch. Whereas, ER values during carbonated water applications were higher in the presence of mulch at the lower wind speeds but only at the 1 cm height during wind speeds between 3.0 and 4.5 m s^{-1}.

Table 4. Efficiency ratios at two different wind speed ranges. Ratios are expressed in (uL L^{-1} CO$_2$ concentration)/(kg CO$_2$ ha^{-1} h^{-1}). Strawberry field experiment, 1986.

		CO$_2$ Application Rate kg ha^{-1} h^{-1}			
		G 360	CW 420	G 630	G 900
	Sampling height cm	Wind speeds below 3.0 m s^{-1}			
Mu	1	0.93	0.88	0.95	1.01
	10	0.63	0.63	0.63	0.58
	20	0.32	0.35	0.30	0.30
Means		0.63	0.62	0.63	0.63
Umu	1	0.54	0.78	0.55	0.52
	10	0.37	0.52	0.31	0.33
	20	0.21	0.32	0.19	0.18
Means		0.37	0.54	0.35	0.34
		Wind speeds between 3.0 and 4.5 m s^{-1}			
Mu	1	0.36	0.36	0.28	0.26
	10	0.30	0.29	0.28	0.22
	20	0.13	0.14	0.23	0.20
Means		0.26	0.26	0.23	0.20
Umu	1	0.28	0.34	0.25	0.24
	10	0.21	0.29	0.19	0.23
	20	0.11	0.16	0.12	0.10
Means		0.20	0.26	0.19	0.19

The efficiency of all CO_2 applications tested in this experiment were reduced by the higher winds (Table 4). However, the degree of reduction varied considerably so as to change the relative efficiencies of the application rates at the different sampling heights. Whereas 900 kg CO_2 ha^{-1} h^{-1} applied in conjunction with mulch yielded the greatest efficiency at the base of the plants (1 cm sampling height) at the low wind speeds, 360 kg CO_2 ha^{-1} h^{-1} and carbonated water were the most efficient at this height when applied under mulch during the higher wind speeds. Also, 630 kg CO_2 ha^{-1} h^{-1} was found to be the most efficient of all application rates at the 20 cm height in the presence of mulch at the high wind speeds, whereas, during application at the lower wind speeds, carbonated water and 360 kg CO_2 ha^{-1} h^{-1}, yielded higher efficiency ratios in conjunction with mulch.

The mulch factor also influenced the degree of enrichment attenuation by the higher wind speeds (Table 4). During application at the low wind speeds, 630 kg CO_2 ha^{-1} h^{-1} without mulch was slightly more efficient than 360 kg CO_2 ha^{-1} h^{-1} at ground level without mulch, however, during the higher wind speeds, 360 kg CO_2 ha^{-1} h^{-1} was the most efficient of the two at 1 cm. For the most part, these changes were minor, and in no case, did mulch or application rate overcome the effects of wind to render enrichment during the higher wind speeds at any of the three sampling heights more efficient than during the lower wind speeds.

The presence of mulch during application affected the efficiencies of 420 kg CO_2 ha^{-1} h^{-1} in carbonated water differently than those of the gas application rates during both wind speed conditions (Table 4). Although, the presence of mulch did enhance the efficiency of carbonated water, gas application rate efficiencies gained more in the presence of mulch than did carbonated water. This difference attributed to mulch rendered carbonated water more efficient than gas application at both wind speeds in unmulched canopies. During wind speeds between 3.0 and 4.5 m s^{-1}, the efficiency of carbonated water at the top of the canopy was greater without mulch than with mulch. In view of this, it appears that CO_2 evolved from carbonated water was dispersed by wind at the top of the canopy to a greater extent in mulched beds than unmulched beds during carbonated water irrigation. Therefore, under the high wind conditions, mulch had a negative effect on enrichment efficiency of carbonated water.

For maximum efficiency during CO_2 enrichment, based on the results in Table 4, wind speeds should be below 3.0 m s^{-1} and CO_2 should be applied under a mulch barrier. Under these wind conditions, carbonated water should be applied for maximum efficiency at the top of the canopy where photosynthetic potential is the greatest. The lack of efficiency advantage gained by increasing gas application rate warranted gas applications no higher than 360 kg CO_2 ha^{-1} h^{-1} during wind speeds below 3.0 m s^{-1}.

Despite the low efficiency ratios yielded by CO_2 application at the higher wind speeds, previous results (Figure 5) indicate that some enrichment can be achieved by applying CO_2 during wind speeds between 3.0 and 4.5 m s^{-1}. Under such conditions, the use of mulch was found to be beneficial. However, the increase in efficiency in the presence of mulch during the higher wind speeds is substantially less than that observed during the lower wind speeds. The most efficient gas application rate for enrichment at the top of the canopy during the higher wind speeds was 630 kg CO_2 ha^{-1} h^{-1}, however, increasing the rate to 900 kg

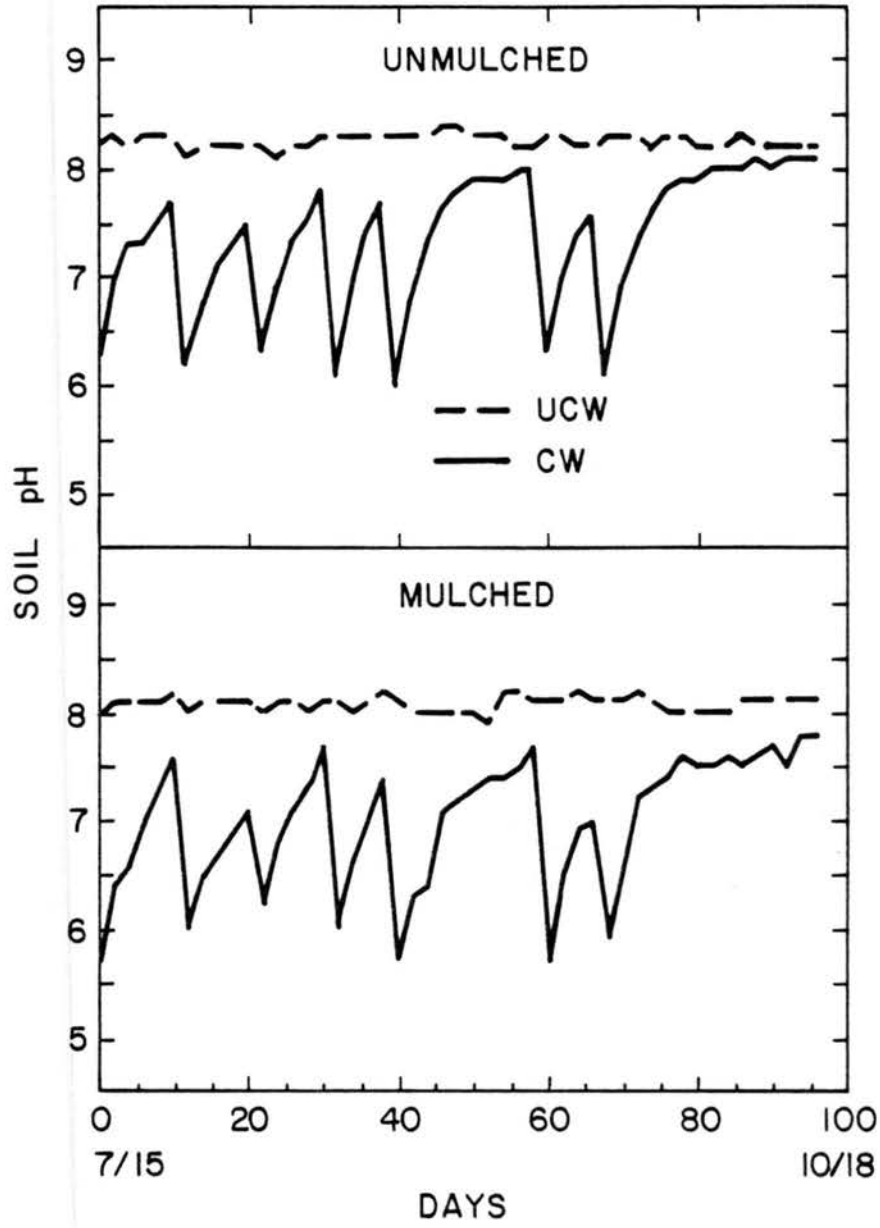
CO_2 ha^{-1} h^{-1} conferred no increase in efficiency at this height. In situations where the use of mulch is infeasible, carbonated water is recommended above gas application during calm conditions to a wind speed of 4.5 $m\ s^{-1}$. Since, the results indicate that enrichment without mulch under the higher wind speed conditions is more efficient than enrichment with mulch at the top of the canopy, the absence of mulch may be particularly beneficial at the higher wind speeds.

Residual Effects of Carbonated Water

Soil pH measurements presented in Figure 7 demonstrate the residual effect of irrigation with carbonated water. Carbonated water resulted in acidification of the calcareous soils in the research plot immediately after irrigation, and irrigation dates are evident by discrete drops in soil pH. Even though the large pH reductions during irrigation were not permanent, the irrigations were spaced such that soil pH remained below the control levels (irrigated with uncarbonated water) over the entire experimental period. The gradual pH increases between irrigation times indicates that carbonated water affected soil chemistry days after application.

This soil acidification would benefit plant growth by increasing availability of micronutrients such as zinc, manganese, and iron, particularly in calcareous soils where micronutrient availability is initially low. Phosphorous and calcium availability might also be increased. Mauney and Hendrix (1988) found that irrigation of pot-cultured cotton plants with carbonated water significantly increased the zinc and manganese content in the leaf blade tissue.

Figure 7. Time courses of soil pH fluctuations at 5 cm depths over 7 irrigation intervals with carbonated water (CW) and uncarbonated water (UCW). Each mean is from four samples taken from four field plot replications (n=16). The first irrigation was on July 15 and the last on September 11. Strawberry field, experiment, 1986.

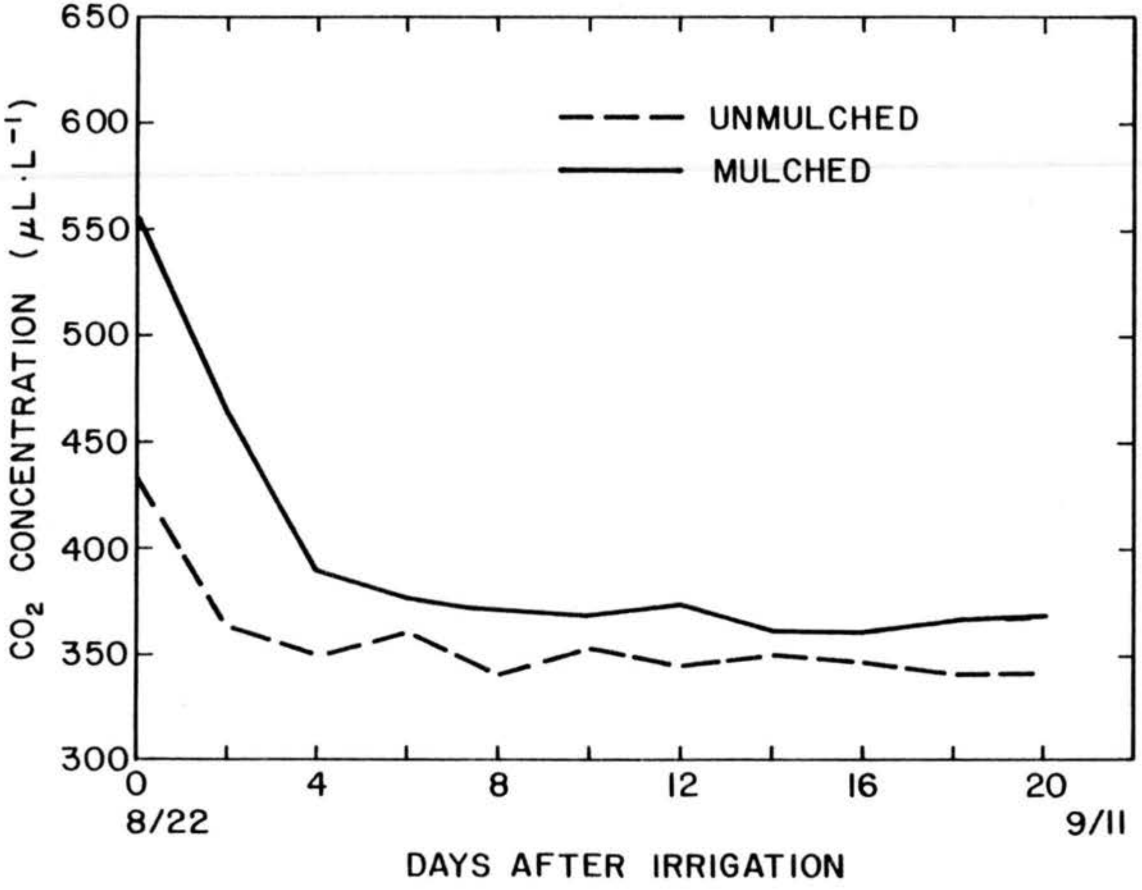

UNMULCHED
MULCHED
UCW
CW
SOIL pH
9
8
7
6
5
9
8
7
6
5
0
20
40
60
80
100
7/15
10/18
DAYS

Reduction in soil pH resulting from carbonated water irrigation was also recorded by Nakayama and Bucks (1980). These authors detected a soil pH decrease from 8.0 to 6.5 during application of CO_2 saturated water. The pH reduction recorded in the Nunn clay Loam of the strawberry experiment site in the experiment ranged from 2.6 units directly after irrigation to 0.1 units 16 days after the final irrigation (Figure 7).

There appeared to be a slightly greater pH reduction in the soil beneath the mulch during carbonated water application, as well as a slight acidification of the control soil by mulch alone (Figure 7). These two occurrences may be attributed to the greater retention of CO_2 by the mulch barrier. The slight reduction recorded in the mulched control soil was most likely due to CO_2 from soil respiration, whereas, the greater pH reduction in the carbonated water irrigated soil was due mostly to the CO_2 in the water. The reduction in pH may be attributed to dissolution of some of the retained CO_2 in the soil solution, increasing the concentration of carbonic acid.

The persistence of soil acidification after irrigation with carbonated water indicates a persistence of carbonation in the soil solution. This residual effect was detected to a smaller degree in mid-canopy CO_2 concentrations (10 cm sampling height) after the August 22 carbonated water irrigation (Figure 8). Elevated CO_2 concentrations persisted for as long as six days above the mulched beds after water application, and as expected from other observations, CO_2 did not persist as long in the canopy of the unmulched beds. However, by the next irrigation date, September 11, CO_2 concentrations above both mulched and unmulched beds had returned to ambient levels. This

Figure 8. Time course of CO_2 concentrations after irrigation with carbonated water. All samples were taken at the 10 cm sampling height. Ambient concentrations averaged 367.4 $uL\ L^{-1}$ CO_2 above mulched beds and 348.2 $uL\ L^{-1}$ CO_2 above unmulched beds. Strawberry field experiment, 1986.



650
600
550
500
450
400
350
300
CO_2 CONCENTRATION ($\mu L \cdot L^{-1}$)
UNMULCHED
MULCHED
0
4
8
12
16
20
8/22
9/11
DAYS AFTER IRRIGATION

indicates that even though there may have been some carbonation persisting in soil solution between the two irrigation dates, no detectable amount of degassing occurred six days after irrigation on August 22. Mauney and Hendrix (1988) found that saturated carbonated water lost half of its CO_2 after 24 hours on a laboratory bench, and assuming a constant rate of degassing, this is much faster than the rate detected from soil solution in this experiment. Degassing from a soil solution, however is likely complicated by many chemical processes in a soil system, particularly acid base reactions, which may slow the rate of degassing from a soil solution.

SUMMARY AND CONCLUSIONS

Field Experiment

Application of CO_2 gas and carbonated water resulted in effective enrichment of a strawberry plant canopy at the three sampling heights tested (1, 10, and 20 cm above the ground). All CO_2 concentrations measured during gas and carbonated water application at wind speeds below 3.0 m s^{-1} were found to be significantly higher than ambient concentrations without enrichment across the entire experimental period. A large reduction in concentrations during enrichment with all three gas application rates (360, 630, and 900 kg CO_2 ha^{-1} h^{-1}) and carbonated water (420 kg CO_2 ha^{-1} h^{-1}) was detected during wind speeds between 3.0 and 4.5 m s^{-1}. However, only 360 kg CO_2 ha^{-1} h^{-1} and carbonated water did not yield significantly higher than ambient concentrations at the top of the canopy (20 cm) during the higher wind speed conditions.

The CO_2 concentrations measured during application of CO_2 gas and carbonated water decreased with increasing vertical distance from the source. Mean CO_2 concentrations yielded during application of 360, 630, and 900 kg CO_2 ha^{-1} h^{-1} were significantly greater at all sampling heights above mulched beds as compared to unmulched beds. In contrast, the mean CO_2 concentrations yielded 20 cm above mulched and unmulched beds during application of carbonated water (420 kg CO_2 ha^{-1} h^{-1}) were not significantly different. Concentration increases at the 20 cm sampling height attributed to the presence of mulch were 11, 18, and 22% respectively for 360, 630, and 900 kg CO_2 ha^{-1} h^{-1}. The increase at 20 cm recorded during application of carbonated water was 6%.

Carbon dioxide concentrations detected at the top of the canopy were considered to be the most important for photosynthetic enhancement. Therefore, conclusions concerning the enrichment effectiveness of each CO_2 application rate during calm conditions (wind speeds below 3.0 m s^{-1} at the beginning of CO_2 application) were drawn through comparisons of enrichment concentrations at the 20 cm sampling height.

Without mulch, the enrichment effectiveness of 900 kg CO_2 ha^{-1} h^{-1} was found to be significantly greater than that of 360 kg CO_2 ha^{-1} h^{-1}. However, no significant advantage was found by increasing CO_2 gas application from 630 to 900 kg ha^{-1} h^{-1} when mulch did not cover the drip tubes. The efficiency ratios, reflective of enrichment efficiency, decreased with increasing gas application from 360 to 900 kg CO_2 ha^{-1} h^{-1} at the 20 cm height without mulch, indicating the impracticality of increasing CO_2 availability at the top of an unmulched strawberry canopy by increasing gas application above 360 kg CO_2 ha^{-1} h^{-1}. Application of carbonated water yielded significantly greater concentrations than 360 kg CO_2 ha^{-1} h^{-1} without mulch. In contrast, no advantage was gained over carbonated water by application of 630 or 900 kg CO_2 ha^{-1} h^{-1} to unmulched beds. This is also reflected in the efficiency ratios, which demonstrate that carbonated water was a more efficient source of CO_2 enrichment at the 20 cm height without mulch than any of the gas application rates tested in this experiment when applied during wind speeds below 3.0 m s^{-1}.

Each of the higher gas application rates resulted in significant increases in CO_2 concentration at the 20 cm sampling above mulched beds. Gas applied at 360 kg CO_2 ha^{-1} h^{-1} yielded the highest efficiency ratio at the top of the canopy at wind speeds below 3.0 m s^{-1}. No difference in efficiency was detected at the 20 cm height during application of 630 or 900 kg CO_2 ha^{-1} h^{-1} during these wind speeds. Applying carbonated water in conjunction with mulch during the lower wind speeds (below 3.0 m s^{-1}) did not yield a significant enrichment advantage over any of the gas application rates in the presence of mulch. However, the efficiency ratios indicate that even in the presence of mulch, carbonated water yielded more CO_2 at the top of strawberry canopy per unit of CO_2 applied than any of the three rates of gas application. Due to the high efficiency and greater effectiveness of carbonated water without mulch, application of CO_2 in water to strawberry plants is recommended when the use of mulch is not feasible. When CO_2 can be applied in the presence of mulch application of 900 kg CO_2 ha^{-1} h^{-1} is recommended for its effectiveness, although some efficiency from the application must be sacrificed.

Wind speeds between 3.0 and 4.5 m s^{-1} attenuated the enrichment efficiencies of all four application rates with and without mulch. Although, the enrichment was not significant, carbonated water was more efficient in increasing CO_2 concentration at the top of the canopy than all other CO_2 applications without mulch during wind speeds in this range. Application of 630 kg CO_2 ha^{-1} h^{-1} resulted in the greatest of the gas rate efficiencies 20 cm height above mulched beds under the high wind conditions, with 900 kg CO_2 ha^{-1} h^{-1} still substantially more efficient at the top of the strawberry canopy than 360 kg CO_2 ha^{-1} h^{-1} or carbonated water in the presence of mulch at these wind speeds.

Interpretation of response surfaces, relating CO_2 concentrations at the 10 cm sampling height to the three gas application rates (360, 630, and 900 kg CO_2 ha^{-1} h^{-1}) and wind speeds ranging from 0.5 to 4.5 m s^{-1} during sampling, demonstrated that mulch enhanced enrichment during all applications. Carbon dioxide concentrations above unmulched beds appeared to be diminished more by wind speeds greater than 3.0 m s^{-1} than concentrations yielded above mulched beds. Mulch was found to decrease the dispersive effects of wind during application of 900 kg CO_2 ha^{-1} h^{-1} to a greater extent than during application of 360 kg CO_2 ha^{-1} h^{-1}. However, without mulch, greater proportions of CO_2 were lost to wind dispersion as application rate increased. This was most evident in the relatively large drop in the CO_2 concentration response at the highest wind speed (4.0 m s^{-1}) during application of 900 kg CO_2 ha^{-1} h^{-1} to unmulched beds.

Although 630 and 900 kg CO_2 ha^{-1} h^{-1} yielded higher CO_2 concentrations than carbonated water with and without mulch during wind speeds both below 3.0 m s^{-1} and between 3.0 and 4.5 m s^{-1}, application of carbonated water was found to be more efficient than any of the three gas application rates tested during both wind speed conditions. This indicates that increasing the CO_2 delivered by carbonated water could more effectively enhance enrichment at the top of a strawberry canopy than could increasing the rate of CO_2 delivered as gas at such winds speeds. Additional advantages of carbonated water were soil pH reductions that lasted up to 16 days after carbonated water irrigation.

Also, a persistence of CO_2 enrichment at the 10 cm sampling height was detected up to 6 days after carbonated water application. Both occurrences were augmented by the presence of mulch.

Increasing the CO_2 concentrations in carbonated water is limited by the pressure restrictions of the delivery system; the higher the pressure of carbonated water the more CO_2 it carries. Another method of increasing CO_2 delivery by carbonated water is by increasing the irrigation rate. The potential of this method depends on crop water requirements and the soil and climatic factors that influence these requirements. The use of plants with high water requirements under conditions that warrant large volume or frequent irrigations are needed to maximize the effectiveness of this method. Additionally, application of carbonated water to basic soils can increase micronutrient availability by reducing pH. However, to avoid aluminum and other trace element toxicities, carbonated water irrigation is not recommended in soils that tend to be acidic.

Use of a multiple line CO_2 delivery system, in which each plant rows or bed is individually supplied with CO_2 appears to be more feasible than relying on horizontal dispersion of CO_2 from line sources distributed throughout a designated area of enrichment. Allen et al. (1974) observed little to no enrichment 15 m downwind from one line source releasing CO_2 gas at rates as high as 580 kg ha^{-1} h^{-1}. Application of CO_2 to small areas, as in the present experiment, reduces the exposure of gas to the bulk atmosphere before it comes in contact with the plant canopy. The availability of gas to all plants is more consistent. Because of the greater complexity of this system, the multiple line method of enrichment would not be feasible with agronomic crops on a large scale. Use of this system should be restricted to high cash value crops that can be densely planted under situations in which mulching with a continuous barrier is feasible.

MATERIALS AND METHODS

Growth Chamber Experiment

Plant Establishment

Strawberry plants (Fragaria x ananassa Duch) of the day neutral cultivar Fern were grown in three Percival M-60 growth chambers under 300, 600, and 900 uL L^{-1} CO_2 concentrations for nine weeks. Nine weeks was considered a sufficient amount of time for the plants to complete a fruiting cycle. The plants were harvested at the end of the growth period and dry weights of seven yield components were measured at harvest to assess plant response to CO_2 enrichment of the growing environment. In addition, fruit production and leaf area expansion was evaluated over the course of the nine week treatment period.

Sixty strawberry plants were uprooted from a greenhouse bench just after a fruiting cycle, potted in four-inch (10.16 cm) standard plastic pots and arranged on 122-cm by 61-cm growth chamber racks placed 72 cm from the top-mounted light source. All but three to five leaves were removed from each plant, and any flower buds were pinched off. A single plant was designated by a single crown, such that each plant had only one crown when placed in the pots. Bare root stock was planted in the greenhouse bench late Spring, 1985.

The plants were randomly assigned to six rows of ten on the growth chamber racks. The rows were arranged from the front of the chamber, as designated by the door, to the back wall. The potting media consisted of one part peat, one part perlite, and one part vermiculite by volume amended with 5768 g limestone ($CaCO_2$), 595 g $MgSO_4$, 372 g treble superphosphate ($CaH_4(PO_4)_2$) per cubic meter of soil, and the following trace elements: 1.86 g Mangenese, 3.03 g iron, 0.56 g Copper, 0.30 g Boron, and 0.0026 g Molybdenom per cubic meter of soil added in the form of 37.17 g of Peters Fritted Trace Elements. Plants in all chambers were watered as needed.

The plants were allowed to acclimate to the growth conditions of the chambers four days prior to establishment of carbon dioxide concentrations. The photoperiod in all three growth chambers was maintained at 16 hours and the light/dark temperatures at 24C/16C throughout the experimental period. The temperatures were monitored with glass and mercury thermometers placed on the back wall of the chambers. Irradiance in each chamber was provided by four 40 watt incandescent bulbs and 10 cool white flourescent bulbs. The irradiance values were measured at photosynthetic photon flux density (400 to 700 nm) with a Licor Photometer using a quantum bar sensor that integrates the incident radiation over the one meter length of the sensor.

Carbon dioxide gas from a standard number two size (64 kg) cylinder was continuously injected at different rates into two of the three chambers during the light cycle to maintain 600 and 900 $uL\ L^{-1}$ CO_2 concentration over the nine week test period. Dry nitrogen gas from the same sized cylinder was injected to maintain the 300 $uL\ L^{-1}$ concentration. The CO_2 concentrations were monitored periodically throughout the light period and the flow into the chambers adjusted to keep the concentrations at the desired levels. The diurnal fluctuation in the

CO_2 concentration maintained in each of the three chambers is presented in Figure 16 of the appendix.

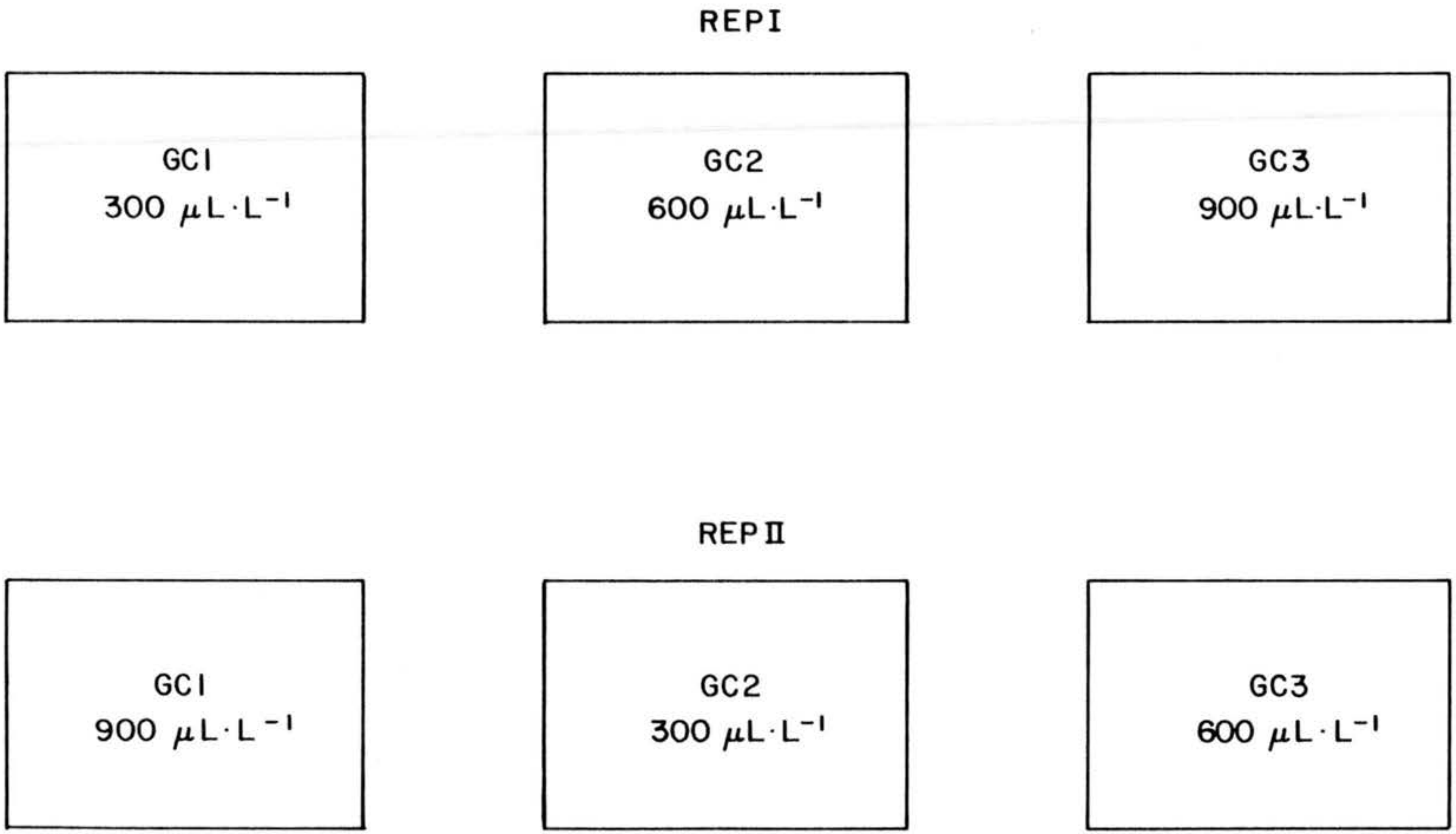
The experiment was repeated once in time, such that the experiment incorporated two replications. The plants for the first replication were placed in the chambers on January 2, 1987 and harvested 67 days later on March 10, 1987. The second replication began on April 3, 1987 and the plants were harvested on June 9, 1987, also 67 days after transplanting. Since photoperiod has not been found to affect fruiting in day-neutral cultivars (Durner et al., 1984) plants from the same greenhouse were used in each replication. Care was taken to harvest plants of uniform size and reproductive stage.

The three CO_2 concentrations were rotated among the chambers between replications to account for any inconsistencies in chamber conditions. The arrangement of CO_2 concentrations among the chambers is presented in Figure 9.

Plant Attributes Measured

The number of flower buds, unripe, and ripe fruit were counted each week in each growth chamber to assess the reproductive response to the CO_2 enrichment. Counting started with the appearance of the first flower bud, and as this occurrence was different for the two replications, measurements were not made at the same relative time after transplanting for each replication. Counts of flower buds, unripe fruit, and ripe fruit were taken from all 60 plants at weekly intervals. The ripe fruit were harvested after counting and each fruit was weighed after harvest. Additionally, the first occurrence of anthesis was determined in each growth chamber within two to three days.

Figure 9. Randomization of three CO_2 concentrations among growth chambers (GC) across two replications in time. Concentrations were maintained during a 16 hour light period every day from January 6 through March 10 for Rep I and from April 7 through June 9 for Rep II. Strawberrry growth chamber experiment, 1987.



REP I		
GC1 300 $\mu L \cdot L^{-1}$	GC2 600 $\mu L \cdot L^{-1}$	GC3 900 $\mu L \cdot L^{-1}$

REP II		
GC1 900 $\mu L \cdot L^{-1}$	GC2 300 $\mu L \cdot L^{-1}$	GC3 600 $\mu L \cdot L^{-1}$

To evaluate the vegetative response to the CO_2 concentrations, the course of leaf area expansion was non-destructively determined from every fully expanded leaf of five plants randomly selected from the 60 in each growth chamber. Length and width measurements were taken from each leaf every week for seven weeks beginning on January 10, 1987 for the first replication and April 11, 1987 for the second replication (8 days after transplanting). Leaf areas were then derived using a linear prediction equation relating the product of leaflet width and length to leaflet area (appendix Figure 17). The relationship was determined prior to the experiment. A Licor model LI 3100 Area Meter was used to measure leaflet areas. Leaves showing loss in leaf area accompanied by yellowing and/or necrosis were assumed to be senescing and were removed. Consequently, only the growth course of actively expanding leaves was evaluated from the five selected plants.

In addition to the leaf area measurements, the number of leaves on all 60 plants were counted in each growth chamber on the same measuring dates. The number of new leaves, old leaves and senescing leaves were determined to assess the effect of enrichment on development and loss of leaves. Necrotic leaves were removed after counting.

Upon harvest, leaf areas, dry weights of leaves, roots, crowns, flowering trusses and runners were measured from each of the 60 plants in each growth chamber. The plant material was dried for 72 hours at 70 C in a forced air drying oven, and leaf areas were determined with the Licor model LI-3100 Area Meter from each plant immediately after harvest.

The plant attributes determined after harvest were leaf area, shoot weight (the sum of flower truss weight, leaf weight, crown weight, and runner weight), root weight, root:shoot ratio, specific leaf area (leaf area/leaf weight), crown weight, and total dry weight (the sum of shoot weight and root weight).

Carbon Dioxide Injection and Monitoring System

The CO_2 and N_2 gas flow injected into the chambers was controlled with a barostat and flow board assembly described by Hanan (1986). The flow needed to maintain the proper CO_2 concentrations in the chambers was determined by periodically measuring the chamber concentrations and adjusting the flow.

The flow rates were increased over the nine week treatment period to maintain constant enrichment concentrations as photosynthetic consumption increased with plant growth. The flow rate of CO_2 during the first replication started at 1.5 ml s^{-1} and was increased to 2.1 ml s^{-1} at the end of the treatment period to maintain 600 uL L^{-1} CO_2, and started at 2.9 ml s^{-1} and was increased to 3.4 ml s^{-1} to maintain 900 uL L^{-1}. During the second replication, the flow rate started at 1.1 ml s^{-1} and was increased to 2.3 ml s^{-1} to maintain 600 uL L^{-1} CO_2, and started at 2.9 ml s^{-1} and was increased to 3.9 uL L^{-1} to maintain 900 uL L^{-1}. These flow changes reflect increases in CO_2 consumption by the plants, however, this is not a definitive measure of photosynthetic use because the chambers were not completely sealed and vents were opened and closed periodically to help maintain the targeted CO_2 concentrations.

To monitor chamber CO_2 concentrations, air samples were drawn from each chamber through a 28-cm 20-gauge hypodermic needle fixed into the chamber through a 5-cm stoppered port located 15 cm above the growth rack and 10 cm from the growth chamber wall. A 10-ml BD Plastipak syringe was used to draw the air samples through the needle. The CO_2 concentration of the air samples was analyzed with a Beckman 865 infra-red gas analyzer using a pulse injection method as described by (Clegg et al., 1978). Two-milliliter aliquots from the samples were injected into a constant 0.45 L min^{-1} stream of dry nitrogen which carried the sample through the infra-red light source to be analyzed. The analyzer was calibrated with 2 ml samples of six known CO_2 concentrations within the range of the targeted chamber concentrations (appendix Figure 18).

Experimental Design and Analysis

The experimental design was comprised of two replications of three treatments, 60 sampling units per treatment, a plant being a sampling unit or experimental unit. Only measurements taken at harvest were from each of the 60 plants; reproductive parameters, leaf numbers and leaf areas taken throughout the experiment were evaluated for all 60 plants collectively.

An analysis incorporating the three treatments and two replications, revealed significant differences in the growth chambers which could not be statistically separated from treatment differences due to lack of replication. This difference was most noticeably manifested in a depression of growth in chamber 3, which could be partially attributed to a clouded light diffusser. Consequently, all the measurements from the 600 and 900 uL L^{-1} treatments for both replications were combined to reduce the effect of any one growth chamber on any one enrichment treatment. The 600 and 900 uL L^{-1} treatments, then, were not evaluated separately but as a joint treatment to determine a generalized response of day-neutral strawberry plants to CO_2 enrichment. A combination of responses from both replications to 600 and 900 uL L^{-1} CO_2 were compared to the combined responses from the two replications of the 300 uL L^{-1} treatment. This enabled a comparison between concentrations substantially above present global ambient levels (600 and 900 uL L^{-1} CO_2) to 300 uL L^{-1} CO_2 which is close to present ambient levels (320 to 350 uL L^{-1}). The 300 uL L^{-1} CO_2 concentration was considered a control treatment.

Independent t-tests were used to compare fruit weights taken throughout the experimental period and plant component dry weights and their ratios at the end of each replication period. Since measurements from two replications of two CO_2 concentrations (600 and 900 uL L^{-1}) were combined without averaging and only two replications for the control, there were twice as many measurements from the enrichment treatment as from the control treatment.

The cumulative number of flower buds, ripe and unripe fruit and leaf areas from 5 plants were regressed against time to generate smooth lines for comparison of the two treatments. As with the plant component measurements taken at harvest, all of the counts and leaf areas measurements from both replications of the enrichment treatment (joint responses to 600 and 900 uL L^{-1} CO_2) and the 300 uL L^{-1} were combined without averaging. Since relative sampling times did not match between replications, each count was treated as a distinct unreplicated data point in all of the regression procedures.

RESULTS AND DISCUSSION

Growth Chamber Experiment

Fruit and Flower Bud Production

The trends in flower bud production characterized by the regression lines in Figure 10, indicate that flower buds were produced earlier by the plants exposed to 600 and 900 uL L^{-1} CO_2 than those exposed to 300 uL L^{-1} CO_2. By the end of the sampling period, production of flower buds in the control environment had caught up to the enriched plants. However, earliness appears to be an advantage in itself, because the cumulative time courses of unripe fruit (Figure 11) and ripe fruit (Figure 12) production suggest that earlier bud production by the enriched plants, gave rise to earlier fruit set (Figure 11) and faster ripening. Earlier fruit production can provide an edge in marketing, and such earliness in response to CO_2 enrichment has also been recorded in tomatoes (Krizek et al., 1974), wheat and sunflowers (Marc and Gifford, 1983) and cowpea (Bhattacharya et al., 1985).

It appears that the early bud formation also hastened anthesis. The mean time to first anthesis was 9 days for enriched plants and 13.5 days for plants grown in the control environments. The enriched plants set fruit 3.2 days after first flowering and the control plants set fruit 5 days after first flowering. The first ripe fruit was produced 26 days after first flowering in the control environment and 22.5 days in the CO_2 enriched environment, an advance of 3.5 days by the enriched

Figure 10. The effect of 300 uL L^{-1} CO_2 (control) and a combination of 600 and 900 uL L^{-1} CO_2 (enriched) on cumulative production of flower buds by 60 plants as characterized by a fitted curve. The plants were maintained in growth chambers at each of the three CO_2 concentrations during 16 hour light periods each day for nine weeks. Regression procedures were used to smooth the responses for comparison. Strawberry growth chamber experiment, 1987.

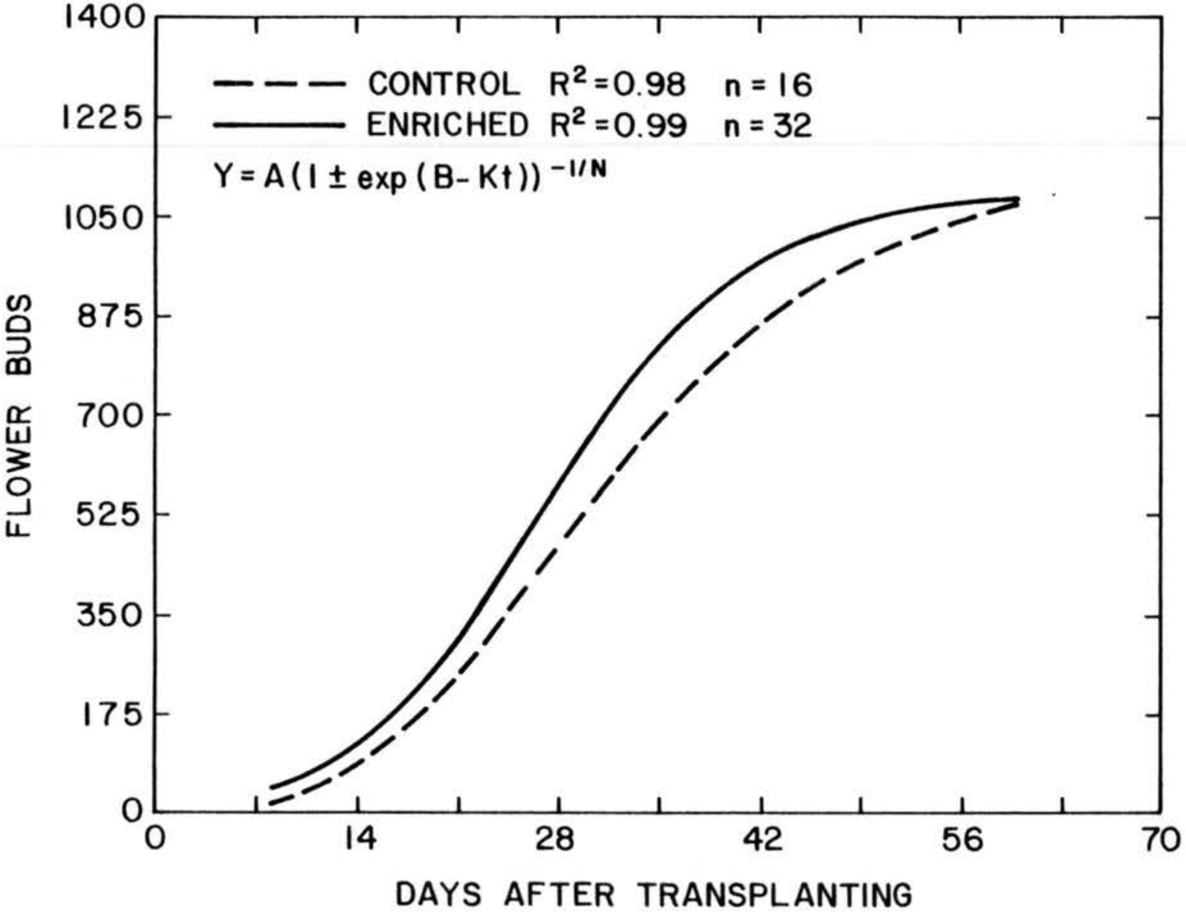

CONTROL $R^2=0.98$ n = 16
ENRICHED $R^2=0.99$ n = 32
$Y=A(1\pm\exp(B-Kt))^{-1/N}$
FLOWER BUDS
0
175
350
525
700
875
1050
1225
1400
0
14
28
42
56
70
DAYS AFTER TRANSPLANTING

Figure 11. The effect of 300 uL L^{-1} CO_2 (control) and a combination of 600 and 900 uL L^{-1} CO_2 (enriched) on cumulative production of unripe fruit by 60 plants as characterized by a fitted curve. The plants were maintained in growth chambers at each of the three CO_2 concentrations during 16 hour light periods each day for nine weeks. Regression procedures were used to smooth the responses for comparison. Strawberry growth chamber experiment, 1987.

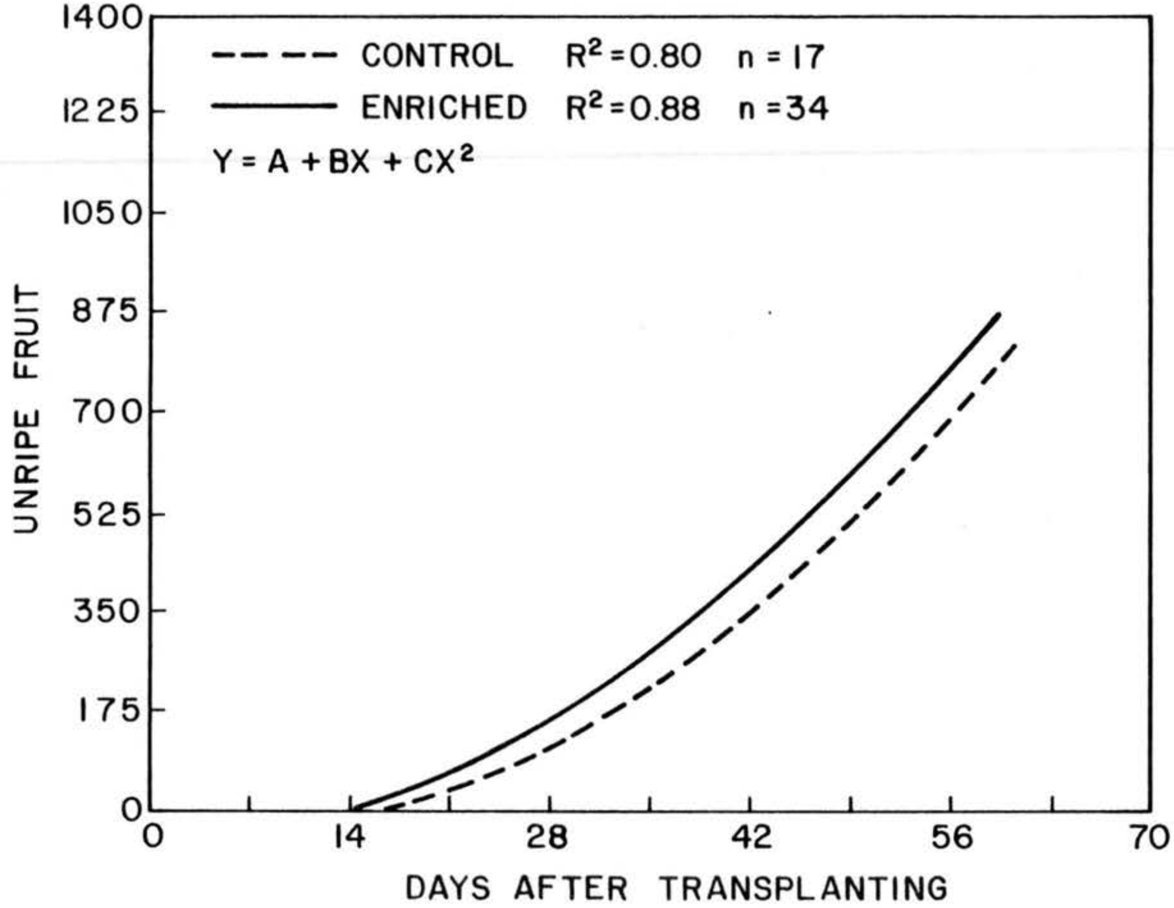
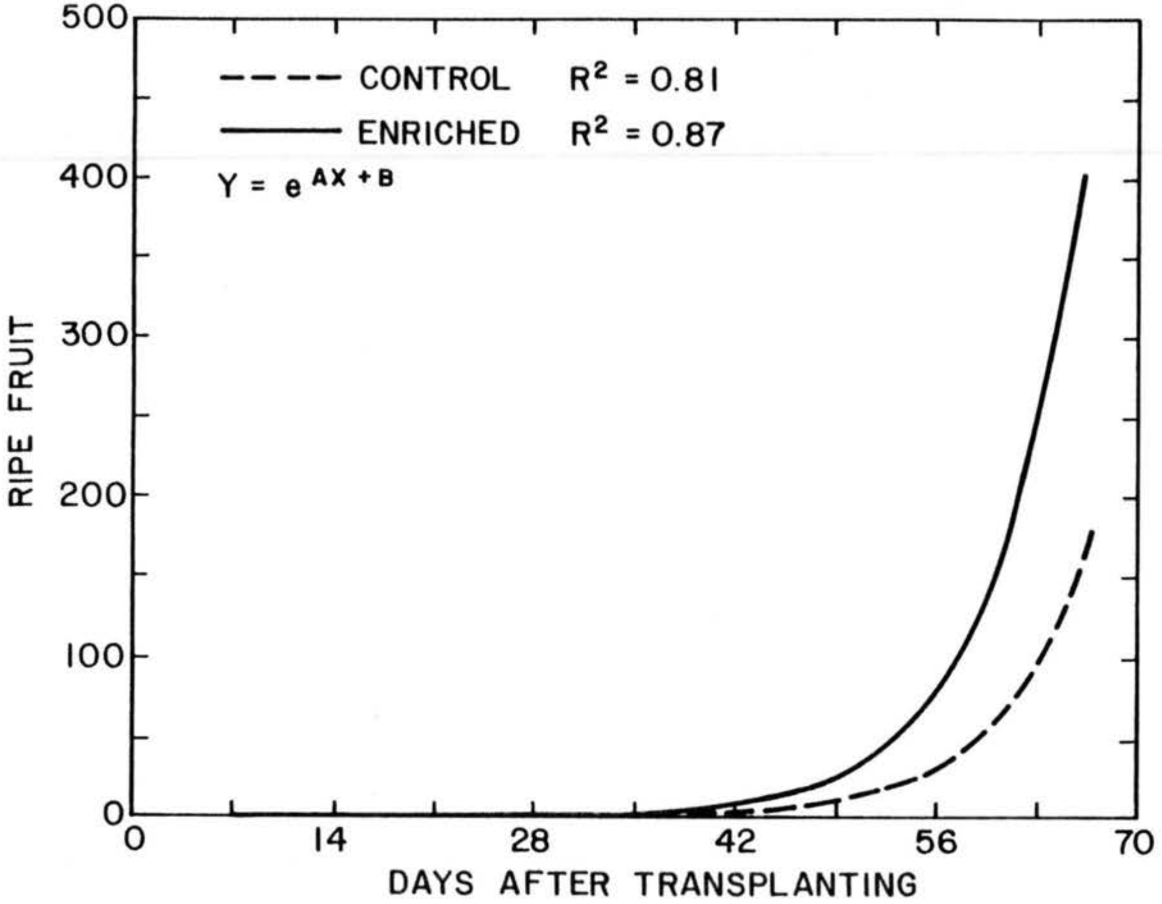

CONTROL $R^2=0.80$ n = 17
ENRICHED $R^2=0.88$ n = 34
$Y = A + BX + CX^2$
UNRIPE FRUIT
1400
1225
1050
875
700
525
350
175
0
0
14
28
42
56
70
DAYS AFTER TRANSPLANTING

Figure 12. The effect of 300 uL L^{-1} CO_2 (control) and a combination of 600 and 900 uL L^{-1} CO_2 (enriched) on the cumulative production of ripe fruit by 60 plants as characterized by a fitted curve. The plants were maintained in growth chambers at each of the three CO_2 concentrations during 16 hour light periods each day for nine weeks. Regression procedures were used to smooth the responses for comparison. Strawberry growth chamber experiment, 1987.


CONTROL $R^2 = 0.81$
ENRICHED $R^2 = 0.87$
$Y = e^{AX + B}$
RIPE FRUIT
0
100
200
300
400
500
0
14
28
42
56
70
DAYS AFTER TRANSPLANTING

plants. Enoch et al. (1976) also recorded advances of 2 to 3 days in ripe fruit production after first flowering by the cultivar Tioga grown in greenhouses atmospheres enriched to 3000 uL L^{-1} CO_2.

Figure 12 shows a greater production of ripe fruit by the enriched plants by the end of the nine-week experimental period. However, since it appears that the fruiting cycle was not completed by the end of the nine-week period, this observed increase in fruit production may not reflect overall production capacity of the enriched plants. More informative are the fruit weight results in Table 5. The mean fresh weight of individual fruit produced by the enriched plants were significantly higher than the mean from the plants grown in the control environment, however, the fruit yield from all harvests was not significantly greater for the enriched plants.

The fruit yield data presented in Table 5 demonstrate that the largest fruit (mean fresh weight of 9.35) were produced by the enriched plants 46 days after transplanting (42 days of enrichment). Enoch et al., (1976) found that fruit yield increases in enriched 'Tioga' plants was due to greater fresh weight per fruit in the first developed fruit and greater number of fruit per bed later in the three and one half month enrichment period. Although, the first fruit were not the largest in the present experiment, there was a marked trend towards reduction in fruit weight of enriched plants following the 46 day harvest. The trend in fruit production and individual fresh fruit weight with harvest date illustrated in Table 5 indicates that fruit number contributed more to total fruit yield than fruit weight as time progressed after 42 days of enrichment.

Table 5. The effect of 300 uL L^{-1} CO_2 (C) and a combination of 600 and 900 uL L^{-1} CO_2 (E) on individual ripe fruit weight, fruit yield, and number of fruit produced, n on each of 12 harvests. Strawberry growth chamber experiment, 1987.

	Ripe Fruit Weight (g)						Fruit Yield/60 plants (g)			
Days After Transplanting	E x	E n	C x	C n	E − C	t-statistic	E	C	E − C	t-statistic
25	3.97	1	0.00	–	–	–	3.97	–	–	–
31	7.12	4	0.00	–	–	–	3.56	–	–	–
32	4.62	1	0.00	–	–	–	4.62	–	–	–
35	7.22	7	0.00	–	–	–	3.61	–	–	–
37	7.59	42	6.48	7	1.11	0.44ns	159.69	45.36	114.33	–
39	7.95	19	2.61	1	5.34	–	75.53	2.61	72.92	–
44	8.32	49	6.68	10	1.84	0.16ns	203.84	66.80	137.04	–
46	9.35	37	6.81	19	2.74	2.67**	172.98	129.39	43.59	–
51	7.71	53	5.05	19	2.66	3.40**	204.32	95.95	108.37	–
53	6.64	115	4.03	63	2.61	5.19**	381.80	253.89	127.91	–
60^z	6.01	255	4.00	119	2.01	5.95**	383.14	238.00	145.14	–
66^z	5.36	199	3.95	111	1.41	4.03**	266.66	219.23	47.44	–
All Harvests	6.50	782	4.32	349	2.18	10.45**	155.31	87.60	67.71	1.36ns

** Significance at P<0.01
ns Not significant

^{z} Data from two replications

Leaf Production

The number of leaves produced by the enriched and control plants were significantly different for the two replications. The fluctuation in the numbers and lack of a smooth increase with sampling time in Table 6 reflects the variability between replications, since leaf numbers were not counted on the same number of days after transplanting in both replications. Significantly more leaves were produced in the first replication than the second. The mean number of leaves from all three chambers and sampling dates was 495 ± 23.4 for the first replication and 410 ± 19.8 for the second replication.

Mean numbers of total leaves, new leaves and senescent leaves produced per sampling date by enriched and control plants were not significantly different (Table 6). This lack of difference may be partially attributed to the variability among the growth chambers, specifically, the effect of the lower light in the third chamber on the two enrichment concentrations. Despite the differences in replications and growth chambers, the enriched plants consistently produced more leaves than the plants in the control environment. In view of this trend, it appears that enrichment enhances leaf production. A conclusion supported by findings made by Enoch et al. (1976) in which a significant 22% increase in leaf number was recorded in day-neutral strawberry plants exposed to 3000 uL L^{-1} CO_2 in a greenhouse.

Although the differences were not significant, enriched plants produced greater percentages of new and senescent leaves than did control plants on each sampling date in Table 6. The difference in new leaves produced by the enriched and control plants (E - C) was larger than the difference for senescent leaves on every sampling day until 25

Table 6. The effect of 300 uL L^{-1} CO_2 (C) and a combination of 600 and 900 uL L^{-1} CO_2 (E) on the production of total number of leaves, new leaves, and senescent leaves per 60 plants. The percent new and senescent leaves of the total leaf number in response to 600 and 900 uL L^{-1} CO_2 is expressed as %TE and %TC in response to 300 uL L^{-1} CO_2. Number of leaves is expressed as n. Strawberry growth chamber experiment, 1987.

	Total Leaves			New Leaves					Senescent Leaves				
Days After Transplanting	E n	C n	E − C	E n	E %TE	C n	C %TC	E − C	E n	E %TE	C n	C %TC	E − C
4[z]	261	258	3	47	18	45	17	2	9	3.3	10	4	−1
7	373	342	31	63	17	51	15	12	15	4.0	11	3	4
11	331	299	32	70	21	59	20	11	27	8.2	20	9	7
15	438	365	73	63	14	50	14	13	17	3.7	7	2	10
18	394	346	48	78	20	61	18	17	26	6.6	22	6	4
22	513	472	41	89	17	73	16	16	25	4.9	12	3	13
25	455	411	44	97	21	85	21	10	45	9.9	25	6	20
29	573	503	70	105	18	90	18	15	35	5.8	15	3	20
32	493	465	28	100	20	91	20	9	78	15.8	55	12	23
39[z]	608	524	84	116	19	88	17	28	88	14.5	57	11	31
46[z]	568	532	36	83	15	65	13	27	96	16.9	69	13	27
53[z]	511	498	13	58	11	42	8	16	91	17.8	72	14	19
60[z]	480	457	23	50	10	40	9	10	72	15.0	61	13	11
All Sampling Dates													
x	421	462	41	79	17.4	64	15.6	15	48	9.7	34	7.6	14

[z] Data from two replications

days after transplanting, after which senescent leaves showed a greater difference. This indicates a faster turnover of leaves at first and then a tendency towards greater senescence. The accelerated senescence may be linked to starch accumulation in the leaves associated with CO_2 enrichment. Starch accumulation has been found to result in feedback inhibition of ribulose bisphosphate carboxylase oxygenase, low activity of which has been found to accelerate leaf senescence (Wittenbach, 1979).

Accelerated leaf senescence attributed to CO_2 enrichment has also been recorded in cowpea by Bhattacharya et al. (1985), by Sionit et al. (1987) in soybean, and by Peet et al. (1986) in cucumbers. Omer and Horvath (1983) attributed their findings of accelerated aging in whole winter annual plants grown in CO_2 enriched greenhouse chambers to possible increase in ethylene production at elevated CO_2 levels. The shortening of whole-plant life span discovered by these authors was strongly correlated with early flower initiation, indicating that elevated CO_2 may shorten the plant's entire developmental period, including time to seed production.

The greater number of senescent leaves found in the strawberry plants of this experiment under CO_2 enrichment may be an indicator of faster turnover of the fruiting cycles in these day-neutral plants. The appearance of earlier buds and fruits in the enrichment chambers supports this as well. However, the exponential relationship of ripe fruit production over the time period sampled (Figure 12) suggests that the fruiting period was not complete six weeks following appearance of the first fruit (25 days after transplanting). Since the designated fruiting cycle for day-neutral cultivars is six weeks, it appears that the fruiting cycle of the 'Fern' plants in this experiment was extended in the growth chamber environment. This may be due in part to the low irradiance levels supplied in the artificial environment.

Figure 13 indicates little difference in leaf area expansion between the two growth environments until 50 days after transplanting, the last day of measurement. At this point, leaf area from the control treatment exceeded that from the enrichment treatment. Desjardins and Gosselin (1987) recorded a greater leaf area per plant of enriched 'Kent' (a Junebearer) ex-vitro plantlets as compared to unenriched plants 20 days after apical meristem cultures were transferred to a rooting media in CO_2 enriched greenhouse chambers. This could be attributed mostly to the high growth rate of the young plantlet leaves. The lack of root growth increase in response to CO_2 enrichment indicates that most of the assimilates were being shunted to shoot growth in the plantlets. In contrast, the leaves from the mature plants of this experiment were at different growth stages during any one sampling time.

Yield Components at Harvest

Comparison of yield component means are presented in Table 7. All yield component means from the enriched plants were significantly greater than those from the control plants with the exception of mean leaf area ratio (LAR - cm^2 g^{-1} total plant dry weight). Although, LAR did not show a significant response to enrichment, the CV (coefficient of variability) values were much greater for this component than any of others. The relatively large amount of variability unaccounted for in the measurements may have obscured any LAR differences due to treatment effect. Because a significant decrease in specific leaf area

Figure 13. The effect of 300 uL L^{-1} CO_2 (control) and a combination of 600 and 900 uL L^{-1} CO_2 (enriched) on production of cumulative leaf area by 5 out of 60 plants as characterized by a fitted curve. The plants were maintained in growth chambers at each of the three CO_2 concentrations during 16 hour light periods each day for nine weeks. Regression procedures were used to smooth the responses for comparison. Strawberry growth chamber experiment, 1987.

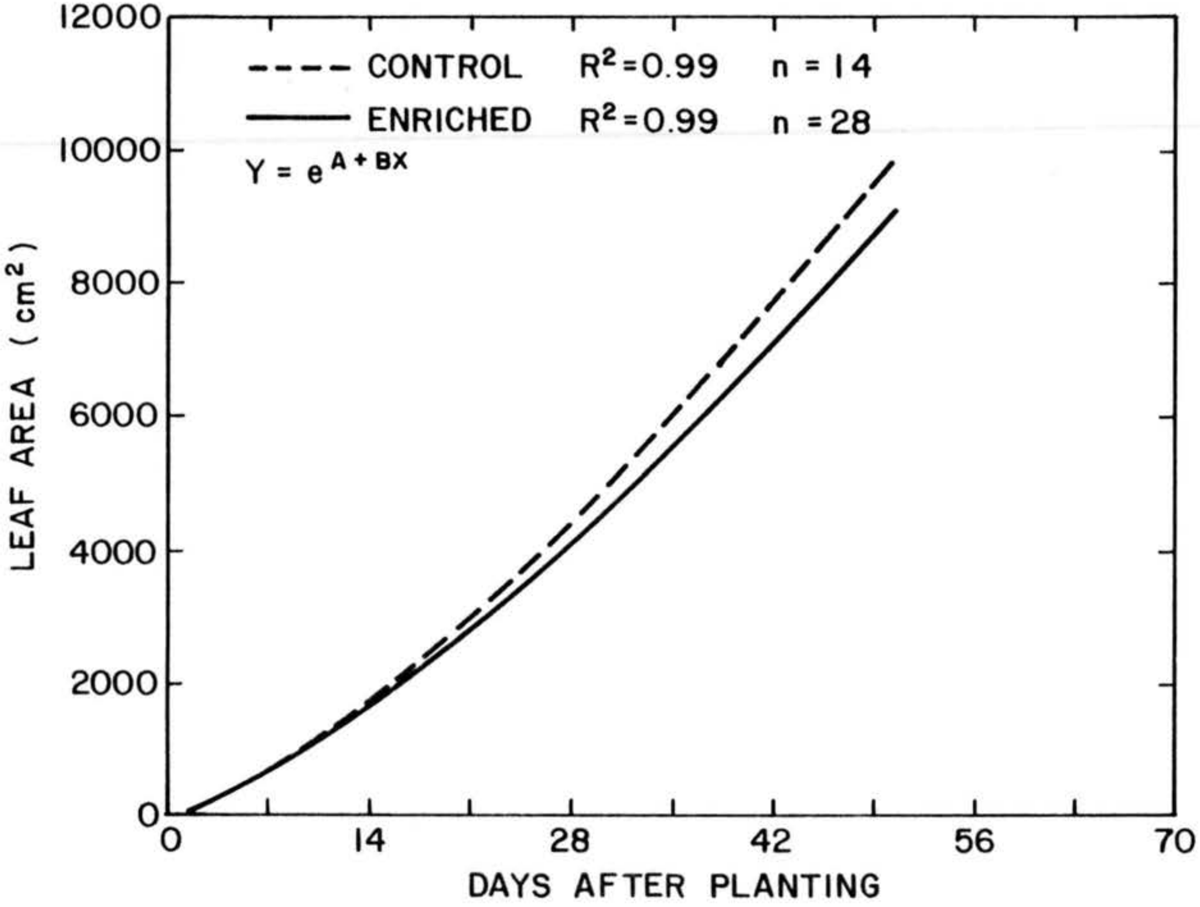

CONTROL R^2=0.99 n = 14
ENRICHED R^2=0.99 n = 28
Y = e$^{A + BX}$
LEAF AREA (cm^2)
12000
10000
8000
6000
4000
2000
0
DAYS AFTER PLANTING
0
14
28
42
56
70

Table 7. The effect of 300 uL L^{-1} CO_2 (C) and combination of 600 and 900 uL L^{-1} CO_2 (E) on yield component means after 67 days of treatment. The percent dry weight contribution by each component to the total dry weight is expressed as %EDW or %CDW. The contribution of each component yield difference (E - C) to the total dry weight difference is expressed as %DW E - C. All g $plant^{-1}$ values are reported on a dry weight basis. Strawberry growth chamber experiment, 1987.

Yield Component	E			%EDW	C			%CDW	E - C	t-statistic	%DW E - C
	x	n	CV		x	n	CV				
Shoot (g $plant^{-1}$)	3.18	240	42.30	47	2.48	120	33.81	49	0.70	5.23**	40
Root (g $plant^{-1}$)	2.17	240	46.09	32	1.38	120	41.21	27	0.79	7.96**	45
Crown (g $plant^{-1}$)	1.45	240	33.06	21	1.18	120	29.39	24	0.27	5.51**	15
Total (g $plant^{-1}$)	6.80	240	33.60	100	5.04	120	26.79	100	1.76	7.77**	100
Leaf Area Ratio (cm^2 g^{-1})	79.71	240	107.88		97.61	120	104.11		65.66	1.74ns	
Specific Leaf Area (cm^2 g^{-1})	234.56	240	72.60		286.33	120	69.47		51.77	2.57**	
Root : Shoot Ratio	0.74	240	40.87		0.60	120	40.87		0.14	3.98**	

** Significance at P<0.01

ns Not significance

(SLA - cm^2 leaf area g^{-1} shoot weight) was found, a significant reduction in LAR was expected.

Production of heavier leaves with little or no increase in leaf area (resulting in higher LAR) has been recorded in several annual species (Ho, 1977; Neales and Nicholls, 1978; Peet, 1986; Sionit et al., 1982) and some perennial species (Hughes and Cockshull, 1972; Thomas and Harvey, 1983) in response to CO_2 enrichment. Leaf expansion (Figure 13) and leaf number results (Table 6) suggest that CO_2 enrichment stimulated new leaf production rather than leaf expansion. The absence of an LAR difference indicates that the new leaves produced in the enrichment environment tended to be smaller and thicker than those produced in the control environment. The smaller SLA mean from the enriched plants further supports this in that the smaller the SLA the thicker the leaves.

Thomas and Harvey (1983) found that increases in soybean leaf thicknesses exposed to CO_2 enrichment were caused mostly by increased palisade cell formation, and to a small extent starch accumulation in the chloroplasts. These authors also observed increases in stomatal frequencies at 520 and 910 uL L^{-1} CO_2. Both these observations suggest that production of thicker leaves during enrichment increases a plant's photosynthetic capacity and may be an adjustment to take advantage of the added CO_2 availability. In support of this, Hughes and Cockshull (1972) reported thicker leaves in environments favoring high photosynthesis (high CO_2, saturating radiation levels, and optimal temperatures) and greater leaf expansion in conditions not favoring such high rates.

Although thicker leaves (lower SLA) have been associated with increases in net assimilation rate (g m^{-2} of leaf area day^{-1}, NAR) (Neales and Nicholls, 1978; Sionit, Hellmers, and Strain, 1982). Rogers et al. (1984) associated lower SLA in soybean leaves with a reduction in NAR response to CO_2 enrichment. Peet et al. (1986) concluded that starch accumulation was responsible for recorded increases in cucumber leaf thicknesses during CO_2 enrichment and attributed a negative growth response to this accumulation. Such results appear to occur during times of low sink availability, and high sink strength has been found to reverse photosynthetic rate depression associated with starch accumulation (Baysdorfer and Bashaam, 1985; Clough et al., 1981; Havelka et al, 1984). Forney and Breen (1985) identified fruit trusses as strong sinks in a day-neutral cultivar. Since, the plants were fruiting during the present experimental period, it is unlikely that the decreases in SLA recorded here after enrichment were inhibitory to uptake of added CO_2.

The increases in shoot, root, and crown dry weights with enrichment (E - C) all contributed to the increase in total dry weight with enrichment (%DW E - C in Table 7), but each of these components contributed different proportions. The root weight differences contributed the highest percentage. Lakso et al. (1986) also found that root weights of CO_2 enriched grape vines increases more than shoot weight. Desjardins and Gosselin (1987), however, did not find the same in 'Kent' *ex-vitro* strawberry plantlets.

Forney and Breen (1985) found that roots of a day-neutral cultivar Brighton accumulated more starch and dry matter than crowns and leaf blades when plants were deblossomed, establishing that roots provided a strong sink for starch accumulation. Crowns were found by these authors to accumulate more dry matter than leaf blades in the deblossomed plants, however whole shoot (leaf blade and petiole) dry weight differences (E - C) from the present experiment (Table 7) contributed more to total dry weight increases than did differences in crown dry weight. Crown weight not only contributed the least to the total dry weight gain associated with enrichment, but contributed a smaller percentage (%EDW) to the total dry weight of enriched plants than did the crowns of the plants grown in the control environment. Nevertheless, enrichment did result in a significant increase in crown weight as compared to the control.

Although there is substantial variation among cultivars, crown size is often positively correlated with strawberry fruit yield (Hancock et al., 1983; Jahn and Dana, 1970). Since number of flowers and fruit are determined during bud differentiation, increases in crown weight recorded in this experiment would not have affected fruit number during the nine-week enrichment period. Crown size, instead, influences the potential for future yield (Strik, 1987). Therefore, the implications are that the larger crown weight of the enriched plants would increase fruit production potential in subsequent fruiting cycles.

As expected from root and shoot %EDW and %DW E - C values in Table 7, the root:shoot ratio from enriched plants is higher than that from plants grown in the control environment. This implies that photosynthetic assimilates were shunted to a greater extent to root growth than to shoot growth under enrichment conditions. The root:shoot ratios for both the enrichment and control treatments were substantially higher than the values derived from data presented by Schaffer et al. (1985 and 1986) from 'Tribute' plants grown in the field, 6 weeks after fruiting.

The shoot dry weight recorded by Schaffer et al. (1986) was nearly twice the mean shoot weight recorded for both enriched and control plants in Table 7, however, the root weight was almost the same as the root weight of the control plants in this experiment. The mean root weight of the enriched plants here was almost twice that recorded by Schaffer et al., indicating a substantial benefit to root growth by CO_2 enrichment. The large difference in shoot production may reflect the different growth conditions of the field and growth chamber and possibly cultivar and plant age differences. Although, it is perplexing that root growth was not restricted more in the growth chamber environment, since the plants were in pots.

Greater root mass presents a substantial advantage to perennial growth by increasing the reserves for overwintering, as well as an advantage in nutrient and water uptake. Consequently, the nine-week enrichment period may have had effects on plant potential reaching beyond the immediate period of enrichment.

SUMMARY AND CONCLUSIONS

Growth Chamber Experiment

Strawberry fruit production over a nine-week period and plant vegetative yield components at harvest were measured to evaluate the effects of 300, 600, and 900 uL L^{-1} CO_2 in growth chamber atmospheres on plant growth and development. Responses to the 600 and 900 uL L^{-1} CO_2 concentrations were combined to form a generalized enrichment treatment with the 300 uL L^{-1} CO_2 concentration treated as an unenriched control.

Although not significant, more fruit were produced by the CO_2 enriched plants, and there was a trend towards earlier anthesis, fruit set and ripe fruit production in the enriched plants as compared to the plants grown under the control environment. Significantly larger fruit were produced by the enriched plants. Fruit size contributed the most to total fruit yield prior to 46 days after transplanting to the growth chambers from a greenhouse bench. An assessment of total fruit production over an entire fruiting cycle could not be made since it appeared that the fruiting cycle was not completed by the end of the nine-week period. No difference was recorded between the fruit yield of the enriched and control plants, however, individual fruit produced during enrichment were found to be significantly larger than those produced in the control environment.

Progressive leaf area measurements of the same leaves from five plants over eight weeks of the enrichment period revealed a slightly higher rate of leaf expansion by the control plants, however, no significant were recorded in LAR at plant harvest. Leaves from the enriched plants harvested at the end of the nine-week enrichment period were significantly thicker (lower SLA) than those from the plants grown in the control environment, indicating that CO_2 enrichment stimulated production of leaf tissue or accumulation of photosynthate as recorded by other authors in response to CO_2 enrichment.

No significant differences were recorded in the number of leaves produced by enriched or control plants throughout the eight-week sampling period. However, the number of leaves counted on the enriched plants was consistently higher throughout the period. More or thicker leaves would have provided extra photosynthetic area for utilization of the added CO_2 accounting for the increase in fruit size produced by the enriched plants.

Until 46 days after transplanting (42 days of treatment), the enriched plants produced a greater percentage of new leaves compared to senescent leaves. After that time, more leaf senescence was recorded than development. In view of this observation and the acceleration in flowering and fruit production, it was concluded that enrichment may shorten the fruiting cycle in this day-neutral cultivar under the growth chamber conditions of this experiment.

All yield components of the enriched plants harvested after the nine-week treatment period were significantly larger than those of the control plants, except for LAR. Increase in root dry weight accounted for the greatest proportion of the total dry weight increase in the enriched plants, followed by shoots and crowns. Unexpectedly, crown dry weight accounted for a relatively greater proportion of the control plant total dry weight than the enriched plant total dry weight. However, the enriched crown weight was significantly greater than that from the unenriched control plants. Since crown size has been closely correlated to fruit production capacity, it appears that CO_2 enrichment stimulated the potential for greater plant vigor and increases in fruit production in future fruiting cycles. The increased root weight, also may have future influence on plant vigor and productivity.

From these results, it was concluded that growth chamber enrichment at 600 and 900 uL L^{-1} CO_2 stimulated dry weight production and specifically root production by strawberry plants. However, due to the limited statistical analyses afforded by the experiment, no definitive conclusions could be drawn concerning flower bud, fruit and leaf production over the course of the nine-week treatment period. The growth chamber bias and variability in plants from the greenhouse bench in terms of flower bud initiation and leaf primordia may have been significant enough to obscure the treatment responses. Additionally, the low irradiance values of the growth chambers may have diminished the response to CO_2 enrichment, since photosynthetic usage of CO_2 is inherently linked to radiation intensity.

Further replication of this experiment is needed before reproductive responses of strawberry to the CO_2 enrichment can be firmly established. Also, studies over several fruiting cycles must be conducted to determine the relationship between vegetative growth and fruit production during enrichment because increases in vegetative growth usually do not affect reproduction within the same fruiting cycle or growth season. Enrichment studies spanning several fruiting cycles may also give insight into the effect of the added CO_2 on runner production, since this factor has been correlated to crown size and number. The use of day-neutral cultivars is recommended for future studies because of the relative insensitivity of their reproductive mechanisms to day-length and for their shortened fruiting cycles.

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APPENDIX

Table 8. Flow rates (FR) in gallons h^{-1} bed^{-1} (1.37 m^2) and total flow (TF) in gallons measured by water meters at the beginning of each header line. Flow rate was determined by the number of beds supplied by each header line (# beds) and the length of the irrigation period. The mulched beds were irrigated for five hours (1000 LST to 1500 LST), and unmulched beds for six hours (1000 LST to 1600 LST). Strawberry field experiment, 1986.

Date 1986	Plain Water Mulched			Plain Water Unmulched			Carbonated Water Mulched			Carbonated Water Unmulched		
	FR	# beds	TF	FR	# beds	TF	FR	# beds	TF	FR	# beds	TF
May 3	9.2	16	736	10.1	12	727						
19	6.5	16	520	7.2	12	518						
June 3	8.6	16	688	7.8	12	562						
16	6.5	16	520	5.9	12	425						
23	5.6	16	448	6.3	12	454						
July 5	7.2	16	760	8.1	12	584						
15	9.1	12	546	10.8	8	518	7.4	4	148	8.6	4	206
27	9.4	12	564	6.3	8	304	18.3	4	166	7.5	4	180
Aug 4	6.9	12	414	5.7	8	272	9.2	4	184	10.2	4	246
14	8.3	12	498	11.2	8	536	8.6	4	171	7.5	4	180
22	11.3	12	678	9.4	8	450	7.3	4	146	8.2	4	196
Sep 12	8.7	12	524	6.4	8	306	10.1	4	202	11.1	4	266
19	12.3	12	740	8.1	8	390	6.5	4	130	7.2	4	172
TOTALS			7636			6046			1147			1446
MEANS	8.4			7.9			8.2			8.6		

Table 9. Water pH and water temperature before carbonation (BC) and immediately after carbonation (IAC) and from the end of the drip tubes supplying mulched and unmulched beds in each field plot replication. The drip tubing means are from three samples and four field plot replications (n = 12), and the BC and IAC means are from three samples (n = 3). Strawberry field experiment, 1986.

Sampling Date 1986	BC		IAC		Drip Tubing			
					Mulched		Unmulched	
	pH	Temp(C)	pH	Temp(C)	pH	Temp(C)	pH	Temp(C)
July 15	6.0	24	3.7	24	4.0	35	4.1	32
Aug 14	6.0	24	3.8	22	4.0	27	4.0	25
Sept 11	5.9	20	3.8	21	4.1	23	4.1	22

Figure 14. Regression of CO_2 concentration in carbonated water on water pH. Carbon dioxide concentrations were determined with acid base titration techniques at water temperatures from 11 to 30 C. Strawberry field experiment, 1986.

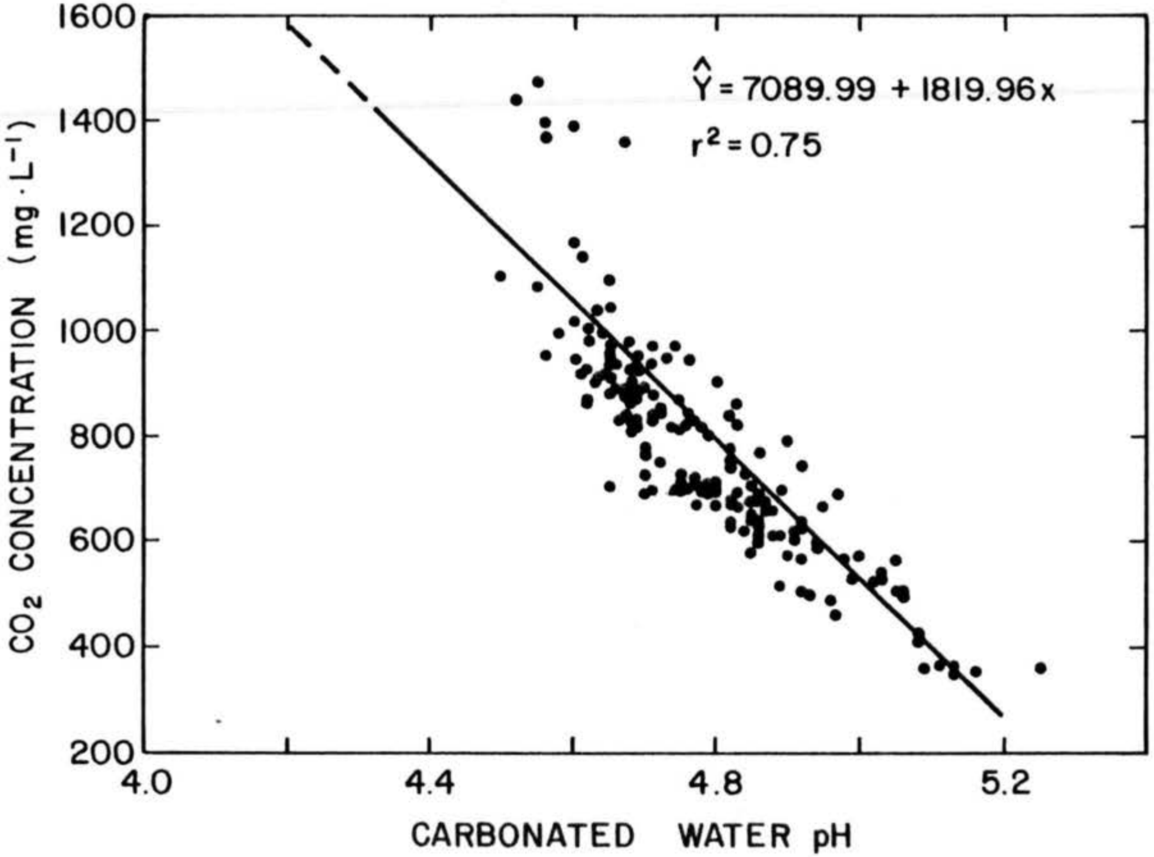
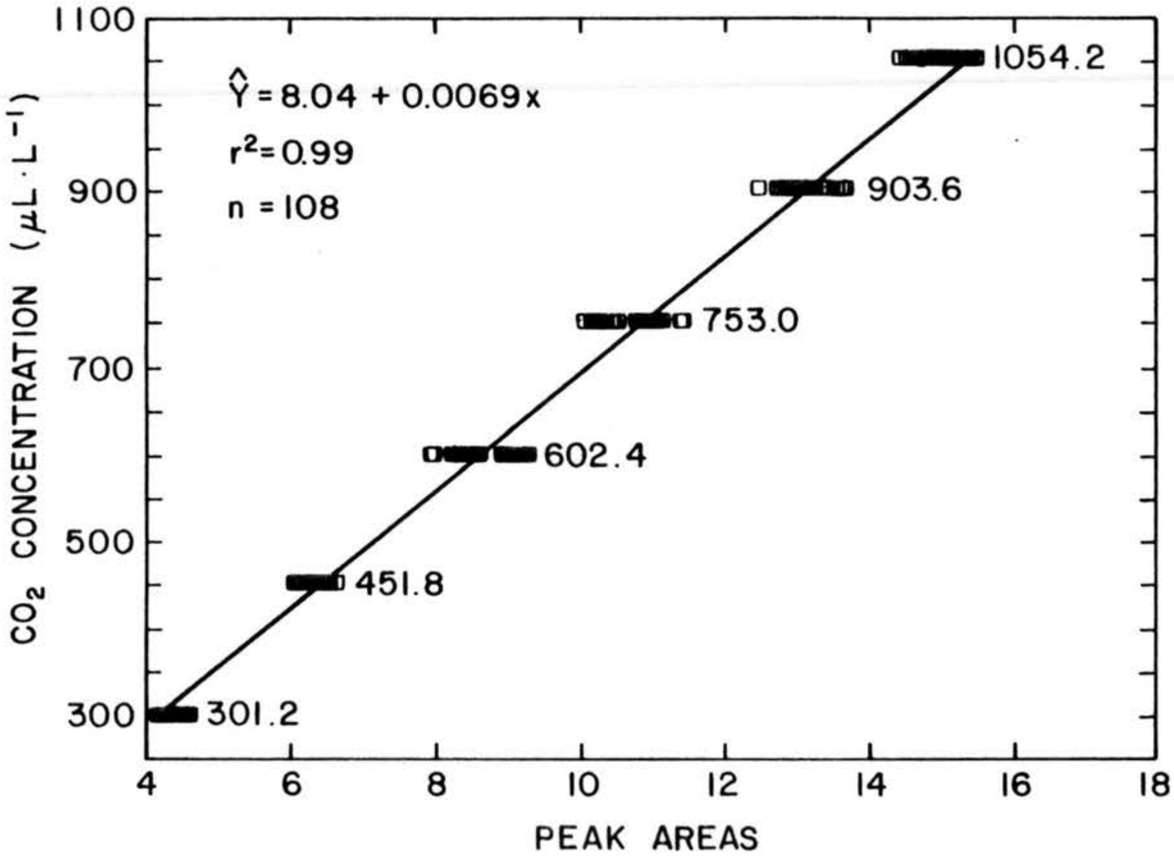

Ŷ = 7089.99 + 1819.96x
r² = 0.75
CO2 CONCENTRATION (mg · L⁻¹)
1600
1400
1200
1000
800
600
400
200
4.0
4.4
4.8
5.2
CARBONATED WATER pH

Figure 15. Calibration curve for the Hewlett Packard 5840A gas chromatograph. Peak areas from 0.5-ml aliquots of six CO_2 concentrations were used to generate the curve using linear regression procedures. Strawberry field experiment, 1986.



$\hat{Y} = 8.04 + 0.0069x$
$r^2 = 0.99$
n = 108
1054.2
903.6
753.0
602.4
451.8
301.2
1100
900
700
500
300
CO₂ CONCENTRATION (μL · L⁻¹)
4
6
8
10
12
14
16
18
PEAK AREAS

Table 10. Environmental conditions during dates of CO_2 gas (G) and carbonated water (CW) application. Strawberry field experiment, 1986.

Date 1986	CO_2 Application	Mean Global Radiation	1200-1400 MST^z Global Radiation	Wind	Temperature C	
	$Kg\ ha^{-1}\ h^{-1}$	$Kwh\ m^{-2}\ day^{-1}$	$Kwh\ m^{-2}\ h^{-1}$	$m\ s^{-1}$	Max	Min
July 6	360 (G)	6.387	0.714	1.4	28	13
8	360 (G)	7.252	0.985	1.7	29	13
9	630 (G)	6.919	0.506	1.6	31	12
12	630 (G)	8.742	1.048	1.9	30	13
15	420 (CW)	6.470	1.002	2.0	35	16
16	630 (G)	6.200	0.709	1.6	32	15
17	900 (G)	6.732	0.655	2.1	31	14
20	360 (G)	4.558	0.923	1.7	25	15
22	900 (G)	7.457	1.002	1.1	31	14
24	630 (G)	6.169	0.881	1.6	29	18
27	420 (CW)	8.306	1.020	1.6	32	14
30	360 (G)	7.991	1.007	2.6	31	14
Aug 1	all rates	6.981	0.808	3.1	30	13
4	420 (CW)	4.115	0.153	2.1	27	13
10	360 (G)	7.405	0.968	2.1	28	16
11	630 (G)	6.379	0.751	1.3	33	14
14	420 (CW)	5.585	0.436	1.3	28	13
17	900 (G)	6.384	0.939	1.8	32	10
22	420 (CW)	6.000	0.860	2.7	28	14
Sept 11	420 (CW)	6.660	0.875	2.1	24	4
12	360 (G)	–	0.781	1.5	31	12
14	630 (G)	6.145	0.772	1.5	31	6
17	900 (G)	–	–	1.6	24	3
19	420 (CW)	–	–	1.3	23	6

[z] Wind run/24 hours

Preliminary Analysis

On each application sampling date (Table 1), measurements were taken from control (unenriched) mulched and unmulched beds at all three sampling heights in each of the four field plot replications, such that there was a set of control responses to match the set of application responses. This was done to detect any change in ambient CO_2 concentration associated with different sampling dates that may have influenced responses to the four CO_2 application rates. An analysis of the control response variance (Table 11) indicated a significant difference between sampling dates (averaged across months), however, the control error mean square due to blocks (field plot replications) was far less (about 25 times smaller) than the error mean square due to blocks associated with the CO_2 application responses. Statistically, this signifies that the two error variances should not be pooled in the same analysis. Practically, this indicates that the differences in control CO_2 concentrations were smaller than those of each application rate both across time and across blocks. Ultimately, this indicates that the differences in ambient concentrations associated with different dates were not big enough to confound the differences due to CO_2 application rate; consequently, adjustments due to differences in control responses were not made in the final analysis.

Averaging across sampling date, the CO_2 concentration response from 360 kg CO_2 ha^{-1} hr^{-1} 20 cm over the unmulched beds (the treatment factor combination expected to yield the lowest response), was significantly greater than the control responses 1 cm over mulched beds (the treatment factor combination expected to yield the highest response) (Table 12). Since the difference between these two treatment factor responses represented the smallest CO_2 concentration difference between the controls and CO_2 applications, the significance in the difference was assumed to hold true between all controls and CO_2 application rate responses. Consequently, the control responses were not incorporated as a zero application rate level in the final comparison of CO_2 application rate responses.

All four CO_2 application rates were sampled on separate dates in July, August, and September. The analysis of variance presented in Table 13 shows that the CO_2 concentrations from the different sampling months were not significantly different. The same was true for the different sampling dates for each application rate as indicated by the lack of significance in the application rate x month interaction. The design analyzed in Table 13 was a straight factorial, however, only the interactions of interest were analyzed. Additionally, sampling height was not incorporated into the factorial because separate analyses for each sampling height showed the same lack of significance between sampling months and application rate x month interaction.

Based on the interpretations of the analyses presented here, each month was considered a replication. This was because no significant difference was found between sampling months. Also, control responses were not compared to CO_2 application rate responses in the final analysis. The final analysis was considerably simplified as a result of these decisions, enabling a clearer comparison of the CO_2 concentrations produced by the four application rates (360 kg CO_2 ha^{-1} hr^{-1}, 420 kg CO_2 ha^{-1} hr^{-1}, 630 kg CO_2 ha^{-1} hr^{-1}, and 900 kg CO_2 ha^{-1} hr^{-1}) over mulched and unmulched beds at the three sampling heights; 1, 10, and 20 cm.

Table 11. Preliminary analyses of CO_2 concentration response variance during no CO_2 enrichment (control) and CO_2 application at three sampling heights above mulched and unmulched beds averaged over sampling month. All measurements were taken during CO_2 application at wind speeds below 3.0 $m\ s^{-1}$. Strawberry field experiment, 1986.

Analysis of Variance
Controls

Source of Variance	df	SS	MS	F
Block Error	69	4993.32	72.36	
Block	3	584.42	194.86	2.69
Sampling date	3	6831.50	2277.17	31.47**
Mulch	1	24156.02	24156.02	333.80**
Sampling Height	2	103008.37	51504.19	711.71**
Date x Mulch	3	792.80	264.27	3.65**
Date x Height	6	3124.80	520.71	7.20**
Mulch x height	2	8853.31	4426.66	61.17**
Date x mulch x height	6	317.12	52.85	0.73

Application Rates

Source of Variance	df	SS	MS	F
Block Error	69	128987.54	1869.38	
Block	3	22132.13	7377.38	3.95
CO_2 Application Rate	3	2857851.73	952617.2	509.59**
Mulch	1	1819743.90	1819743.90	973.44**
Sampling Height	2	5460308.31	2730154.15	1460.46**
Rate x Mulch	3	529044.45	176348.17	94.33**
Rate x Height	6	749153.10	124858.85	66.79**
Mulch x Height	2	429406.58	214703.29	114.85**
Rate x Mulch x Height	6	196292.81	32715.47	17.50**

** Significance at $P<0.01$

Table 12. Analysis for comparison of CO_2 concentration measured during application of 360 kg CO_2 ha^{-1} hr^{-1} 20 cm above unmulched beds and during no CO_2 enrichment 1 cm above mulched control beds. All measurements were taken during CO_2 application at wind speeds below 3.0 m s^{-1}. Strawberry field experiment, 1986.

Analysis of Variance

Source of Variance	df	SS	MS	F
Block Error	15	3098.85	206.59	
Block	3	533.98	178.00	0.86
Control vs 360	1	1424.50	1424.50	6.90*
Month	2	1194.26	597.12	2.90
Month x Control vs 360	2	55.68	27.84	.13

* Significance at $P<0.05$

Table 13. Analysis of sampling month and mulch variance averaged over sampling height. All measurements were taken during CO_2 application at wind speeds below 3.0 m s^{-1}. Strawberry field experiment, 1986.

Analysis of Variance

Source of Variance	df	SS	MS	F
Total Block Error	56	175462.41	3133.26	
Block	3	22132.13	7377.38	2.35
CO_2 Application Rate	4	2857851.73	952617.24	304.03**
Mulch	1	1819743.90	1819743.90	580.78**
Rate x Mulch	4	529044.45	176348.15	56.28**
Month	2	9768.15	4884.41	1.56
Month x Date	6	37719.28	6286.55	2.01

** Significance at $P<0.01$

Table 14. Carbon dioxide concentration means (uL L^{-1}) for each sampling date from unenriched controls at three sampling heights above mulched (Mu) and unmulched (Umu) beds. Each mean is from four field plot replications (n = 4). Strawberry field experiment, 1986.

Controls

	Sampling height cm		Sampling Dates 1986				Monthly Mean
			July 8	July 15	July 12	July 17	
Mu	1		399.0	394.5	390.1	424.9	402.1
	10		357.6	357.9	356.4	381.2	363.3
	20		340.1	342.2	335.3	332.0	337.4
		Mean	365.6	364.8	360.6	379.4	367.6
Umu	1		360.8	351.8	364.3	385.8	365.7
	10		344.6	342.9	348.6	361.9	349.5
	20		331.7	327.6	331.1	332.6	330.8
		Mean	345.7	340.7	348.0	360.1	348.6
	Daily Mean		355.6	352.8	354.3	369.7	
			Aug 10	Aug 14	Aug 11	Aug 17	
Mu	1		386.7	400.7	380.8	417.6	396.5
	10		354.1	361.5	356.1	368.5	360.0
	20		333.0	354.7	340.4	343.3	342.8
		Mean	357.9	372.3	359.1	376.4	366.4
Umu	1		356.0	368.9	368.4	373.1	366.6
	10		342.6	339.9	351.3	354.9	347.1
	20		328.7	337.2	336.9	332.8	333.9
		Mean	342.4	348.7	352.2	353.6	349.2
	Daily Mean		350.2	360.5	355.6	365.0	
			Sept 12	Sept 11	Sept 14	Sept 17	
Mu	1		392.4	387.6	413.9	405.7	399.9
	10		364.3	357.8	365.8	367.2	363.8
	20		340.6	333.0	345.6	344.4	340.9
		Mean	359.5	365.8	375.1	372.4	368.2
Umu	1		362.1	358.1	372.1	370.8	365.7
	10		344.4	342.9	353.6	351.5	348.1
	20		334.6	329.0	337.0	337.4	334.5
		Mean	343.3	347.0	354.2	353.2	349.4
	Daily Mean		351.4	356.4	364.7	362.8	

Table 15. Carbon dioxide concentration means (uL L^{-1}) for each sampling date from three gas (G) application rates and carbonated water (CW) application three sampling heights above mulched (Mu) and unmulched (Umu) beds. Each mean is from four field plot replications (n = 4). Strawberry field experiment, 1986.

			CO_2 Application Rate kg ha^{-1} h^{-1}				
			(G) 360	(CW) 420	(G) 630	(G) 900	
	Sampling height cm		Sampling Dates 1986				Monthly Mean
			July 8	July 15	July 12	July 17	
	1		760.2	744.2	941.4	1280.3	931.5
Mu	10		604.4	613.2	759.2	903.2	720.0
	20		470.6	470.8	517.7	585.8	393.6
		Mean	611.7	609.4	739.4	923.1	556.0
	1		574.3	693.1	643.7	899.3	702.6
Umu	10		480.5	577.4	517.0	666.8	560.4
	20		418.6	463.4	431.8	491.1	451.2
		Mean	491.1	577.9	530.7	685.7	571.4
	Daily Mean		551.4	593.7	635.0	804.4	
			Aug 10	Aug 14	Aug 11	Aug 17	
	1		726.8	754.2	1035.2	1346.4	646.2
Mu	10		592.2	602.0	772.8	895.2	965.6
	20		445.0	511.9	545.2	607.5	715.5
		Mean	588.0	622.7	784.4	949.7	527.4
	1		561.7	684.9	654.4	796.0	736.2
Umu	10		475.9	519.4	526.3	640.4	674.3
	20		399.8	472.2	457.0	486.3	540.5
		Mean	479.6	558.8	545.9	640.9	453.8
	Daily Mean		533.6	590.8	665.1	795.3	
			Sept 12	Sept 11	Sept 14	Sept 17	
	1		697.1	788.3	995.3	1349.4	957.5
Mu	10		572.6	652.1	756.0	888.0	717.2
	20		442.0	489.6	530.7	626.5	522.0
		Mean	570.6	643.3	760.7	954.6	732.3
	1		559.8	707.1	737.7	854.4	714.7
Umu	10		472.9	587.3	596.6	662.9	597.9
	20		399.8	456.6	466.5	516.1	459.7
		Mean	477.5	583.6	600.3	667.8	582.3
	Daily Mean		524.0	613.5	680.5	816.2	

Table 16. Parameter values and regression statistics for equations relating wind speed and CO_2 gas application rate (360, 630 and 900 kg ha^{-1} h^{-1}) to CO_2 concentration 10 cm above mulched and unmulched beds. Wind speeds ranged from 0.5 to 4.5 m s^{-1} during application of gas to mulched beds and between 0.5 and 4.0 m s^{-1} during gas application to unmulched beds. Strawberry field experiment, 1986.

Mulched
Adjusted R^2 - 0.97

Variable Name	Regression Coefficient	T-Statistic	Contribution To R^2
Intercept	276.36	4.27**	-
Wind	-49.55	-3.10**	0.01
Rate	1.48	7.55**	0.06
$Rate^2$	-0.0007	-4.81**	0.02
Rate x Wind	-0.071	-3.31**	0.01

Unmulched
Adjusted R^2 - 0.94

Variable Name	Regression Coefficient	T-Statistic	Contribution To R^2
Intercept	-104.49	-0.95ns	-
Wind	132.64	2.65*	0.01
Rate	1.63	6.14**	0.08
$Wind^2$	-22.87	-2.70*	0.01
$Rate^2$	-0.00068	-3.47**	0.02
Rate x Wind	-0.15	-5.22**	0.05

* Significance at $P<0.05$
** Significance at $P<0.01$
ns Not significant

Figure 16. Diurnal fluctuation in CO_2 concentration of three growth chambers. Carbon dioxide or nitrogen gas were release from 0600 to 2200 h to obtain 300, 600, or 900 uL L^{-1} in separate chambers. The 95% confidence intervals are based on sampling repeated on different days. Strawberry growth chamber experiments, 1987.

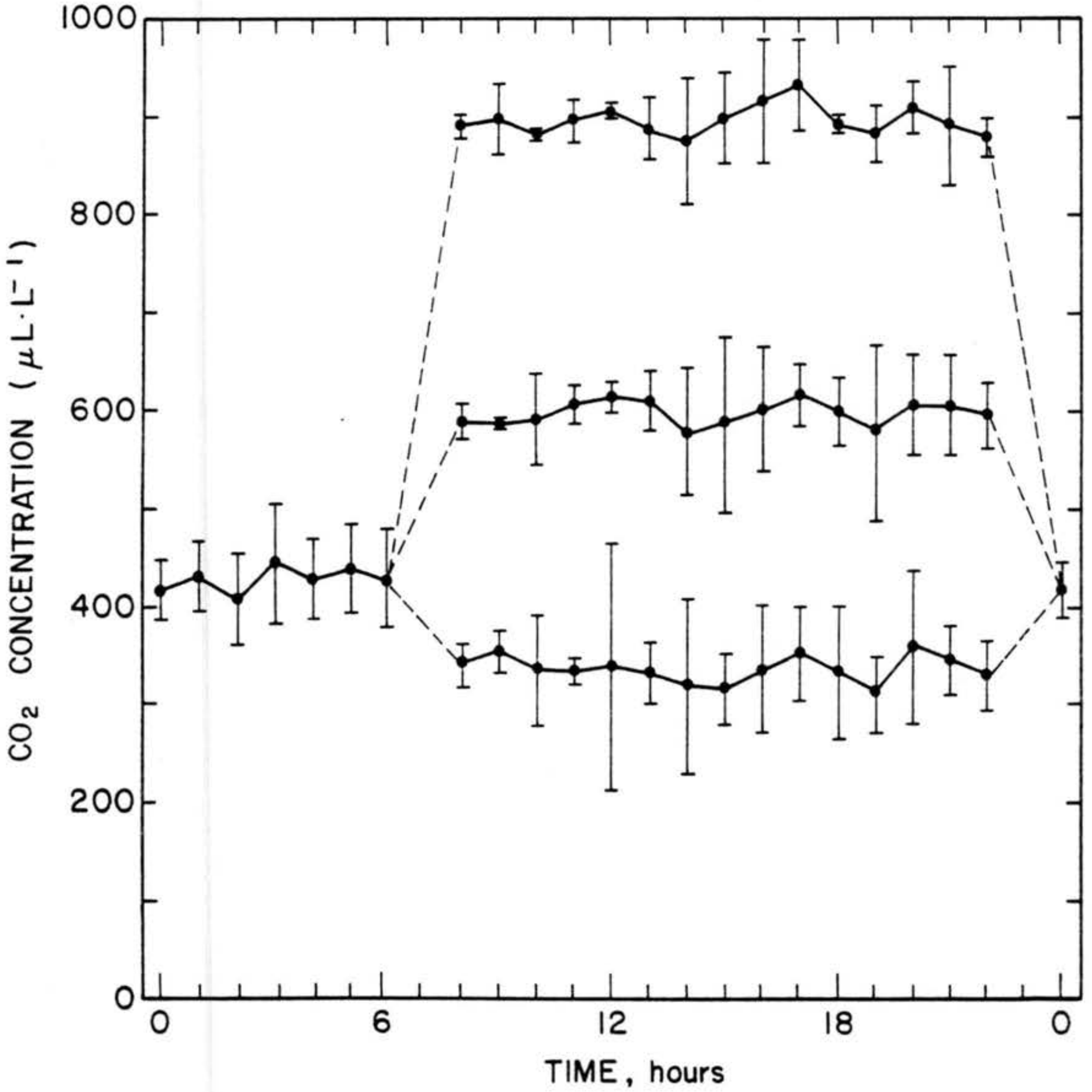
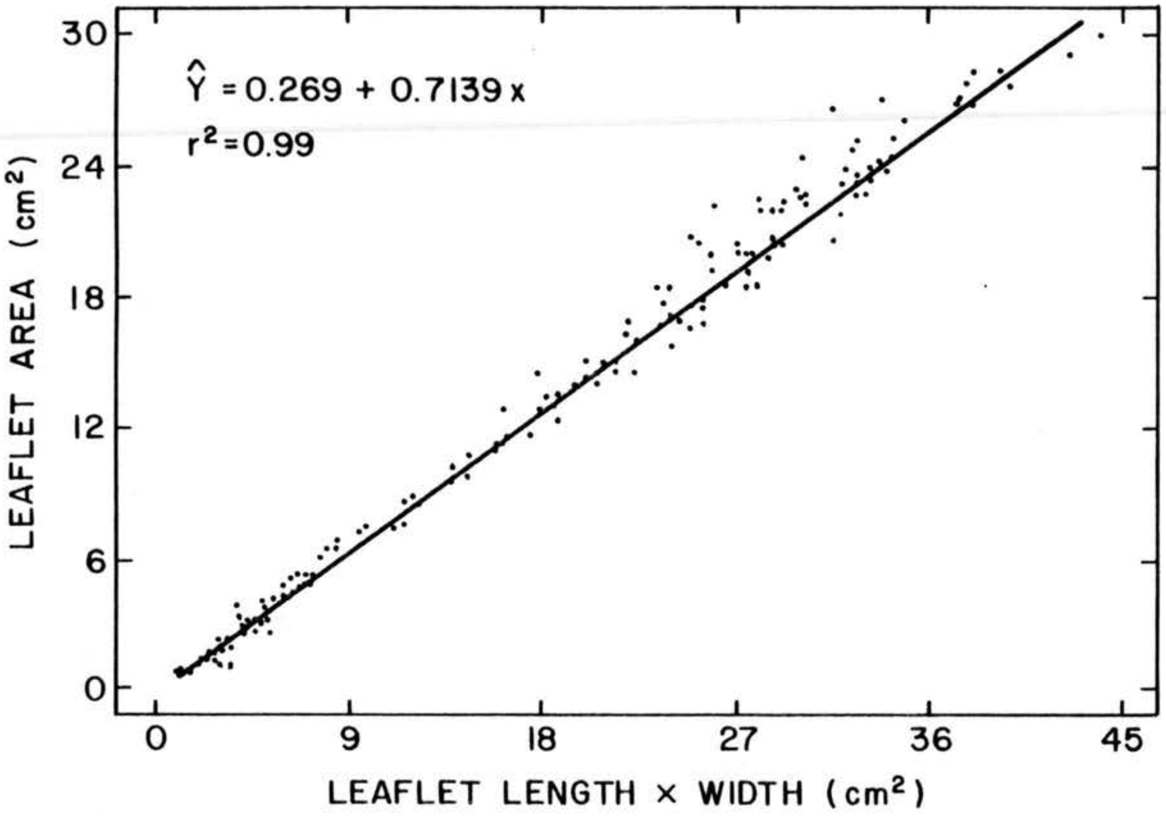

1000
800
600
400
200
0
CO_2 CONCENTRATION ($\mu L \cdot L^{-1}$)
0
6
12
18
0
TIME, hours

Figure 17. Linear correlation of leaflet length, width and area for prediction of leaflet area from non-destructive measurements. Strawberry growth chamber experiment, 1987.



$\hat{Y} = 0.269 + 0.7139x$
$r^2 = 0.99$
LEAFLET AREA (cm^2)
LEAFLET LENGTH × WIDTH (cm^2)
0
6
12
18
24
30
0
9
18
27
36
45

Figure 18. Calibration curve for the Beckman 865 infrared gas analyzer (IRGA). IRGA meter readings from 2-ml aliquots were used to generate the curve from linear regression procedures. Strawberry growth chamber experiment, 1987.

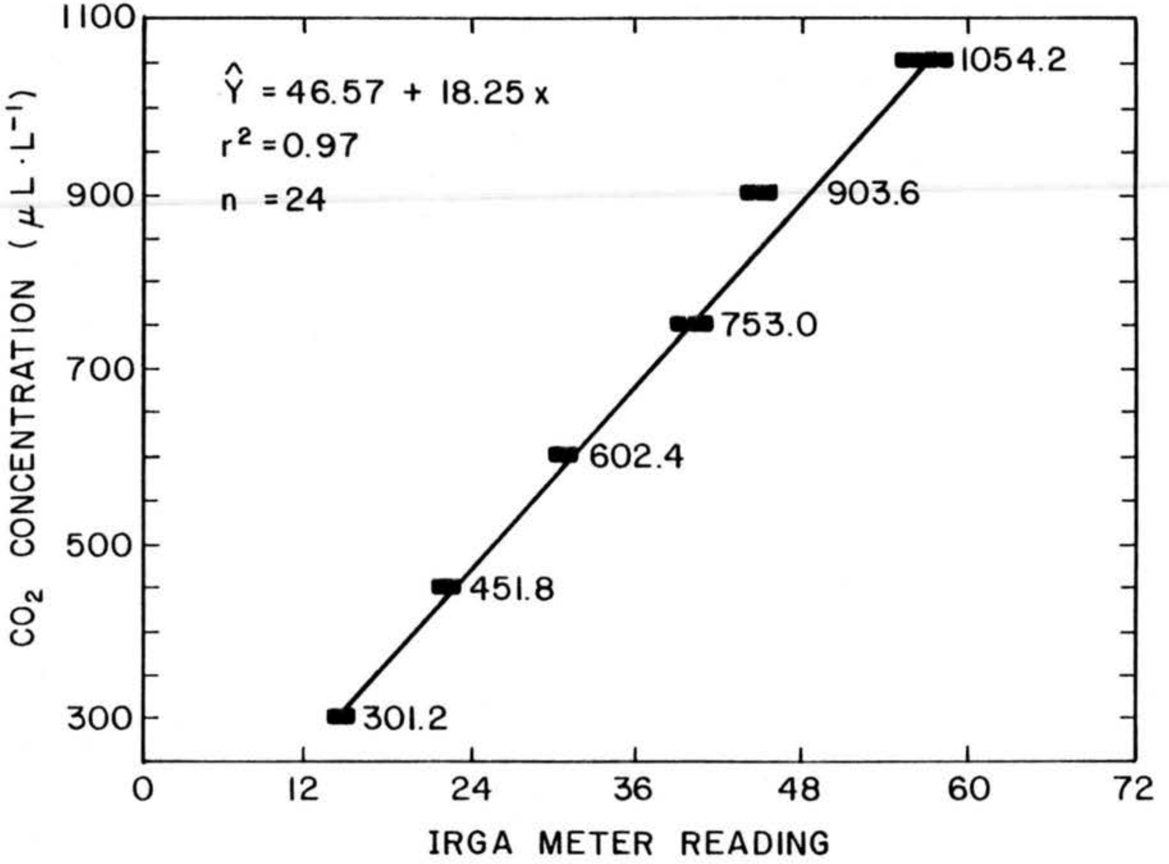

$\hat{Y} = 46.57 + 18.25x$
$r^2 = 0.97$
n = 24
1054.2
903.6
753.0
602.4
451.8
301.2
1100
900
700
500
300
0
12
24
36
48
60
72
CO_2 CONCENTRATION ($\mu L \cdot L^{-1}$)
IRGA METER READING

Figure 19. Differences in CO_2 concentration means at three heights above mulched and unmulched beds during CO_2 gas (G) and carbonated water (CW) application. Each mean was from four field plot replications sampled on three dates July - September (n=12). Wind speeds on the sampling dates were below 3.0 $m\ s^{-1}$ at the beginning of CO_2 application. Strawberry field experiment, 1986.

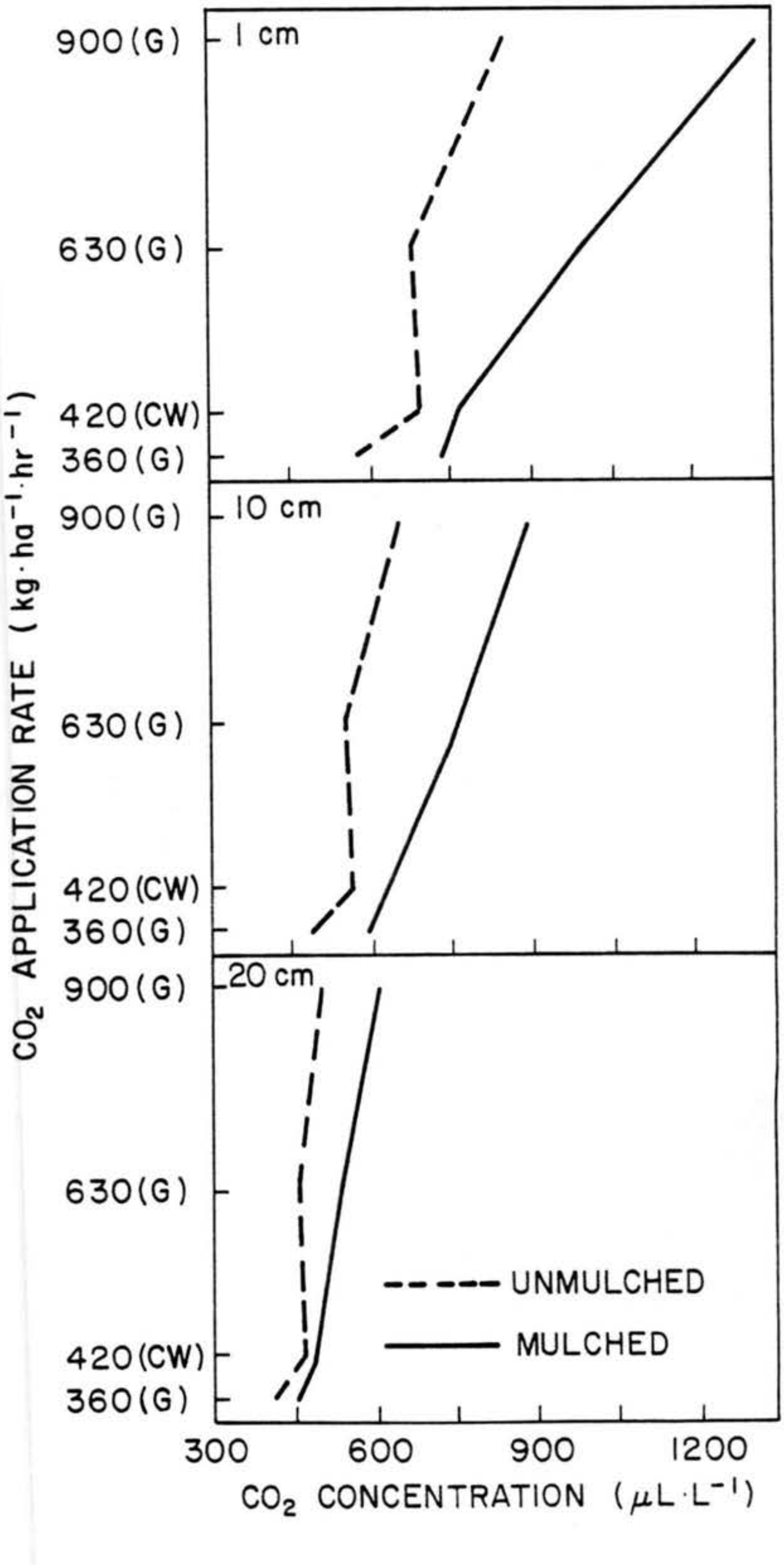

1 cm
10 cm
20 cm
900(G)
630(G)
420(CW)
360(G)
CO2 APPLICATION RATE (kg·ha⁻¹·hr⁻¹)
300
600
900
1200
CO2 CONCENTRATION (μL·L⁻¹)
UNMULCHED
MULCHED

Figure 20. Differences in CO_2 concentration means at three heights above mulched and unmulched beds under ambient conditions with no CO_2 enrichment (C) and application of CO_2 gas and carbonated water (CW). Each CO_2 application mean was from four field plot replications and three dates July - September (n=12). The (C) means were from samples taken during 12 separate dates July - September. Wind speeds on the sampling dates were below 3.0 $m\ s^{-1}$ at the beginning of CO_2 application. Strawberry field experiment, 1986.

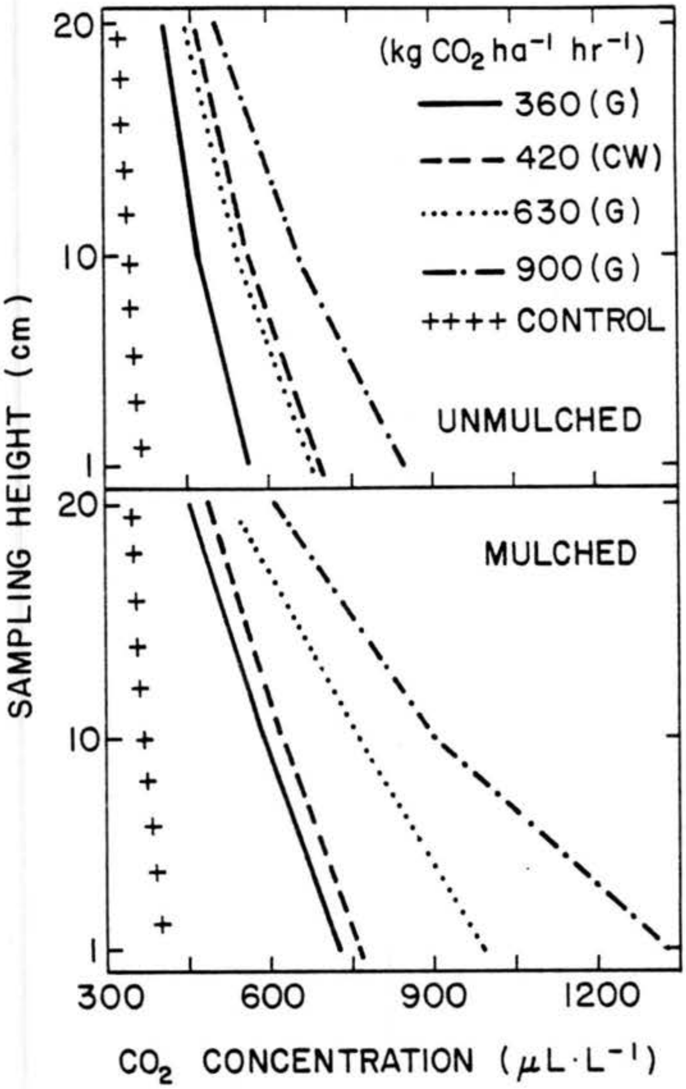

(kg CO₂ ha⁻¹ hr⁻¹)
360 (G)
420 (CW)
630 (G)
900 (G)
++++ CONTROL
UNMULCHED
MULCHED
SAMPLING HEIGHT (cm)
20
10
1
300
600
900
1200
CO₂ CONCENTRATION (μL·L⁻¹)

Figure 21. Mean hourly air temperatures measured during the July CO2 sampling dates (n=4). Strawberry field experiment, 1986.

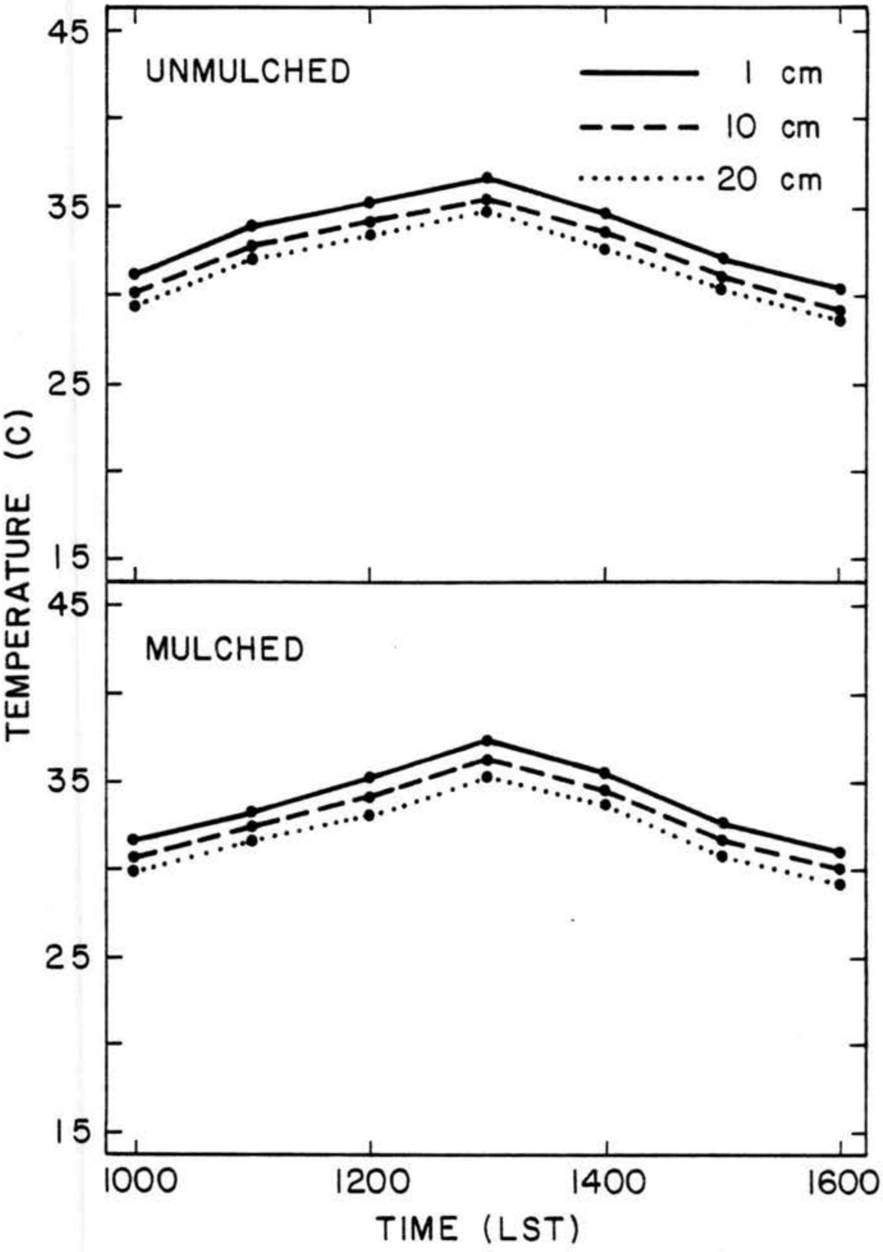

UNMULCHED
MULCHED
1 cm
10 cm
20 cm
TEMPERATURE (C)
45
35
25
15
1000
1200
1400
1600
TIME (LST)

Figure 22. Mean hourly air temperatures measured during the August CO_2 sampling dates (n=4). Strawberry field experiment, 1986.

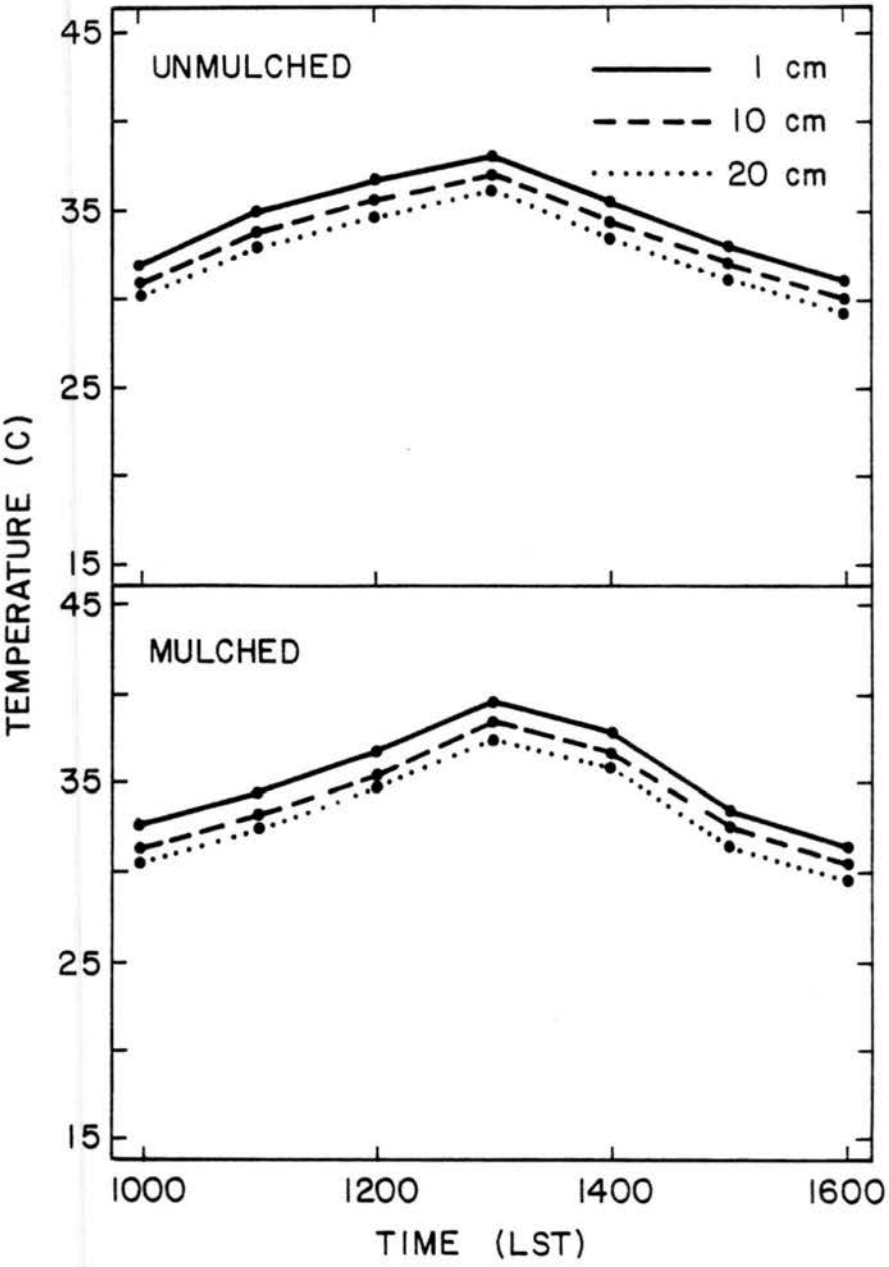

UNMULCHED
MULCHED
1 cm
10 cm
20 cm
TEMPERATURE (C)
45
35
25
15
TIME (LST)
1000
1200
1400
1600

Figure 23. Mean hourly air temperatures measured during the September CO_2 sampling dates (n=4). Strawberry field experiment, 1986.

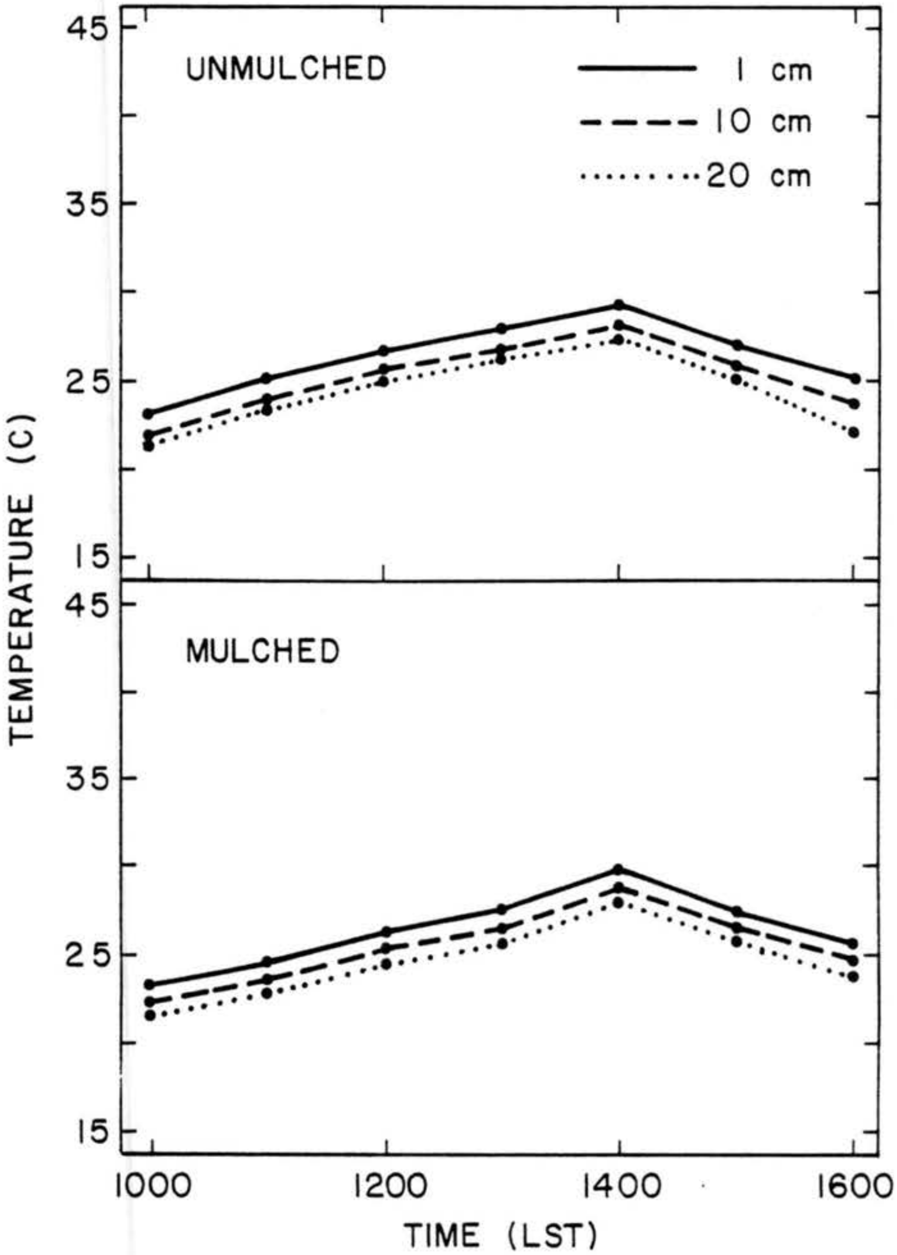

UNMULCHED
1 cm
10 cm
20 cm
MULCHED
TEMPERATURE (C)
45
35
25
15
45
35
25
15
1000
1200
1400
1600
TIME (LST)

Table 17. Data set for three-dimensional response surface associated with mulched and unmulched beds. All CO_2 concentrations (CC) were determined from the 10 cm sampling height during designated wind speeds (WS). Strawberry field experiment, 1986.

		Unmulched		Mulched	
Sampling Date 1986	CO_2 Application Rate kg ha^{-1} h^{-1}	WS m s^{-1}	CC uL L^{-1}	WS m s^{-1}	CC uL L^{-1}
Aug 1	360	3.4	385.2	3.3	481.6
Aug 1	360	3.4	470.8	3.3	463.4
Aug 1	360	3.4	405.3	3.3	461.1
Aug 1	360	3.4	375.2	3.3	404.3
July 20	360	1.4	470.0	1.4	603.4
July 20	360	1.3	506.6	1.3	625.1
July 20	360	2.3	452.1	2.3	566.3
July 20	360	1.7	425.9	1.7	593.8
July 20	360	2.0	436.1	2.0	581.8
July 20	360	1.0	429.2	1.8	598.3
Aug 1	630	4.1	484.5	4.3	526.1
Aug 1	630	4.1	423.3	4.3	478.5
Aug 1	630	4.1	359.5	4.3	539.4
Aug 1	630	4.1	422.6	4.3	562.3
July 16	630	1.3	683.1	1.3	807.6
July 16	630	1.0	636.6	1.0	785.6
July 16	630	1.7	655.4	1.7	766.6
July 16	630	2.4	618.4	2.4	726.2
July 16	630	1.6	670.1	1.6	750.6
July 16	630	1.4	702.3	1.4	770.8
Aug 1	900	3.5	549.4	4.1	589.5
Aug 1	900	3.5	546.3	4.1	550.4
Aug 1	900	3.5	484.4	4.1	492.6
Aug 1	900	3.5	574.1	4.1	571.6
July 22	900	0.9	813.4	0.9	936.6
July 22	900	0.6	831.3	0.6	957.8
July 22	900	1.0	784.2	1.0	916.4
July 22	900	1.4	734.1	1.4	881.3
July 22	900	1.2	756.5	1.2	889.2
July 22	900	1.2	765.3	1.2	865.3