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CARBON DIOXIDE EXCHANGE OF BLUE GRAMA AS INFLUENCED BY SEVERAL ECOLOGICAL PARAMETERS, 1971

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ABSTRACT

Progress to November 1971 consisted of improving environmental control and sampling procedures for both a field system and a laboratory system. A new environmental control unit was constructed for the field system so that temperatures could be controlled more precisely (±1.0°C) and all sensor responses could be recorded onto a multipoint recorder. The laboratory unit consisted of a closed gas exchange system where the carbon dioxide (CO_2) exchange rate was determined by changes in CO_2 concentrations over time.

Carbon dioxide exchange of blue grama (*Bouteloua gracilis*) sods under field conditions was determined from early June through October 19 (Appendix I). Peak assimilation rates on untreated native sods were observed on June 16 to be 4.4 g $CO_2/(m^2 \times hr)$ leaf area (one side). There was little rainfall in July and August at the Pawnee Site, and living blue grama foliage decreased. Therefore, the photosynthesis trailer was moved to the Environmental Stress Area in mid-July to observe gas exchange rates of fertilized and irrigated blue grama vegetation. Prior to the change of location, the average fixation rates of blue grama vegetation were about 0.1 g $CO_2/(m^2 \times hr)$ leaf area.

The laboratory system was used to determine effects of soil water potential, temperature, and irradiance (335 to 660 nm) on photosynthetic rates of blue grama. A split plot (3 × 3 × 3 factorial design) was implemented with observation on three replications of blue grama sods for each of the above variables. The mean maximum photosynthetic rate of blue grama was 0.29 mg CO_2/g dry wt/min. This rate was observed at a soil water potential of 0 and a temperature of 30°C, with both 1.12 and 1.54 langleys/min, as well as 40°C and 1.54 langleys/min. All three variables, soil water

potential, temperature, and irradiance, significantly affected photosynthetic rates of blue grama. Decreases in photosynthetic rates were noted at high temperatures (40°C), low irradiance (0.30 langleys/min), and high soil water stress (-30 bars). Interactions among these variables also significantly affected photosynthesis of blue grama.

RESEARCH OBJECTIVES DURING 1971

The photosynthesis project is intended to provide data contributing to a photosynthesis process model. Measurements of carbon dioxide (CO_2) gas exchange of important shortgrass prairie species will provide information on rate of energy capture by the primary producers in the shortgrass ecosystem. Data for assimilation and respiration rates as affected by light, temperature, water potential, and stress situations will aid the modelling effort in predicting the amount of energy fixed by producers per unit of leaf area or weight per unit of time. Results obtained from this study should therefore help explain causes for variations in producer biomass through time.

Objectives for 1971 were to (i) monitor carbon dioxide gas (CO_2) exchange of blue grama (*Bouteloua gracilis* (H.B.K.) Lag.) vegetation under field conditions at the Pawnee Site during the growing season, (ii) obtain response characteristics of CO_2 exchange from representative samples of blue grama vegetation for variations in light intensity (irradiance), temperature, and soil water potential, (iii) develop a micro-cuvette system suitable for field use for measuring photosynthesis of shortgrass species under controlled experimental conditions, and (iv) continue improving the environmental control and monitoring in the dome field system.

BACKGROUND AND PROGRESS

Two assimilation chamber systems have been used to accomplish the 1971 objectives. The dome system as described by Moir et al. (1969) and Dye and Moir (1971) was used to measure CO_2 exchange of blue grama vegetation in the field. This system was modified during the winter and early spring to

increase the cooling capacity of the system to provide a smaller temperature differential between incoming and outgoing air. Additional equipment was purchased to monitor other abiotic parameters such as temperature, solar radiation, humidity, and water potential. A closed gas exchange system developed by Ronco (1969) was utilized in greenhouse experiments. The closed gas exchange system allows for controlled experimental conditions where soil water potential, light intensity (irradiance), and temperature can be varied in an experimental fashion to determine their effects on photosynthetic and respiratory rates of shortgrass species.

In addition to the two previously mentioned gas exchange systems presently being utilized, a third gas exchange system is under construction. This micro-cuvette system (Fig. 1) has been designed and components have been purchased. The cuvette is made of acrylic plastic tubing which can contain several sprigs of blue grama foliage. Other plants of small stature can also be placed in the chamber. The heat exchanger consists of air passing over a Peltier block. Cuvette air temperature will be controlled by using an environmental control unit similar to that of the dome system. The complete system should be operational by May 1973.

After testing, the micro-cuvette system will initially be used simultaneously with the dome system in the field. Data of CO_2 differential and temperatures will be recorded on the multiple channel recorder and automatic data acquisition system being used for the dome system. In the micro-cuvette chamber, soil and vegetation components of the ecosystem can be separated using RTV silicone rubber at the interface. Therefore, net assimilation rates and respiration rates of the foliage alone can be determined. Data obtained from the micro-cuvette system will be compared with data taken

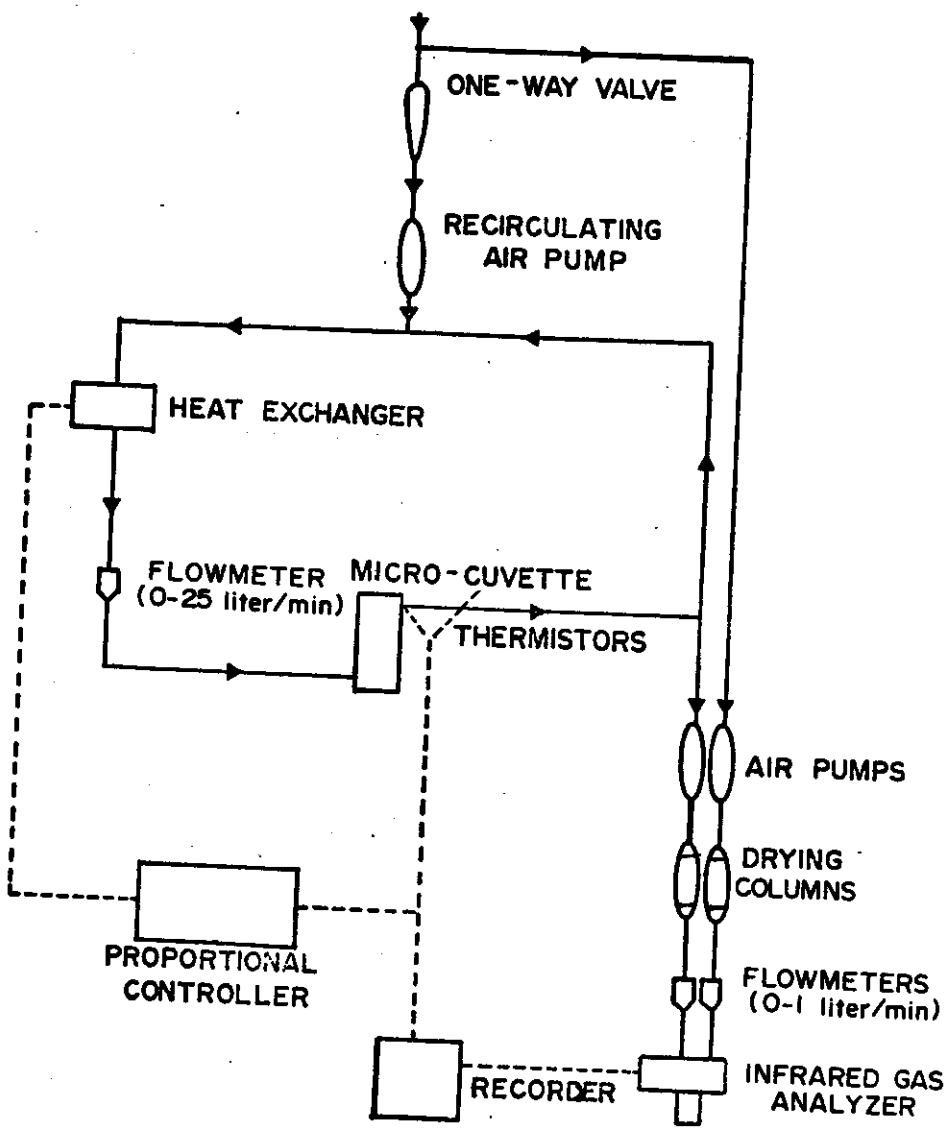

Fig. 1. Diagram of micro-cuvette system for observing net assimilation of shortgrass vegetation under field conditions.

simultaneously from the dome system to approximate the amount of CO_2 contributed by the soil block.

When completed, the micro-cuvette system can be used to study single plants of several species under a variety of field experimental conditions. The system could be housed in the instrumentation trailer or in a pickup camper and thus be very mobile. However, a recorder, data acquisition system, and power source will be needed before the micro-cuvette system can be operated separately from the dome system.

EXPERIMENTAL MATERIALS AND METHODS

Field System

The photosynthesis trailer was moved to the Pawnee Site in May 1971. Line power was still needed for operation; therefore, the trailer and equipment were located within the enclosure surrounding the lysimeter. All data from untreated blue grama sods (through July) were collected near the southwest corner of the enclosure, about 100 m south of the lysimeter. Four aluminum base plates (60-cm inside diameter) were driven into the ground enclosing sods which were essentially stands of pure blue grama of approximately similar leaf areas. These four areas were chosen to exclude mixed stands which might contain plants representative of two different carbon fixation pathways (Hatch and Slack, 1970). After determining carbon dioxide (CO_2) exchange over a sod, the sod was allowed a rest period of at least 3 days before another determination, or run, was made.

Sampling unit. The sampling unit was a small hemispherical plexiglass dome, as described by Moir et al. (1969). However, some modifications were made to increase flow rates through the closed-loop cooling cycle. The total

air volume of the unit is approximately 90 liters. An aluminum base plate was hammered 10 to 12 cm into the ground. An aluminum air ring (6 × 8-cm inside dimensions) was placed upon the base plate. The ring had uniformly spaced 1-cm holes drilled into the inner wall to allow cooled air to mix thoroughly with dome air around the perimeter of the sod. The dome was then positioned upon the ring, and adjustable clamps were used to fasten the dome and ring to the base plate. The air ring was sealed to the base plate and dome with gaskets to reduce gas leakage.

Air flow through the heat exchanger was accomplished by using a Dayton blower with a capacity of approximately 400 cfm (cubic feet per minute). There were two efflux air ducts (7.5-cm diameter) on opposite sides of the dome. These two air ducts were connected together by flexible hose into one 10-cm hose which was attached to the vacuum side of the blower. The heat exchanger consisted of four 15 × 20-cm radiator cores connected in series. A water-ethylene glycol mixture was constantly circulating within the cores. When additional cooling of dome air was necessary, colder water-ethylene glycol mixture was pumped from a reservoir chilled by a 3/4-hp compresser which ran continuously. The cooled air was returned to the sampling unit through a 10-cm hose and then into two smaller hoses (7.5-cm diameter) and entered the dome atmosphere through the holes in the inner wall of the cooling ring described above. Fig. 2 is a diagrammatic representation of the dome instrumentation system. Air, with ambient concentrations of CO_2, was pumped into one of the efflux ducts, and a sample of dome air was withdrawn from the opposite efflux duct at a somewhat lower flow rate. The ambient air intake was located 6 m above the soil surface.

Depending upon the photosynthetic activity of the sod, one to three Reciprotor pumps were used to provide adequate ambient air flow rates to

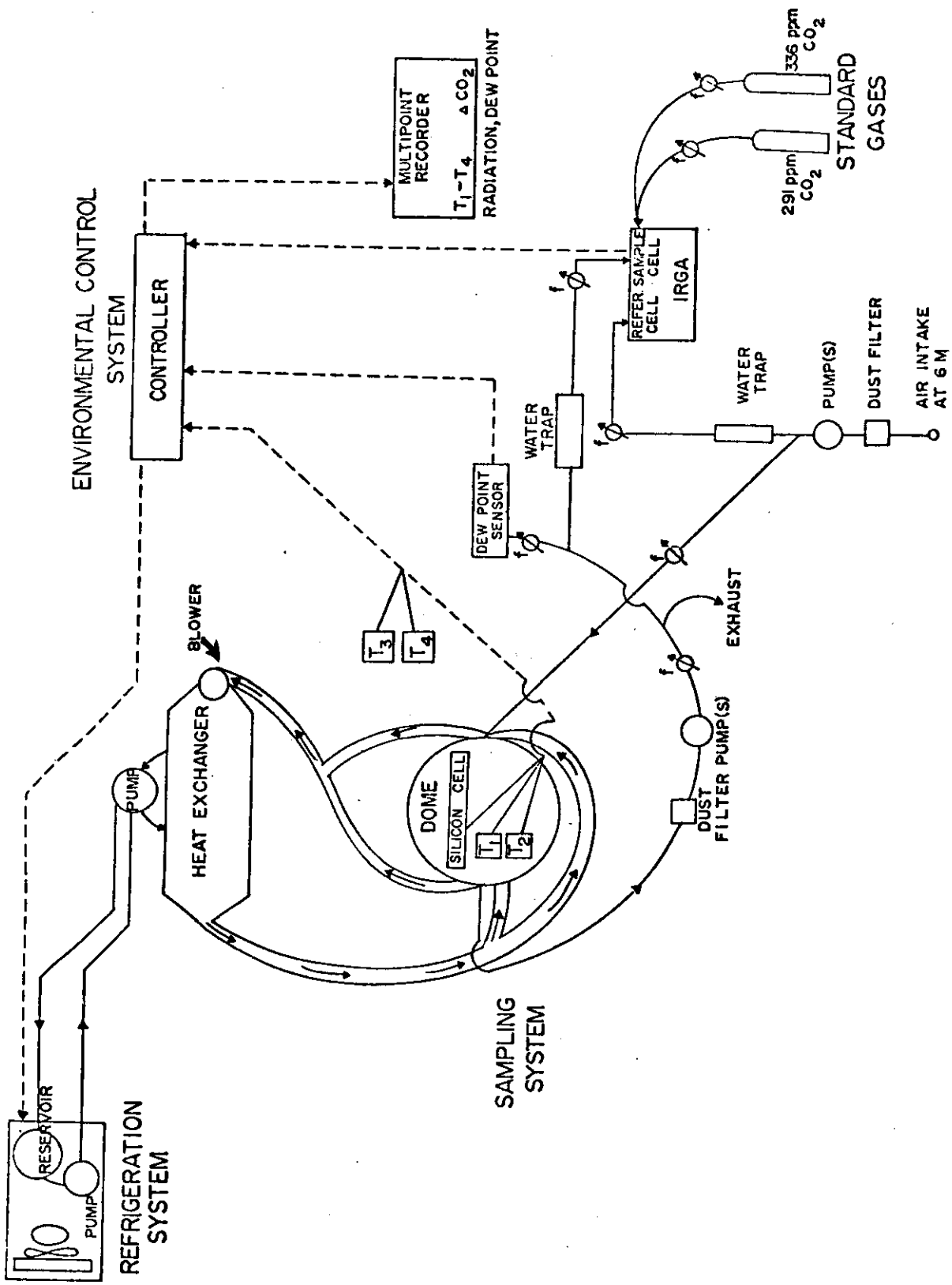

Fig. 2. Schematic diagram of the field instrumentation system for CO_2 exchange studies at the Intensive (Pawnee) Site of the U.S. IBP Grassland Biome.

the dome. Approximately 2 liters/min of the ambient air stream were used to flush the reference cell of the differential Beckman 315A infrared gas analyzer (IRGA). The remaining ambient air flow to the dome was monitored by a Gilmont flowmeter (75 liters/min capacity). The air sample withdrawn from the dome environment was subsampled. About 1 liter/min of sample air was passed over the sensing element of a dew point hygrometer (EG&G--Cambridge, Vapor Mate II), and 2 liters/min were passed through the sample cell of the IRGA. The remainder of the sample was exhausted into the air. At various intervals, known concentrations of CO_2 were passed through the sample cell of the IRGA to check for zero-drift of the analyzer and recorder and to determine ambient CO_2 concentrations. Zero-drift of the IRGA was also checked by dividing the ambient intake line into two streams and allowing gas of the same CO_2 concentration to purge both cells of the IRGA.

A through-bulkhead-fitting attached to the wall of the plexiglass dome allowed for quick coupling of abiotic sensors. Two thermistors were placed within the dome environment. One thermistor normally was placed about 15 cm inside the perimeter of the sod and within the grass canopy, while the other thermistor was placed at varying locations to sense temperature gradients such as incoming air temperature, soil temperature, etc. A silicon cell was also placed under the dome to monitor incoming visible radiation.

The incoming air temperature was generally 4 to 5°C lower than the internal dome air temperature, and under high solar radiation the differential was 5 to 7°C. The radiator temperature was essentially the same as incoming air temperature, and there was little or no condensation of water on the radiator surfaces. The return air hoses from the heat exchanger to the air ring were wrapped with mylar to reduce CO_2 diffusion through the walls.

Around this was taped an insulating air duct material to improve cooling efficiencies.

Environmental control unit. The control system for the dome unit was designed and constructed by Bill Rice, principal electronics research technician for the Intensive (Pawnee) Site. The unit functions as an electromechanical feedback system which senses differential temperatures. Linear thermistors (#44002) (-5 to +45°C) sense the various temperatures and transmit their signals to the controller. A reference thermistor located in the grass canopy outside the dome environment is used to establish a base temperature around which the thermistor under the dome will be allowed to fluctuate. When the differential between the reference and sample thermistor is greater than 0.1°C, an electronic signal causes a pump to either start or stop pumping chilled water-ethylene glycol to the heat exchanger.

Dome air temperature is controlled by either an automatic (ambient track) or manual mode of operation. On manual control a temperature value on a potentiometer will function as the base temperature. The differential between the thermistor under the dome and programmed resistance will determine if more or less cooling is needed. Under manual operation, the temperature within the canopy can normally be controlled to within ±0.5°C of the desired value. Such control is contingent upon ambient environmental conditions. For example, scattered clouds will cause rapid fluctuations in the energy budget. The relatively large mass of coolant prohibits an instantaneous response to a change in incoming energy levels. The same air temperature might fluctuate 4 to 5°C around changing ambient air temperatures

because of the lag in response time. The ambient air temperature within the dome can be cooled to 14°C below that of external ambient conditions.

In the automatic mode of operation, problems similar to those above are encountered on cloudy days. The differential resistance in this case is between a thermistor inside the dome and one thermistor outside in the environment. Both sensors are placed 2 to 5 cm above the soil surface within the grass canopy. In relation to the manual mode of operation, accuracy is not as great when tracking ambient conditions. Normally, on cloudless days the temperature under the dome will be ±1.0°C of the ambient temperature outside. Fluctuations in ambient wind speed can influence heat flux, and the ambient thermistor may change rather rapidly. The lag time before the two values coincide again is from 1 to 4 min.

Solid state circuitry with printed circuit boards are used in the control unit for the various temperature sensors, silicon cell, IRGA, and dew point hygrometer. All outputs from the controller are 0 to 10 mv and are sequentially recorded onto a 24-channel multipoint recorder (Texas Instruments). Data from all sensors can also be scanned visually on the controller unit by use of a channel selector and microammeter.

Vegetation measurements in the field. The leaf area index (LAI) for each blue grama sod was determined at periodic intervals by the crew of Dr. Dennis Knight, University of Wyoming (Knight, 1971). Leaf area index was determined by using an inclined point frame as described by Warren-Wilson (1963). By putting the photosynthetic rates on a leaf area basis, direct comparisons can be made between sods, even though the amounts of green material may vary. Aboveground biomass was clipped from sods in the

Environmental Stress Area (ESA), thus allowing comparisons to be made on a dry weight basis also. Periodically, ektachrome and infrared photographic exposures of each sod were also taken for leaf area determinations.

Change of location. On July 15, the photosynthesis trailer was moved to the environmental stress area in order to measure CO_2 exchange of sods which were still green and actively growing. At this time, the vegetation in the lysimeter area was under extreme water stress, green leaf area was small, and exchange rates were low. Observations were continued in the ESA until October 19. Most determinations of CO_2 exchange were made over sods in the irrigated only treatment.

Field data processing and analysis. Too often the process of choosing sections of data, and observations within sections, from strip chart records is very time consuming. Therefore data analyses may lag as much as 6 months to 2 years behind collection because of complications arising from manual data reductions. The data from our strip charts were transcribed to computer cards automatically by using an Auto-Trol X-Y digitizer (Appendix II). The digitizing process includes placing a section of strip chart on a table which has a two-way adjustable sensor mounted on tracks. The sensor records distances away from the origin, in X and Y coordinates, to the nearest 1/1000 inch. The coordinates are automatically punched onto a computer card with an identification code for each datum point. A set of computer cards could be punched for any given determination with four or five variables in 30 to 40% of the original recording time.

A computer program was written to compute gross photosynthesis in mg of CO_2 per unit leaf area per unit of time. This continuous evolution of CO_2 from the soil block necessitates a correction factor to be added to apparent net

photosynthesis. The magnitude of correction was determined by darkening the dome for a 10- to 12-min period to observe the increase in CO_2 concentration when photosynthesis was halted. Equilibration was usually reached in 8 to 10 min, depending upon temperature. No attempt was made to separate that part of respiratory CO_2 attributable to plant roots alone.

The equation used for the calculation of gross photosynthesis (P_s) is:

$$P_s = \frac{(\Delta CO_2)\ (\text{flow rate})\ (1.58 \times 10^{-6})}{\text{leaf area}}.$$

By summing the absolute differentials observed between light and dark conditions ΔCO_2 (in ppm) was determined. The flow rate was recorded manually several times during each determination. There was very little fluctuation in the flow rates attributable to variations in pump speed. When the flow rate was different for determinations of dark CO_2 evolution, then the differential was adjusted to correspond to flow rates under illuminated conditions. The coefficient (1.58×10^{-6}) includes a correction to standard temperature and pressure (STP) for the flowmeter and also includes the corrections necessary to report CO_2 as the volume fraction in ppm corrected to STP. The flowmeter temperature was generally 35 ± 5°C. Therefore, over this narrow temperature range, only one mean temperature correction factor (35°C) was used (Brown, 1968). The leaf area was simply calculated by multiplying the measured LAI times the area enclosed by the ring (3000 cm^2). A linear change in leaf area was assumed between measurement dates of LAI.

The computer output listed the averages of the dependent variable (CO_2 uptake) and four independent variables (radiation and (three) temperatures). The averages were calculated over various time intervals (3, 15, and 60 min) within a single determination. The data have also been processed through a stepwise multiple regression program.

The Greenhouse System

Description. A closed system for analysis of carbon dioxide exchange was borrowed from Ronco (1969), Rocky Mountain Forest and Range Experiment Station, U.S. Forest Service. The system basically consists of a (i) temperature control system capable of maintaining constant temperatures from 15 to 45°C ± 0.2°C, (ii) bank of seven 300-w reflector spotlights capable of producing light intensities from 0 to 1.54 langleys/min in the visible spectrum after being filtered through an 8-cm continuous flow water bath for removal of much of the infrared radiation, and (iii) gas injection unit allowing the operator to reestablish carbon dioxide concentration in the system before determining photosynthetic or respiration rates.

The entire closed system is diagrammed in Fig. 3. A fan provides continuous internal air circulation within the assimilation chamber and alleviates the problem of variations in rate determinations caused by variations in airflow rates. The temperature control system utilizes a modified drinking fountain cooler as a coolant reservoir. A three-way valve regulates the amount of coolant circulated through about 12 m of copper tubing in the walls of the assimilation chamber to maintain a desired chamber temperature. The light bank is the main source of heat; however, the heat given off by the lights is not sufficient to maintain temperatures above 35°C in the assimilation chamber. Therefore, the system was modified to provide heating when high temperatures within the assimilation chamber were needed. For a more detailed description of the entire system refer to Ronco (1969).

Carbon dioxide concentrations were measured with a differential Beckman 315A IRGA. Since it is a closed system, a steady state of carbon

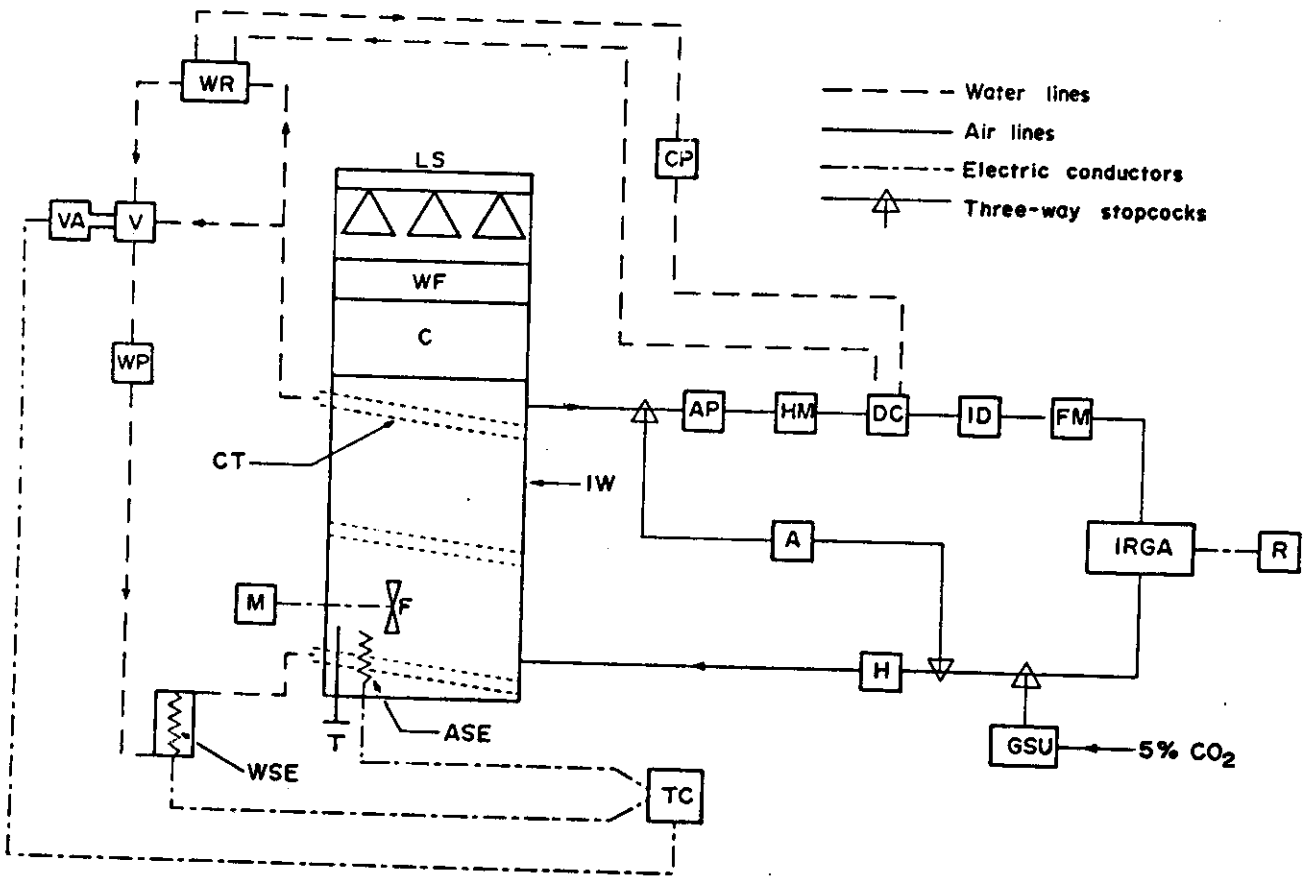

Fig. 3. Schematic diagram of closed system apparatus for measuring photosynthesis as described by Ronco (1969).

A - ascarite column
AP - air pump
ASE - air temperature sensing element
C - assimilation chamber
CP - centrifugal water pump
CT - copper tubing
DC - water-cooled condenser
F - fan
FM - flowmeter
GSU - gas sampling unit
H - humidifier
HM - relative humidity meter
ID - indicating drierite ($CaSO_4$)
IRGA - infrared gas analyzer
IW - internal copper wall of chamber
LS - light source
M - fan motor
R - strip chart recorder
T - thermometer
TC - temperature controller
V - three-way valve
VA - valve actuator
HF - heat filter
WP - water pump
WR - water reservoir, cooler-heater
WSE - water temperature sensing element

dioxide concentration could not be maintained. Instead, a steady rate of depletion was recorded. Experimentation with blue grama showed that the photosynthetic rate was essentially unaffected by CO_2 concentration over the range of 370 ppm to 190 ppm CO_2. This indicated that CO_2 depletion occurred at a steady rate between these two concentrations of CO_2 within the closed system; however, all determinations were made between 360 ppm and 280 ppm CO_2.

Detailed modelling of photosynthesis requires the exclusion of the soil block contribution of carbon dioxide to the system. Polyethylene glycols (carbowax) of different molecular weights (and consequently different melting points) were used in an attempt to seal the soil-atmosphere interface. The objective was to exclude the diffusion of CO_2 from the soil block. The liquid polyethylene glycol was poured onto the soil surface and allowed to solidify around the grass culms, thus covering the soil surface and preventing any gaseous diffusion between the soil component and the atmosphere. The proper ratio of different molecular weights of polyethylene glycol was determined to establish a mixture with a melting point of 40°C. This sealant is reportedly nontoxic and had no visible detrimental effects on the plants up to 10 days following application. When the physiological effects were determined by the gas exchange system, it was discovered that polyethylene glycol had an immediate detrimental effect upon assimilation rates of blue grama. Therefore, mineral oil was utilized as a substitute sealant. Mineral oil was found to be impervious to carbon dioxide diffusion, had no toxic effect on blue grama, and had little if any effect on assimilation rates.

A Wescor chamber thermocouple psychrometer and microvoltmeter were utilized for leaf water potential determinations. Thermocouple psychrometers

were constructed according to Brown (1970) for use in determining soil water potential.

An airflow planimeter was constructed similar to that described by Mayland (1969) to provide leaf area determinations. The planimeter has since been modified to give greater accuracy for surface area determinations of grass leaves.

Irradiance provided by the variable light source of the system was measured at plant height using an Eppley pyranometer equipped with a filter to provide irradiance in langleys in the visible spectrum only. The range of irradiance was from 0.30 langleys with only one 300-w spotlight in operation to 1.54 langleys with all seven lights in operation.

Experimental procedure. An experiment was conducted to determine the effects of three parameters (soil water potential, temperature, and irradiance) on photosynthetic rates of blue grama. Leaf water potentials were determined as an exterior variable for regression analysis. A split plot (3 × 3 × 3 factorial design) was implemented with three levels of soil water potential (0, -15, and -30 bars), three levels of temperature (20, 30, and 40°C), and three levels of irradiance (0.30, 1.12, and 1.54 langleys/min). Each set of variables was replicated three times.

Relatively undisturbed sods of blue grama were cut at the Pawnee Site, potted in no. 10 cans, and brought into the greenhouse on June 29, 1971. The sods were collected randomly in the same afternoon from an area of Ascalon soil of approximately 15 × 15 m. The collection area was purposely kept small so that soil type and water content of each sod would be similar. One thermocouple psychrometer was installed in the spatial center of each sod. The sods were immediately weighed. The original weight of each sod

was used throughout the soil water potential measurements to determine (by subsequent weighing) the exact amount of water present in relation to the original amount. This procedure was followed to provide a check on the sometimes erratic readings obtained from thermocouple psychrometers. The sods were watered, and blue grama vegetation was allowed to grow for approximately 2 weeks, during which time (with subsequent wetting and drying cycles) a large number of soil water potential readings were taken. All psychrometer readings were taken at least 3 days after watering on the drying part of the hysteresis curve. Soil water potentials were plotted against the relative weight of water in the sod at the time of measurement, and a regression line was drawn through the points, thus reducing error caused by possible erratic thermocouple psychrometer readings.

When a sod reached one of the three desired soil water potentials (about 0, -15, or -30 bars), the soil surface was sealed with mineral oil and a sequence of photosynthetic and respiration rate determinations was made on the aboveground foliage. The sequence consisted of measuring the photosynthetic rate of that sod at a given soil water potential under three levels each of irradiance and temperature, respectively.

Respiration rates for each blue grama sod were measured in darkness at each of the three temperatures. Thus, a total of 12 carbon dioxide exchange rate determinations were observed on each sod at a known soil water potential. All determinations were made at night to avoid variations in irradiance caused by sunlight.

A physiological equilibration period of approximately 15 min was allowed between each change in level of light intensity, and 30 min equilibration was allowed between each temperature transition. Approximately 8 to 9 hr were required for each set of 12 rate determinations of CO_2 flux.

Since it was not considered practical to clip 12 leaves for leaf water potential determinations from a sod of only 186 cm^2 in soil surface area, leaf water potential was determined at the beginning and at the end of each set of the 12 CO_2 determinations.

After CO_2 determinations were completed, each sod was clipped. Aboveground biomass and green leaves were weighed separately, leaf areas were determined, and samples were oven-dried at 60°C and reweighed. Both net and gross photosynthesis were calculated, each on a basis of square decimeters of leaf area (one side), dry weight of photosynthetic material, and dry weight of total aboveground biomass (photosynthetic and nonphotosynthetic plant material).

INITIAL RESULTS OF THE 1971 MEASUREMENTS

The preliminary results for the 1971 field season have not yet received critical examination. Therefore, the following results are truly initial results subject to change after additional data analyses have been conducted.

Field System

Average rates of CO_2 assimilation for blue grama sods in the lysimeter area are presented in Fig. 4. The data for September and October are from the control plot in the Environmental Stress Area (ESA). Reliable results were not obtained from the dome system until June 9. Therefore, productivity in May can only be estimated from LAI measurements and abiotic data. Peak productivity from our observations was observed on June 16, following a 6- to 7-mm rainfall on June 14. From June 16 until the instrumentation trailer was moved from the lysimeter area in mid-July, there was an exponential decrease in photosynthetic rates. This rapid decrease in fixation rates was probably

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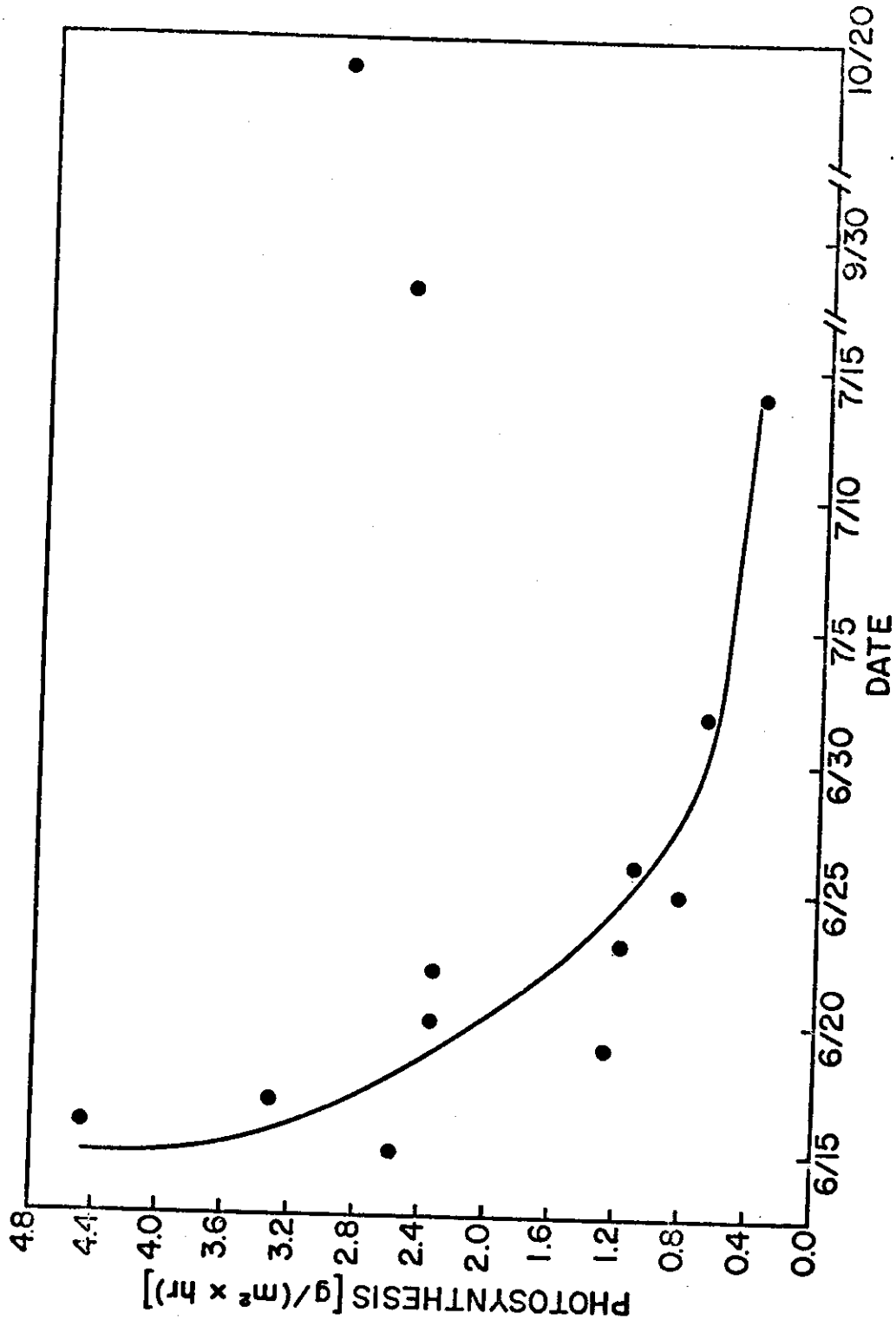

Fig. 4. Seasonal change in average daily CO_2 assimilation rates over untreated blue grama sods at the Pawnee IBP Site in 1971. (Daily averages from about 1000 to 1130 hr).

due to the depletion of soil water. Measurements were not continued in late July and August in the control plots of the ESA because of extremely dry conditions and a small amount of green vegetation. Precipitation in early September caused renewed growth activity for blue grama. The period from mid-July to early September could probably be represented by the asymptotic extension of the curve toward zero assimilation. The only significant assimilation of CO_2 during such harsh environmental conditions would probably occur in the early morning and perhaps late in the afternoon when leaf water stress was less.

The photosynthetic rates are expressed as grams of CO_2 assimilated per square meter of leaf surface area (one side) per hour. Rough calculations from a diurnal run indicate that about 63% of the mean rate of assimilation from 1030 to 1130 hr (MST) can be used as a factor to multiply by the number of daylight hours for obtaining an average value of productivity for a 1-day period. By selecting values from the curve of Fig. 4 for the critical days, one can approximate the total amount of CO_2 assimilated during the growing season. From June 1 to September 1, a randomly chosen square meter of blue grama leaves should assimilate about 1136 g of CO_2, or produce roughly 568 g of carbohydrates.

During periods of rapid growth when soil water stress is relatively low, the incoming solar energy may be the limiting factor for plants which fix carbon by the Hatch and Slack pathway (Björkman, Pearcy, and Nobs, 1971). Field observations in early June indicate that a drop of 20 to 30% in dome temperature resulted in about a 10% reduction in fixation rates. However, when the radiation intensity was reduced about 10%, there was roughly a 40 to 50% decrease in fixation rates. These responses were not observed in

late June when soil water stress was relatively high. When soil water was not limiting, the results from regression analyses were highly variable because of interactions among variables and the varying ranges of incoming energy over which a determination occurred. For example, over the range of 0.2 to 1.0 langleys/min the response in CO_2 assimilation to increasing radiation was essentially linear, but at the low and high extremes of radiation, CO_2 assimilation rates were nonlinear. When CO_2 assimilation rates were linear, then predictive equations could be shown with a relatively large r^2 value ($r^2 = 0.81$).

Photosynthetic rates for blue grama are plotted in Fig. 5 with incoming solar radiation represented on the horizontal axis. Even at 1.3 langleys/min, the photosynthetic activity is apparently not light saturated. To propose that the productivity of a shortgrass ecosystem might be limited by incoming energy is somewhat of a departure from previous thinking. Yet, during the normal periods of rapid growth the soil water content is relatively high, and if more energy were available then production should be increased.

The average rates of fixation over a 10-hr period on June 22, 1971, are shown in Fig. 6. With radiation as the only variable, a regression equation was computed which accounted for 81% of the variability in CO_2 flux.

Some attempts were made to determine temperature curves for photosynthesis when other factors were held essentially constant (Fig. 7). The data points in Fig. 7 represent 15-min means. In this example, the increasing levels of solar radiation should have caused increased CO_2 uptake, but, in fact, the increase in temperature appears to be the more important factor. The 10°C change from 32 to 42°C resulted in about a 25% reduction in the CO_2 assimilation rate. The soil water content for this determination was about

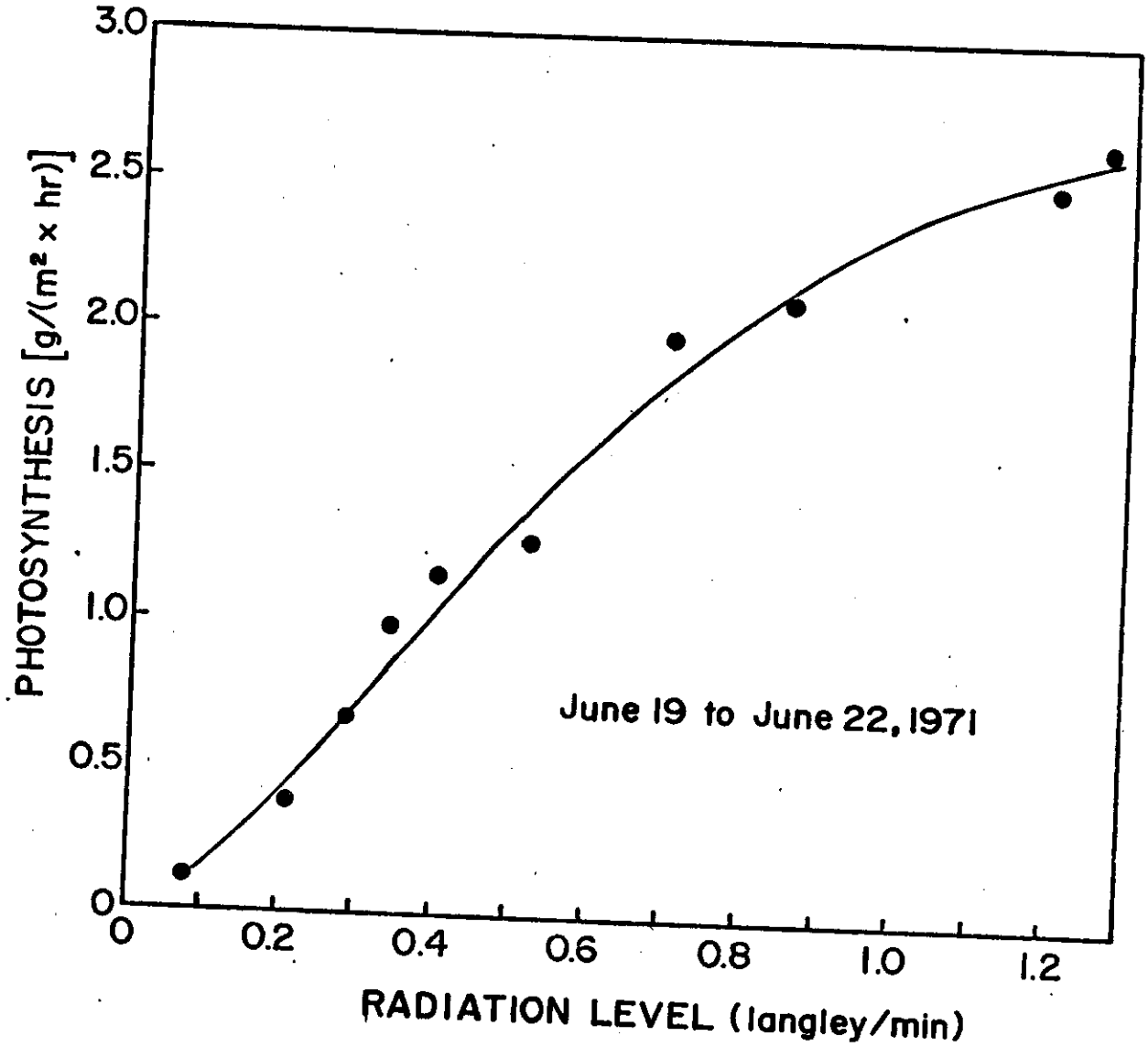

Fig. 5. Photosynthetic CO_2 uptake by blue grama at the Pawnee Site as a function of light intensity (irradiance).

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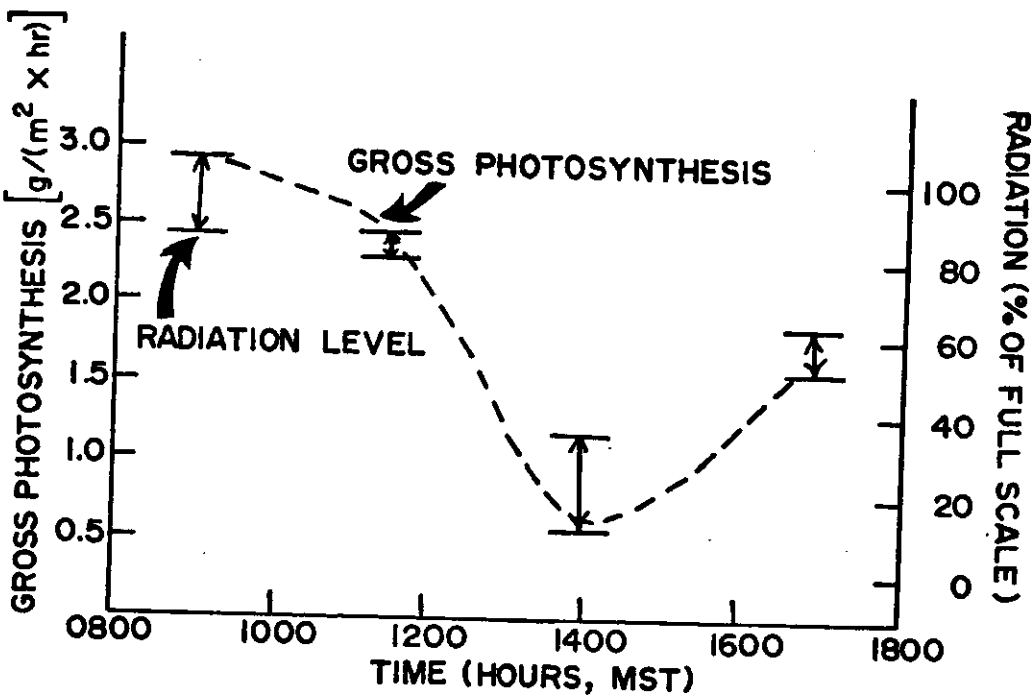

Fig. 6. Daily trend of photosynthetic rates of blue grama sod at the Pawnee Site as a function of incoming solar energy on June 22, 1971.

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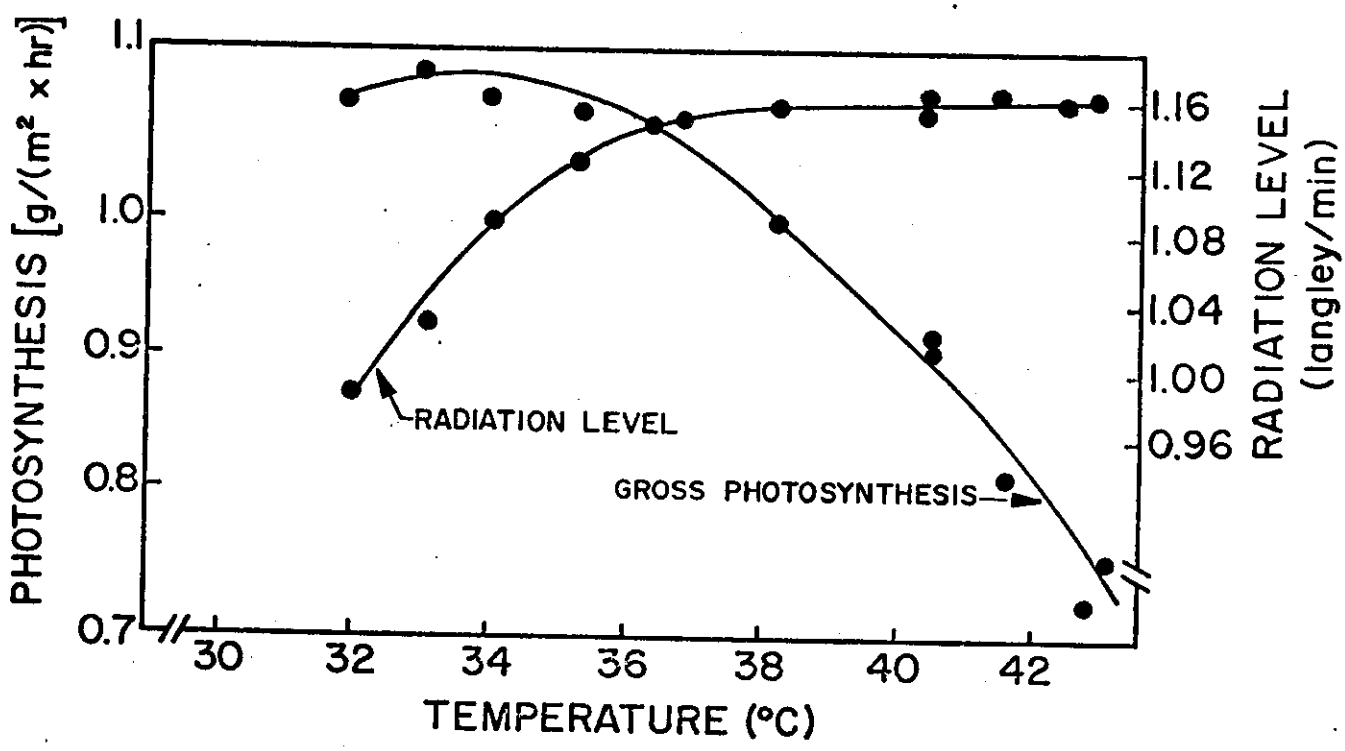

Fig. 7. Photosynthesis of blue grama vegetation at the Pawnee Site as a function of irradiance and temperature on June 26, 1971, from 0815 to 1045 hr (MST).

2.1 cm for the upper 22-cm horizon. The optimum temperature for CO_2 fixation by blue grama appears to be around 33 to 34°C at this soil water content.

The results of CO_2 exchange of blue grama vegetation in the Environmental Stress Area (ESA) have not received sufficient study to warrant sweeping conclusions. In general, the rates of CO_2 assimilation from irrigated blue grama sods without fertilization were comparable to photosynthetic rates in mid-June for blue grama in the lysimeter area when moisture levels were relatively high.

Some values are plotted in Fig. 8 which represent mean fixation rates from determinations of CO_2 flux over sods in the irrigated plots. Irrigation was halted on August 17, and peak fixation rates were observed on August 20. This peak rate was very similar to the 4.4 g/(m^2 × hr) reported from the untreated sod of June 16. The fixation rate was observed to decline until August 25, at which time 5 mm of rainfall was received. The response was roughly a 50% increase in increased photosynthetic activity within 24 to 30 hr. Photosynthetic activity then declined through September 3. Rain fell again on September 4, 7, and 8 (4, 3, and 18 mm, respectively). A determination of CO_2 exchange made on September 9 indicated that exchange rates were approximately equal to those observed when water was regularly applied through irrigation.

The fixation rates of blue grama on July 30 are shown in Fig. 9. The soil water content at this time was near field capacity (about 2.9 cm). Ambient temperature within the dome is presented on the abscissa. When compared to the results presented in Fig. 7, it is apparent that the optimum temperature has shifted upward 3 to 5°C. The rapid drop in photosynthetic activity above 35°C was not observed when the soil water content

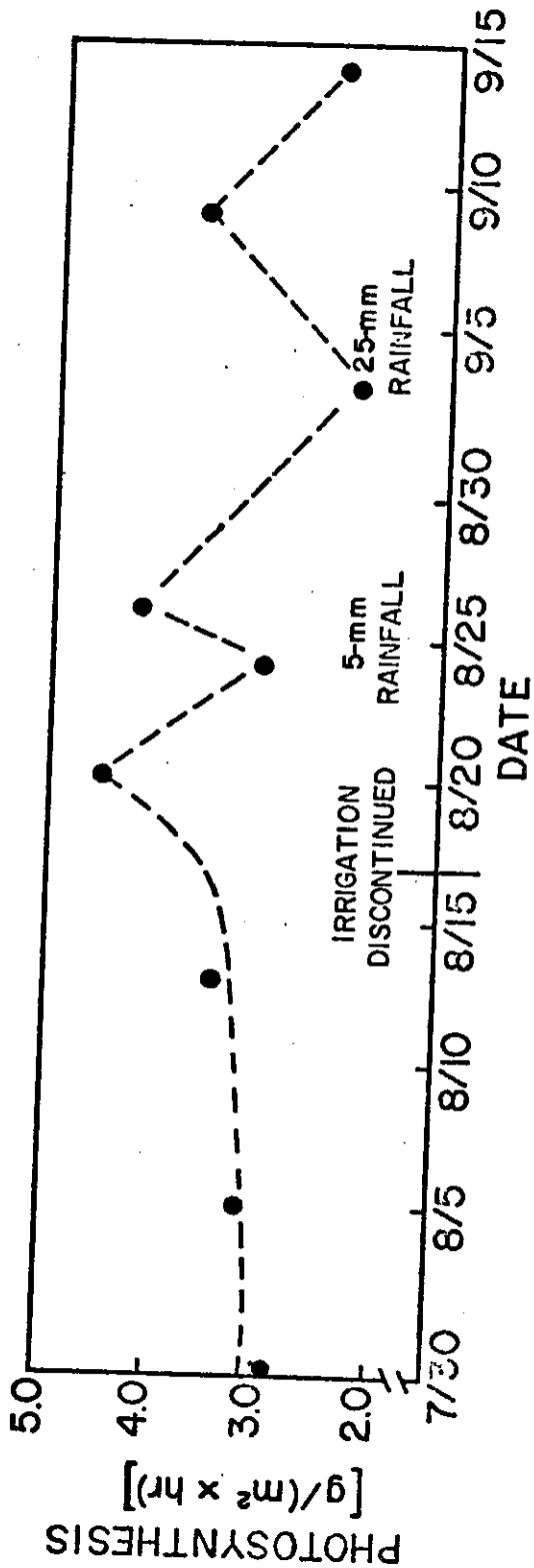

Fig. 8. Seasonal trends of CO_2 uptake by blue grama sods on irrigated only treatment in 1971 at the Pawnee Site of the Grassland Biome.

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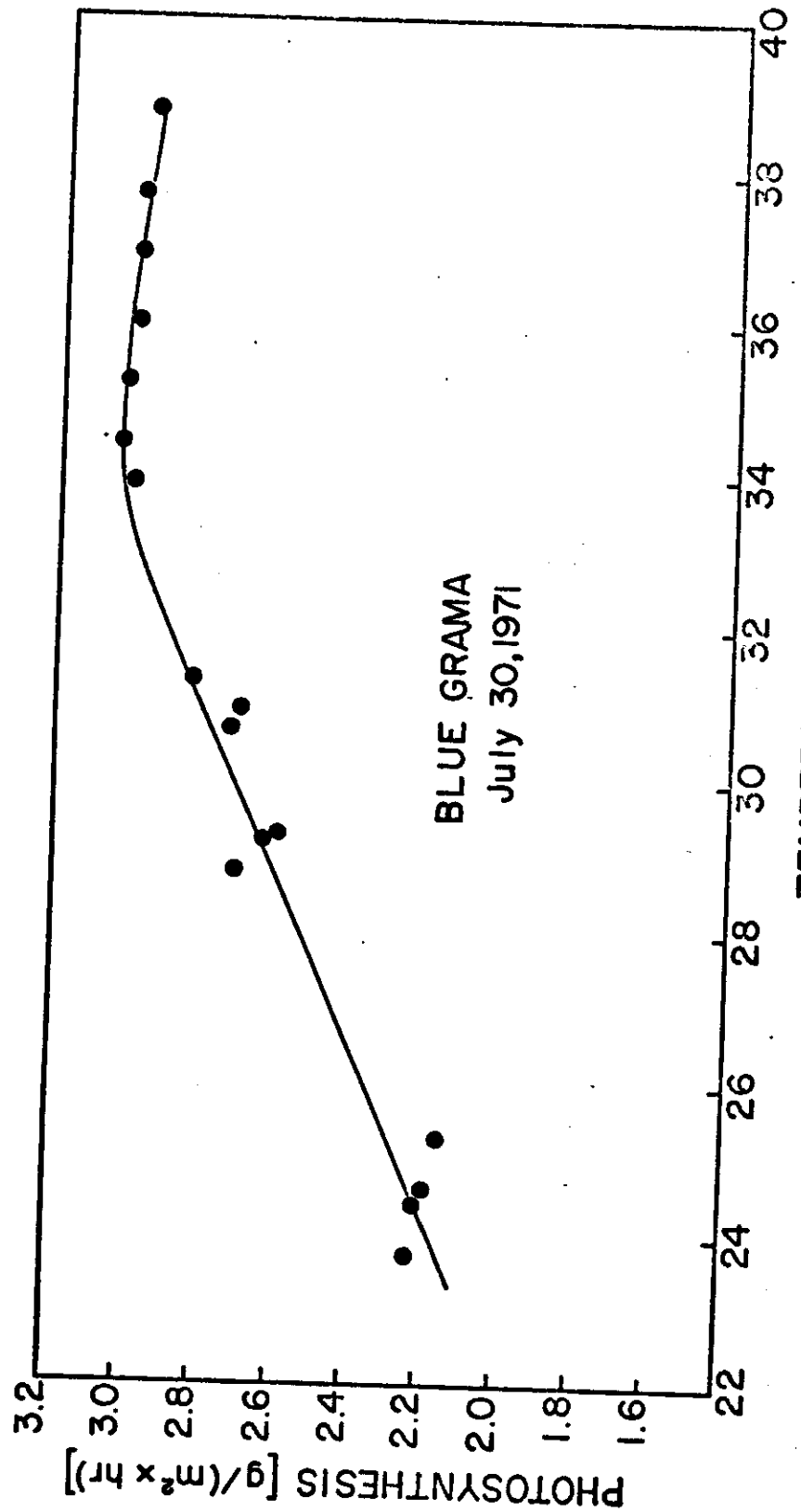

Fig. 9. Photosynthetic CO_2 uptake of blue grama sod as a function of ambient air temperature. Soil water content was near field capacity during measurements.

was near field capacity. The level response from 36 to 39°C may be indicative of solar radiation as a limiting factor.

Greenhouse Study

Analysis of variance of the data obtained in the greenhouse experiment showed all three main treatments (soil water potential, irradiance, and temperature) significantly affect ($P < .01$) both net and gross photosynthetic rates of blue grama (Table 1). Three of the four interactions among these variables were also significant ($P < .01$).

Analysis of variance for dark respiration rates of blue grama showed that each of the two main treatments of temperature and soil water potential significantly affected ($P < .01$) respiration. The interaction between soil water potential and temperature was also significant ($P < .05$).

Average net and gross photosynthetic rates of blue grama for variations in soil water potential, irradiance, and temperature are shown in Table 2. Photosynthetic rates are reported only on the basis of dry weight of photosynthetically active tissue because these values are believed to be most accurate and representative. Photosynthetic rates of blue grama based on total weight of aboveground tissue (live and dead) and leaf area were also determined and followed somewhat similar patterns. Photosynthesis as a function of leaf area is not discussed here because it was felt that our techniques for determining leaf area (airflow planimetry) were not developed to a satisfactory degree of accuracy at that time.

On the assumption that blue grama exhibits no photorespiration, gross photosynthesis was calculated by adding the measured values of net photosynthesis and respiration. All CO_2 exchange rates were computed by the equation:

Table 1. Analysis of variance of net photosynthesis (mg CO_2 × dm^{-1} × min^{-1}) of blue grama vegetation under three levels of soil water potential, irradiance, and temperature.

Source	df	MS	F
Replications	2	0.001	0.25
Water (W)	2	0.064	19.29**
Error (A)	4	0.003	
Irradiance (I)	2	0.022	46.72**
Temperature (T)	2	0.032	68.60**
W × I	4	0.006	12.60**
W × T	4	0.004	8.70**
I × T	4	0.001	2.10
W × I × T	8	0.002	5.02**
Error (B)	48	0.0005	
Total	80		

** Indicates significance at the 0.01 level of probability.

Table 2. Average net and gross photosynthetic rates of blue grama (based on dry weight of photosynthetically active tissue) as influenced by soil water potential, irradiance, and temperature.[a/]

Soil Water Potential (bars)	Irradiance (langleys/min in visible spectrum)	Temperature (°C)	Net Photosynthetic Rate (mg CO_2/g/min)	Gross Photosynthetic Rate (mg CO_2/g/min)
0	0.30	20	0.0944	0.1240
0	0.30	30	0.0962	0.1727
0	0.30	40	0.0125	0.0990
0	1.12	20	0.1342	0.1638
0	1.12	30	0.2099	0.2864
0	1.12	40	0.1138	0.2003
0	1.54	20	0.1188	0.1484
0	1.54	30	0.2136	0.2902
0	1.54	40	0.1936	0.2800
-15	0.30	20	0.0817	0.0822
-15	0.30	30	0.0893	0.1190
-15	0.30	40	0.0184	0.0775
-15	1.12	20	0.1154	0.1159
-15	1.12	30	0.1217	0.1514
-15	1.12	40	0.0423	0.1014
-15	1.54	20	0.1248	0.1253
-15	1.54	30	0.1525	0.1823
-15	1.54	40	0.0414	0.1005
-30	0.30	20	0.0438	0.0474
-30	0.30	30	0.0395	0.0661
-30	0.30	40	-0.0028	0.0390
-30	1.12	20	0.0694	0.0760
-30	1.12	30	0.0483	0.0749
-30	1.12	40	-0.0028	0.0390
-30	1.54	20	0.0734	0.0770
-30	1.54	30	0.0450	0.0687
-30	1.54	40	-0.0011	0.0407
	Grand Mean		0.0847	0.1240

[a/] Each value represents an average rate for three replicates.

$$\text{mg } CO_2/\text{min} = \frac{[44{,}010(\text{mg})][\Delta\text{ppm} \times 10^{-6}/\text{min}][\text{volume(liter)}][273(°\text{C})][\text{pressure(mm Hg)}]}{[22.414(\text{liter})][\text{temp}(°\text{C})][760(\text{mm Hg})]}$$

where Δppm = change in CO_2 concentration for the period of time

volume = the total volume of the system (this replaces the flow rate in the equation for determining carbon dioxide exchange in the field)

pressure = average atmospheric pressure

temp = 273°C + ambient temperature of the assimilation chamber

Fig. 10 depicts the means of net photosynthesis of blue grama at each of the three levels of each main treatment. Decreasing soil water potential from 0 to -30 bars caused an almost linear decrease in apparent photosynthesis. Increasing irradiance from 0.30 to 1.12 langleys/min nearly doubled apparent photosynthesis; however, increasing irradiance from 1.12 to 1.54 langleys/min caused only a small increase in photosynthetic rates. Fig. 10 shows an increase in photosynthetic rate from 20 to 30°C and a very sharp decrease from 30 to 40°C. Considering the 32 to 36°C optimum CO_2 fixation temperature of blue grama in the field, the decrease must be even more extreme from those temperatures to 40°C. It is also interesting to note that 20°C allowed higher photosynthetic rates than 40°C.

Several regression analyses of the data have been performed to determine the various effects of the independent variables of net and gross photosynthesis of blue grama. Surprisingly, the best predictive equation ($r^2 = .84$) was obtained by a decreasing stepwise multiple linear regression on gross photosynthesis using the measured values of the three parameters with no transgenerations. The equation is:

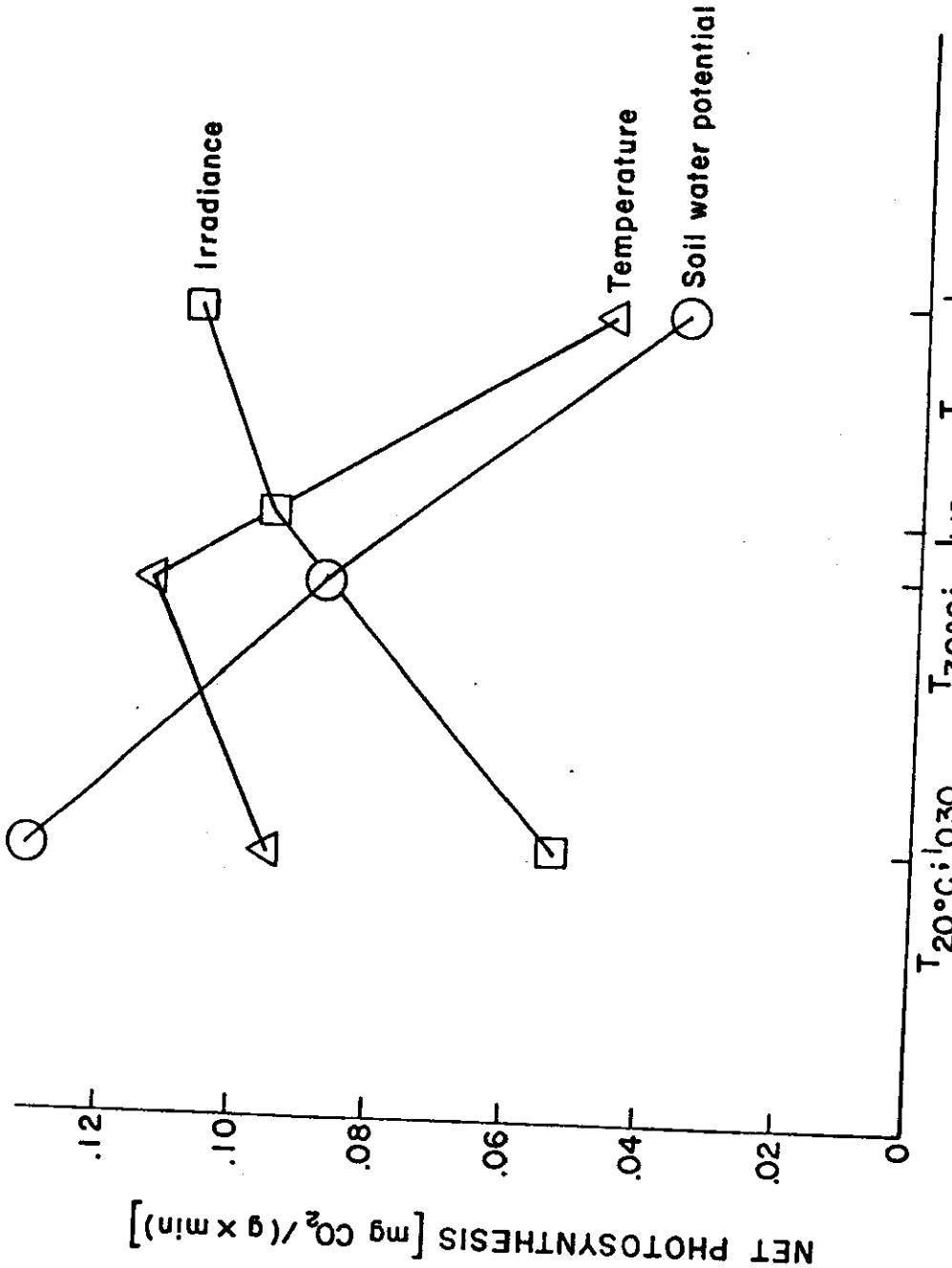

Fig. 10. Average net photosynthetic rates of blue grama at each of the three levels of each of the three main treatments of soil water potential, temperature, and irradiance.

$$\text{gross photosynthesis} \atop (\text{mg } CO_2/\text{g(dry wt live)/min}) = 0.000 + 0.004(\text{temp}) + 0.004(\text{soil water potential}) + 0.087\ (\text{irradiance})$$

Fig. 11 shows the two-way interaction effects of soil water potential and irradiance on net photosynthesis of blue grama. Photosynthetic rates at low irradiance were not reduced significantly by soil water stress up to -15 bars. However, the interaction between soil water potential and irradiance caused significant reductions in photosynthetic rates of blue grama at higher light intensities and lower soil water potentials.

Fig. 12 shows the two-way interaction effect of soil water potential and temperature on net photosynthesis of blue grama. The graph illustrates that the optimum temperature for photosynthesis of blue grama is lower as soil water potential becomes extremely limiting. Observed effects of low soil water potential (< -15 bars) were probably caused by stomatal closure due to moisture stress. Data of interaction effects on gross photosynthesis followed trends similar to that of net photosynthesis.

A summary of the general conditions responsible for maximum, mean, and minimum gross photosynthetic rate determinations are shown in Table 3. The maximum calculated gross photosynthetic rate was 0.29 mg CO_2/g/min (dry weight live tissue), while the minimum gross photosynthetic rate was 0.04 mg CO_2/g/min. The abiotic conditions which were observed in conjunction with maximum, mean, and minimum gross photosynthesis indicated that for maximum rates of photosynthesis of blue grama, low soil water stress, high irradiance, and warm temperatures were necessary. As soil water stress increased, or irradiance decreased, or temperatures dropped below (or went above) optimum, gross photosynthesis of blue grama was decreased (Table 3).

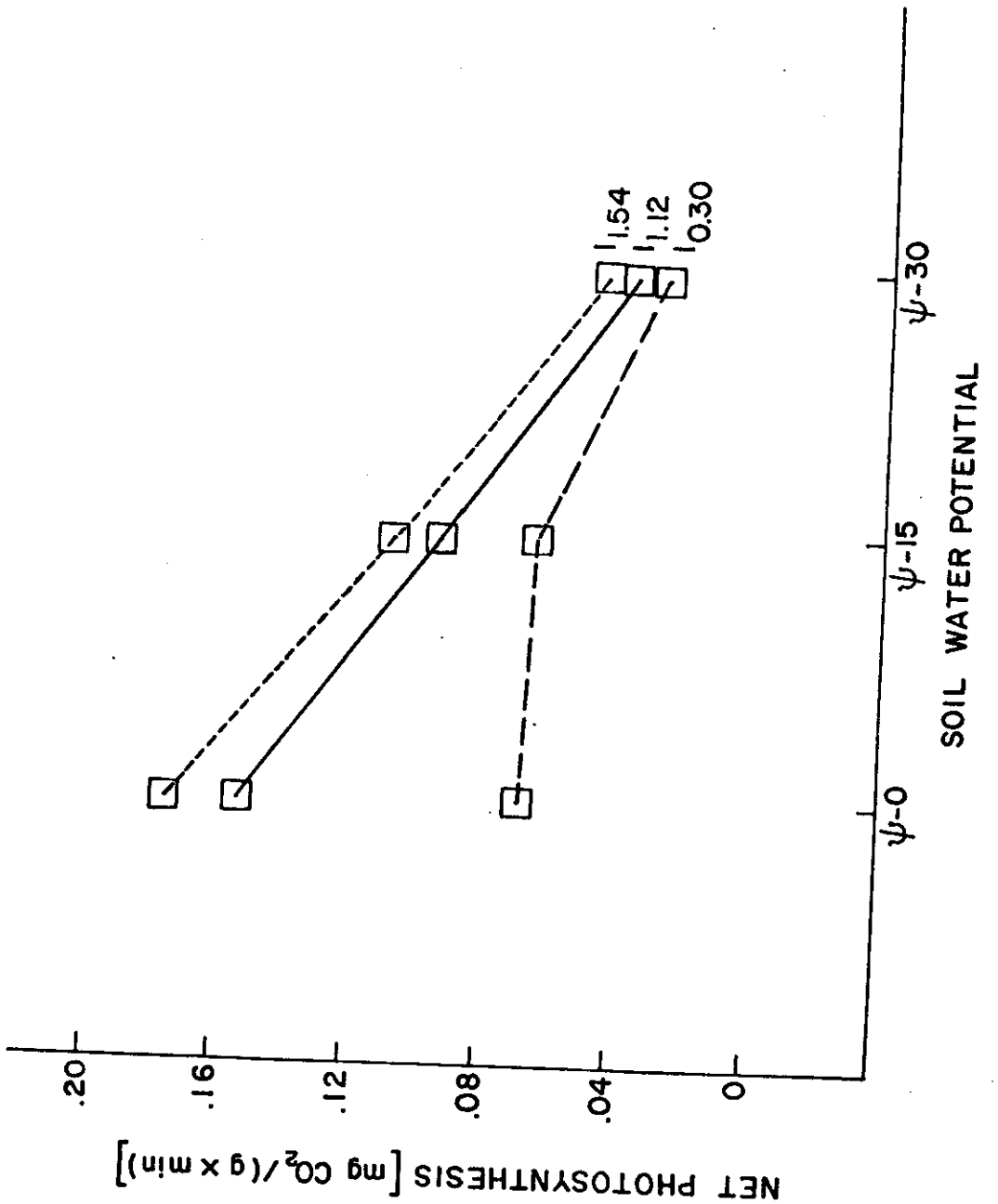

Fig. 11. Two-way interaction effects of soil water potential and irradiance on net photosynthesis of blue grama.

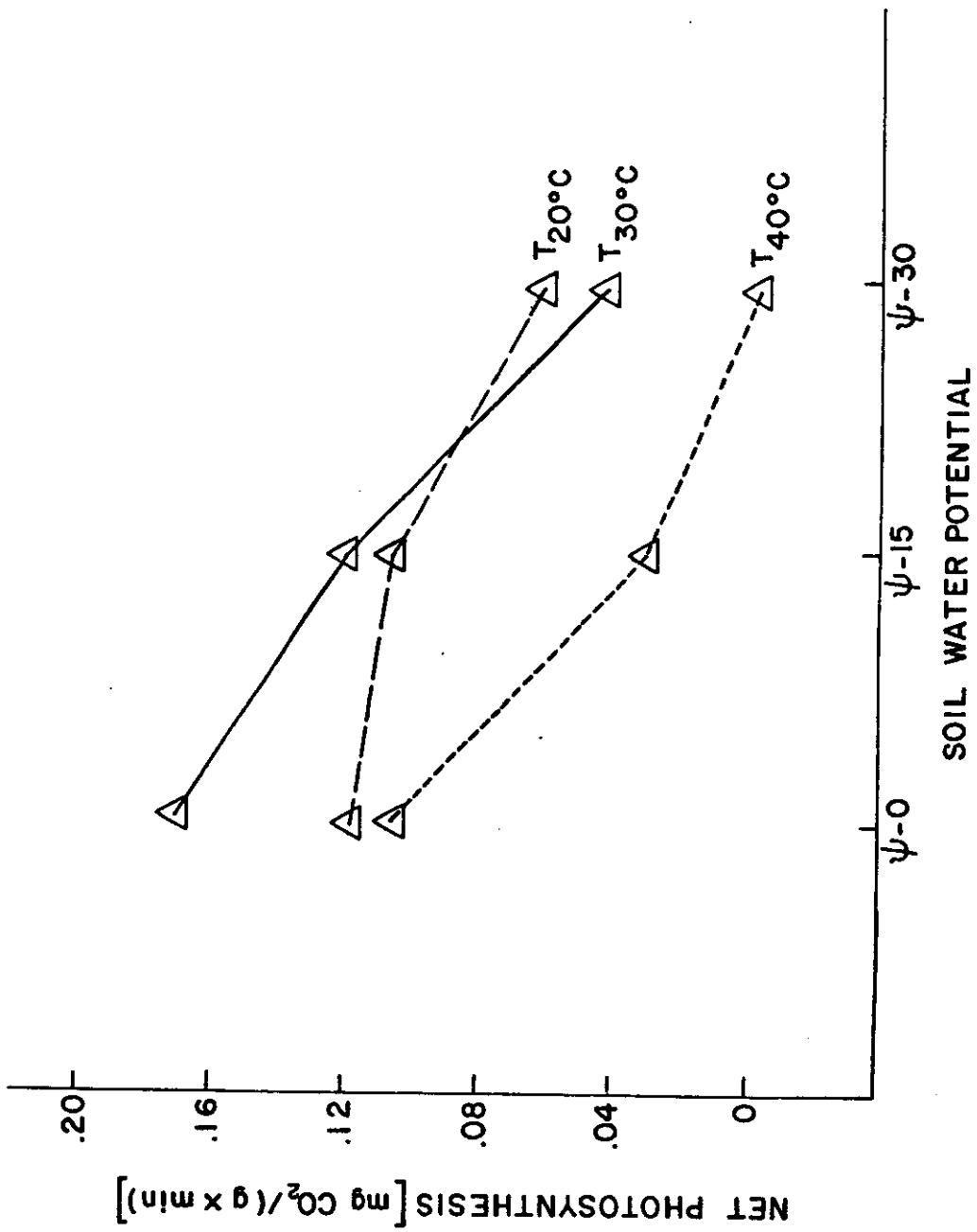

Fig. 12. Two-way interaction effects of soil water potential and temperature on net photosynthesis of blue grama.

Table 3. Maximum, mean, and minimum gross photosynthetic rates of blue grama as influenced by soil water potential, irradiance, and temperature.

Gross Photosynthetic Rate (mg CO_2/g/min)	Water Potential (bars)	Irradiance (langleys/min)	Temperature (°C)
	Maximum gross photosynthetic rates		
0.29	0	1.12	30
0.29	0	1.54	30
0.29	0	1.54	40
	Mean gross photosynthetic rates		
0.12	0	0.30	20
0.12	-15	0.30	30
0.12	-15	1.54	20
0.12	-15	1.12	20
	Minimum gross photosynthetic rates		
0.04	-30	0.30	20
0.04	-30	0.30	40
0.04	-30	1.12	40
0.04	-30	1.54	40

Fig. 13 depicts the effects of temperature and soil water potential on dark respiration rates of blue grama. As expected, increasing temperature caused significant increases in respiration. Decreasing soil water potential from 0 to -15 bars significantly decreased respiration rates of blue grama, with smaller decreases occurring from -15 to -30 bars. This indicated that low soil water potentials and temperatures caused reductions in respiration, thus reducing energy utilization by the plant.

The interaction effects of soil water potential and temperature on respiration are shown in Fig. 14. As soil water potential decreased from 0 to -15 bars, respiration was greatly reduced. Little change in respiration rates were noted between -15 and -30 bars soil water potential, except at 40°C. The decrease in respiration at 40°C was almost linear as soil water potential decreased from 0 to -30 bars. Decreases in respiration rates at 20°C as moisture stress increased from 0 to -15 bars was not as great as at 30°C, probably because the respiration rate was initially low at the lower temperature. Increasing soil water stress from -15 to -30 bars had little influence on respiration rates of blue grama at 20 or 30°C.

The effects of these variables on both photosynthesis and respiration of blue grama aid in emphasizing the very important role of these variables in determining energy capture by primary producers. These results indicated that the factors limiting blue grama growth and productivity throughout a normal growing season are a web of interactions. During a normal growing season, the most important limiting factor in the early spring may be low temperatures. During late spring with higher temperatures and minimal soil water stress, solar irradiance may become the major factor limiting blue grama productivity. In the summer when temperatures and irradiance are optimal, soil water probably becomes the dominant limiting factor.

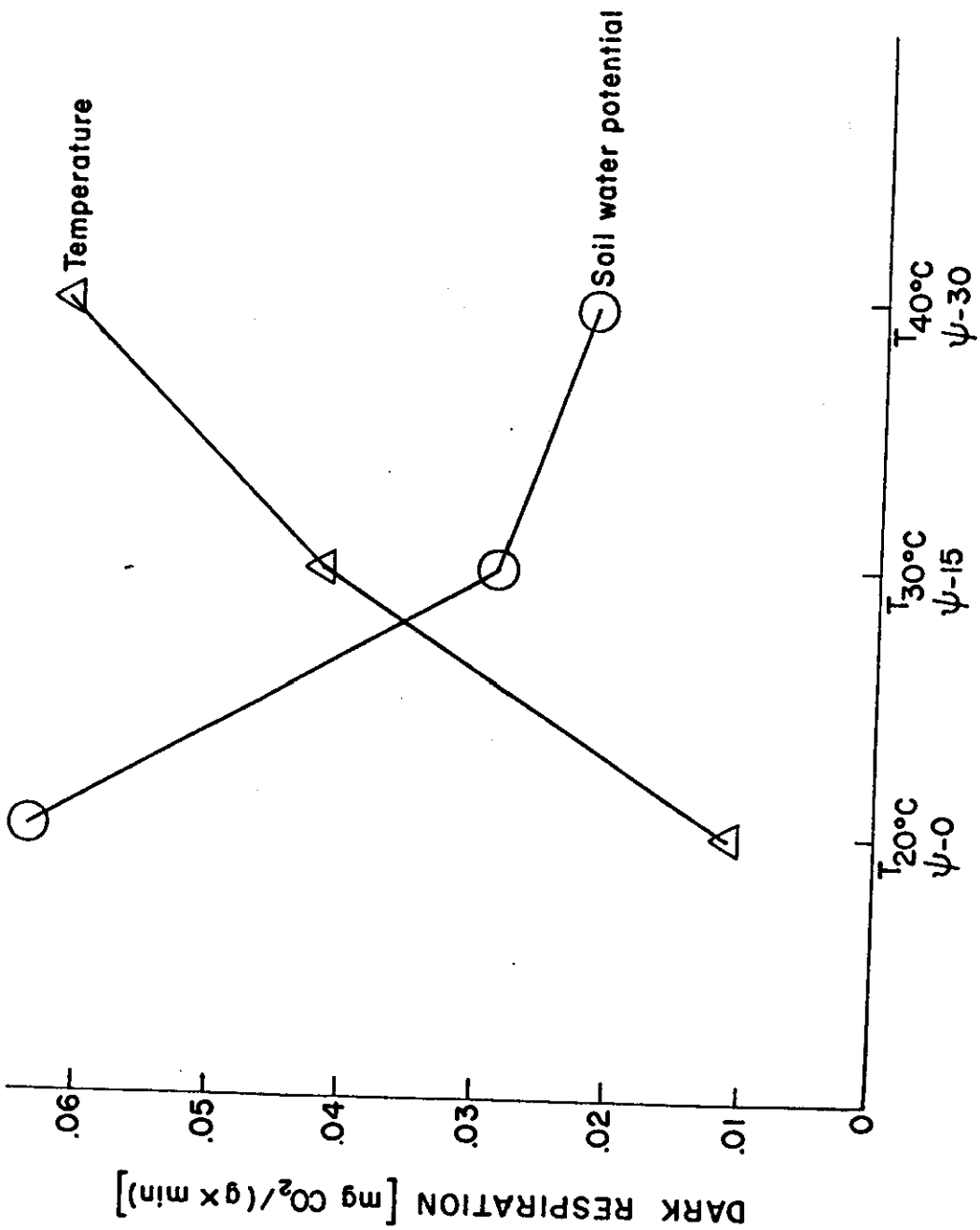

Fig. 13. Mean dark respiration rates of blue grama at each level of the two main treatments of soil water potential and temperatures.

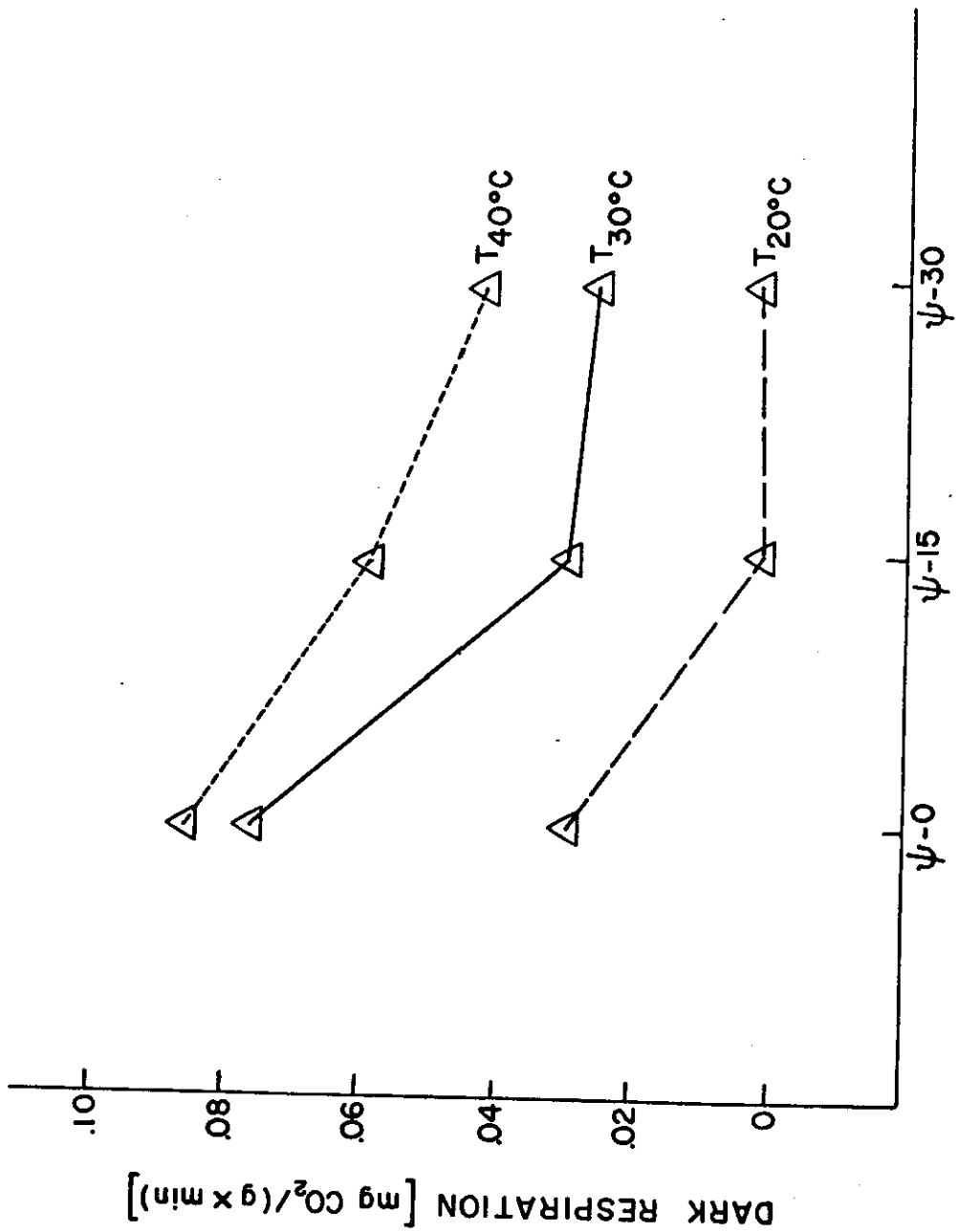

Fig. 14. Two-way interaction effects of soil water potential and temperature on dark respiration of blue grama.

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APPENDIX I

SAMPLING DATES

Data on CO_2 assimilation rates of blue grama sods at the Pawnee Site were collected on the following dates in 1971 at two study areas.

Lysimeter Area

June 9, 10, 11, 12

June 15, 16, 17, 18, 19, 20

June 22, 23, 25, 26

July 1, 2, 3, 4, 5

July 9, 14

Environmental Stress Area

July 19, 20, 22, 28, 30

August 3, 5, 9, 11, 13

August 16, 17 (over *Opuntia* sods)

August 24, 25, 26, 29

September 14, 23, 28

October 8, 19

APPENDIX II

FIELD DATA

Raw Photosynthesis Data

The 1971 Pawnee photosynthesis data are Grassland Biome data set number A2U00PB. A description of these data and a listing of the data from one run on one natural sod follow. A FORTRAN readable summary of these data by 3-, 15-, and 60-min time intervals after conversion to meaningful units is also available at the Natural Resource Ecology Laboratory.

Data Description

These data are read from strip charts and are punched on an X-Y digitizer, which records inches from an origin to .001-inch tolerance. A code is also provided to identify which line (parameter) was read from the strip chart. The parameters measured and their associated codes are:

1. CO_2 concentration
2. Dew point temperature
3. Solar radiation
5. Dome temperature
9. Soil temperature (when possible)

The data are punched in sets, with each set consisting of an x-value (time), a y-value (response parameter), and the code for the parameter being recorded. Six of these sets are punched per card with all the cards containing coordinates for one parameter grouped together, followed by the cards for another parameter, and so forth, within one data run. The format for any one card is 6(2F5.3,I3).

Data runs are physically separated by blank cards. Each run has three associated header cards. The first of these cards contains:

1- 6	Date (year, month, day)
7-10	Time at beginning of run (hr, min)
11-12	Sod number
13-17	Flow rate (in light)
18-22	CO_2 concentration when dark (ppm)
23-27	Flow rate when dark

These are fixed values for that run. The next two cards are commentary and usually contain the same information in no standardized format.

*** EXAMPLE OF DATA ***

```
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