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PHOTOSYNTHESIS OF SHORTGRASSES UNDER FIELD CONDITIONS

W. H. Moir
J. P. Boratgis
R. Sherman
G. Paetsch

GRASSLANDS BIOME

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ABSTRACT

Progress to September 1969 consisted mainly in developing and improving an instrumentation system for measuring carbon dioxide gas exchange in plants growing under field conditions. The observation system now includes a rigorous gas flow and temperature control.

By August 1969 major components of the photosynthesis measurement system had been tested and found satisfactory, although further improvements and modifications of some subsystem components are envisioned. The response of shortgrasses to diurnal ambient changes was measured during two weekends near the end of the growing season. Additional responses in gas exchange were measured during short periods of the active growing season, and the results are discussed.

Plans for the 1970 season include replication of photosynthesis measurements at up to six field sites, continuous diurnal observations correlated with major phenological events, measurements of soil respiration under field conditions, and measurements of the influence of plant moisture stress to carbon dioxide exchange rates.

RESEARCH OBJECTIVES DURING 1969 SEASON

The photosynthesis project is intended to provide field data contributing to a photosynthesis process model. Measurements of carbon dioxide gas exchange (apparent photosynthesis) under field conditions for dominant grasses of the Pawnee arid steppe are intended to show response characteristics to environmental conditions of light, temperature, water stress, defoliation, and other abiotic factors. Our endeavors during the 1969 season were to (1) develop and test the photosynthesis observation system, and (2) obtain response characteristics from representative samples of shortgrass vegetation.

THE FIELD INSTRUMENTATION SYSTEM

We have developed a photosynthesis field measurement system of considerable flexibility of application. The electronic components are housed in a small trailer. A satellite to this trailer is a small hemispherical dome that can be located anywhere within a 30 mile radius of the trailer. The total system is portable and is powered by either line current or by a 2500 watt generator. Levels of carbon dioxide within the dome and at up to five additional intake sites can be measured simultaneously with a precision of ±2 ppm. A typical open system of measurement is shown in Fig. 1. Under conditions of low photosynthetic activity the system of Fig. 1 can be converted to a closed gas flow system. Particular effort has been made to keep the grass environment within the dome as natural as possible. In the discussion below we describe critical features of the various instrumentation components of Fig. 1.

Environmental Cuvette (Dome)

The environmental growth chamber, cuvette, or most simply, the field dome is the sample observation unit. A rust-proof base plate is hammered 2-4 cm into the ground. This circular plate defines an area of vegetation of radius 29 cm (0.26 m^2). A hemispherical plexiglass dome of thickness of two mm fits in an airtight manner upon this plate and allows transmittance of visible light at about 92%. Air intake is provided by circular ducts along the circumference of the base plate. At present there is a "dead space" between the ducts and the wall of the base plate. This will be eliminated in subsequent base plate design. Air is sampled from a small outlet on the dome roof. The environment within the dome is homogenized by turbulent mixing of sensible heat, carbon dioxide, and water vapor. The air temperature within the dome is measured by a #44005 thermister (3000 ohm at 25°C) located near the mouth of the efflux air duct near the base of the plastic dome.

Environmental Control System

As soon as the dome is positioned onto the base plate, the plant environment undergoes mild to drastic modification (depending on external conditions). Our main engineering effort in the summer of 1969 was to restore this modified environment to as nearly natural conditions as possible. We used three methods to bring the energy balance components of green leaves (leaf temperature, sensible and latent heat flux) inside the dome to existing conditions outside the dome: air temperature control, maintenance of a suitable level of turbulent convection around leaves, and periodic or continuous, slow or rapid rates of flushing the dome with ambient air.

Air temperature is regulated by an 0.5 hp compressor-cooler switched on by means of an electronic feedback system (Fig. 1). The resistance of the dome thermister is compared with that of a 1% matched thermister that measures the leaf air temperature external to the dome. Under "ambient control" the cooler is on whenever the dome thermister exceeds the ambient sensor by 1°C. Under "manual control" the cooler is on whenever the dome thermister exceeds a constant, preset value. Under either type of control the dome temperature is kept within ±1°C of its specified value. We tested this system under stringent environmental conditions at the Pawnee site. On a clear, hot day (ambient air temperature at 37°C, surface soil temperature at 48°C) we were able to maintain the dome air temperature about 10°C below ambient. On less extreme days a greater range of controlled dome environments can be achieved. However, under a rapidly flushed, open system the range of controlled dome temperatures would be reduced (although it would be easier to maintain the dome air temperature at ambient).

A variac regulator allows circulation within the dome at simulated wind speeds. The slight flutter of leaves indicates leaf turbulence of about 130 cm/sec (3mph), a value around which leaf boundary layer resistance is reduced (Slatyer 1967), leaf temperatures coincide with air temperature (Gates 1968), and energy exchanges between leaf and environment are maintained by forced convection.

Atmospheric composition (carbon dioxide and water vapor) in the dome is controlled by a flushing system. As CO_2 levels buildup or decline, ambient air is manually brought into the dome at precise, metered rates. At present the metering system consists of calibrated Gilmont flowmeters, but we will modify this system to allow greater flushing rates whenever rapid photosynthesis or respiration activities dictate. At present the air input to the dome is maintained at slight pressure to compensate for possible air leakage in the pumping and duct system.

Precise humidity control has not been engineered into the dome system, and high levels of vapor have been observed especially during early morning hours. The internal vapor pressure is partly reduced by lowering air below the dew point in the cooling circuit, but a further drying system may be required. Flushing to dome with greater volumes of pre-dried ambient air will also help reduce internal humidity.

Air Sample Flow System

This system consists of tubing, pumps, air mixers, driers, valves, flowmeters, and an eight-channel gas switch. The flow circuitry can be varied to accomodate a variety of gas sampling possibilities under different field conditions. The pumps are leak proof and have been used with satisfaction in other carbon dioxide sampling systems (Harris 1968, Lemon 1968). Tubing is aluminum, whenever possible (Brown 1968). The air mixers are designed to reduce variation in carbon dioxide short term levels (Lemon et al. 1969). The eight-channel switch is leak proof and allows simultaneous sampling from different field sources of carbon dioxide. Thus, in addition to monitoring the dome atmosphere, we can observe carbon dioxide at several ambient levels (the open air, or aerodynamic, method of carbon dioxide measurement), can obtain concomitant values of soil respiration (discussed below), and have a zero check on the gas analyzer.

Carbon Dioxide Sensing and Recording System

A LIRA analyzer (Mine Safety Appliances) senses CO_2 levels by infrared absorption. The instrument range is between 275-425 ppm but values beyond this range can also be monitored by use of appropriate instrument settings. The analyzer outputs the difference in gas concentration between sample and reference cells, but use of a constant gas in the reference cell effectively converts the analyzer to an absolute output value. The output was somewhat noisy when the trailer was buffeted by high wind, but otherwise the analyzer performed well during the 1969 season. The millevolt signal was recorded on a Heath servo-recording system, employing chart paper.

Carbon Dioxide Calibration Gases

Atmospheres of known CO_2 concentration are used to periodically check for instrument drift end to scale the output record. Downscale, midscale, and upscale concentrations (respectively about 300, 325, and 425 ppm) are periodically read through channels seven and eight of the gas switch and are recorded on the Heath recorder. The Matheson carbon dioxide standards are periodically recalibrated by ascarite absorption (Brown and Rosenberg 1968). Our standard cylinders are refilled whenever their gas content falls below 500 psi in order to avoid slight concentration changes (Harris 1968).

PHOTOSYNTHESIS OF SHORTGRASS VEGETATION, INITIAL DATA

We report here some of our interpretable results during the 1969 growing season. We realize that much of the interpretation is subject to more rigorous examination, and that much of the necessary concomitant environmental data for interpreting plant response (e.g. light intensity, soil temperature, leaf temperature, stomatal conditions, species composition of vegetation under the dome, their leaf areas, etc.) was unavailable at the time the gas exchange measurements were taken. Thus, these are preliminary results only, and in some cases are more of a voucher for the adequacy (or inadequacy) of the developing instrument system than for a realistic documentation of field photosynthesis.

Some results of field photosynthesis are shown in Figs. 2-4, from observations from plots containing *Bouteloua gracilis* (dominant), *Carex heliophila* (minor), and *Buchloe dactyloides* (subdominant or minor). Fig. 2 was redrawn directly from our chart data. From 1100 to 1200 hours we observed a very low carbon dioxide level within the dome on this clear, warm day. Shortly after noon the dome was plunged into darkness by inverting a large cardboard carton over the entire dome. There was an immediate increase in atmospheric CO_2 concentration as photosynthesis ceased. At the same time the leaf stomata doubtless closed up (Turner 1969) as the radiation flux density dropped below about 10^4 ergs cm^{-2} sec^{-1} and tissue CO_2 concentrations increased. The dome was kept dark for about eight minutes and then re-exposed to the insolation of the clear sky. Immediately atmospheric CO_2 levels declined, and steady state was reached in about 12 minutes, but at about 1/3rd the pre-darkened level. As a cloud briefly passed over the dome (the event is documented photographically) there was again a photosynthesis decline and a rapid return to steady state about five minutes after the cloud had passed (Fig. 2). Progressive increasing cloudiness resulted in gradual photosynthesis decline after 1300 hours. Failure to return to low CO_2 levels after darkening the dome can be attributed to the stomata remaining partly closed, possibly the result of leaf moisture stress. The low CO_2 levels between 1100-1200 hours might be an artifact of unusually high mid-morning humidities that were observed within the dome environment.

The lowest trace of Fig. 2 gives the zero reference line ($\Delta CO_2 = 0$). Ambient levels of CO_2 remained more or less constant from 1200 to 1300 hours, at generally higher values than levels within the dome. This would be a logical consequence of wind mixing outside the dome.

Fig. 2 is instructive in several ways. It suggests that shortgrasses have a rapid response to changing light conditions. Gas exchange properties of shortgrass vegetation needs to be studied along with water vapor, stomatal, and leaf water stress observations. The data suggest that air temperatures varying between 30-35°C under full light conditions (**ca.** 9200 fc) appear not to have a marked effect upon photosynthesis. Most important, perhaps, the record suggests that short period observations (1-2 hours) can produce some very informative data for modelling photosynthesis.

Diurnal observations of shortgrass vegetation are given in Figs. 3 and 4 from 10 minute averages of the chart records. In Fig. 3 both absolute carbon dioxide concentrations within the dome atmosphere and these concentrations expressed as departures from external (ambient) CO_2 concentrations (measured at 25 cm above the ground) are given as separate graphs. The compensation intensity was reached about one hour after sunrise and about two hours before sunset. Fairly high midday CO_2 depletion (to about 302 ppm) and sustained night-time respiratory levels (at about 335-340 ppm) were observed. The short-term CO_2 fluctuations have remarkably high amplitude when compared with data of Lemon et al.(1969). We feel that this is a real phenomena of the biological system and not a consequence of instrument noise. The spectral periodicity of fluxes within the dome is similar to that of the external air (from visual inspection). At least part of the explanation for this resides in the open system of observation - external or ambient air was continually brought in the dome, as indicated in the scheme of Fig. 1.

Fig. 4 summarizes two periods of measurement near the end of the summer growing season at a time when the grasses had visibly yellowed.

The measurements of 9-10 August are of interest because of the suggestion of a midday decline in carbon dioxide assimilation rates - possibly because of high leaf temperature, severe moisture stress, or both. The greatest carbon dioxide depletion within the dome (expressed as a departure from external carbon dioxide levels) occurred in mid-morning (around 0800) and late afternoon (1730-1930) of this clear day. The following week's observations (dashed line) are not strictly comparable because of partly cloudy sky conditions and other differences in meteorological factors. However, daytime CO_2 levels within the dome are definitely below night-time levels, indicating metabolic activity of green plants at this season, and there seems to be a general rise, or upward respiratory shift, in carbon dioxide trends over the previous week's observations. The intriguing suggestion that this upward shift reflects lessened photosynthetic capability at the tail end of the growing season awaits next year's measurements for substantiation.

ANTICIPATED RESEARCH DURING 1969-1970

1. Winter Greenhouse Studies.

We intend to continue modifying and improving the instrumentation system during the winter by using shortgrass sods brought into the greenhouse. Responses of sods containing nearly pure swards of the dominant shortgrass species can be examined under experimental greenhouse environments.

2. Instrumentation System Modifications.

We need to redesign the base plate of the dome assembly to improve rapid air flow and to minimize dead air space within the chamber. A gas metering system that permits large quantites of air to be accurately gauged will also be installed to permit rapid dome flushing. An infrared filter to replace drierite columns will be installed in the IRGA. Humidity sensors and a radiometer will be installed inside the dome. A meteorological mast system will be designed for field use, enabling gas intake at 3-4 heights above the soil and vegetation surface. A simple system for observing "soil respiration" will consist of small, inverted coffee cans that can be placed for short periods over field sites in which green material has been removed. For observing water stress we will develop small hydraulic porometers (Fry and Walker 1967) and set up equipment for measuring relative turgidity (of Rychnovska and Kvet 1965, Rychnovska 1967).

3. Records of Photosynthesis under Field Conditions.

Commencing in March 1969 our equipment will be set up at the Pawnee study area. We intend to house the trailer in the exclosure in the heavy-grazed pasture. Six dome plates will be set up in pairs: two in plant communities dominated by *Bouteloua gracilis* in the heavy-grazed pasture, two in areas dominated or codominated by *Buchloe dactyloides* in the same pasture, and two on vegetation types within the 30-year exclosure. All of these sample types have been found to occur within 30 miles of the trailer. From each of the six 0.26 m^2 sample plots we will obtain (serially) measurements of CO_2 in relation to temperature, light, soil moisture (from data in the nearby neutron access tubes in the watersheds), and humidity. The first two abiotic factors above can be controlled by our temperature regulation system and by use of shading materials placed over the dome. Plant responses to the other abiotic factors will be measured under a variety of meteorological conditions in order to obtain a range under which gas exchange is taking place. These measurements will be undertaken throughout the 1970 growing season, but with particular attention given to phenology and community periodicity. Thus, in addition to vegetative and reproductive stages of growth of the dominant plants, we will also measure photosynthesis during seasons when community green leaf dominance is provided by *Carex heliophila*, *Buchloe dactyloides*, and *Bouteloua gracilis* in progressive phases of community aspectation.

4. Soil Respiration.

We hope to explore some simple, inexpensive procedures for compartmentalizing that part of background atmospheric carbon dioxide produced through soil respiration. A soil respiration intake can be hooked to channel 6 of our gas switch, and measurements made without interfering with existing CO_2 measurements. Some relatively simple intake systems have been described by Reiners (1968), Witkamp (1966), and others. The main problem at the Pawnee grassland study area concerns changes in heating and wind convection under closed or semi-closed gas collecting chambers. The use of highly reflective, small coffee cans placed no more than five-minute periods over the soil surface may be promising. These cans will be flushed with precision metered ambient air, and the flow streams from several cans will be pooled for a single soil respiration determination.

5. Stomatal Physiology and Photosynthesis Response to Water Stress under Field Conditions.

Except for Rychnovska's work on xeromorphic grasses (principally Stipa) in Czechoslovakis (see references) there is almost no work on drought resistance and photosynthetic response of native arid steppe grasses to tissue moisture stress. Yet this may be the over-riding factor regulating both instantaneous photosynthesis (through stomatal regulation and leaf inrolling) and long term seasonal growth. Indeed, any photosynthesis model for arid steppe species would be grossly inadequate without prediction of drought physiology. An immediate issue concerns whether a possible mid-day dip in photosynthetic rates (Fig. 4) is the consequent of high midday temperatures (Idso and Baker 1967), to stomatal closing, or both. The effects of low light intensities on full daylight grasses also needs investigation. Stomatal and turgidity measurements can also be used as a daily check of artifacts in the dome environment, by comparing leaves inside and outside the dome chamber (some destructive sampling of green leaf material in the dome must be allowed here).

Therefore, we intend to initiate studies on water stress physiology during the field season of 1970. Some preliminary measurements can be taken on greenhouse grown shortgrass species maintained under a variety of soil moisture tensions, leaf temperatures, and light intensities. In addition the porometry and relative turgidity techniques can be developed on greenhouse plants.

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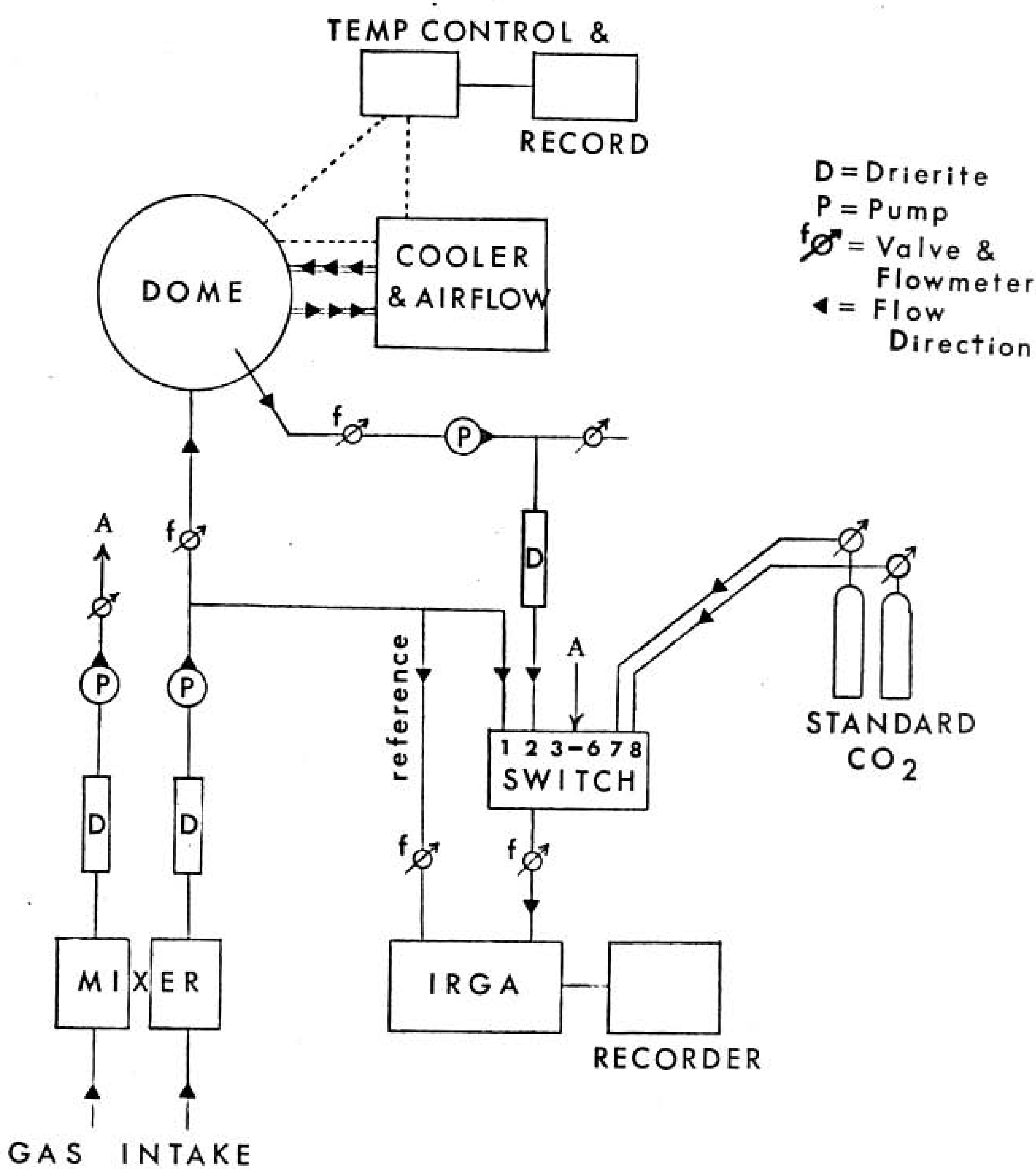

Fig. 1. Instrumentation system for observing photosynthesis of shortgrass vegetation under field conditions.

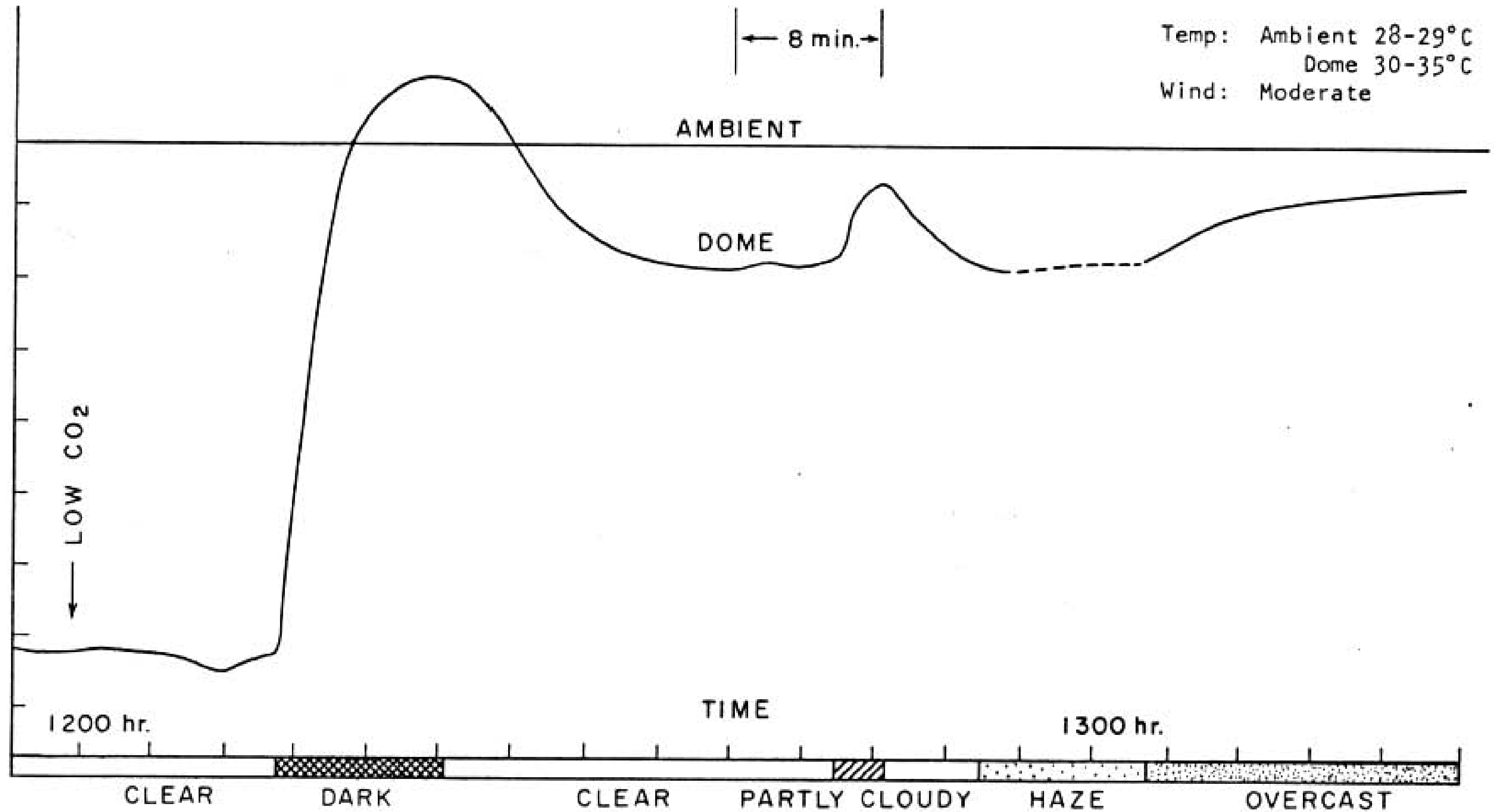

Fig. 2. Carbon dioxide depletion by shortgrasses growing under dome as compared with ambient levels of CO_2 and sky conditions at Pawnee Site on 5 July 1969.

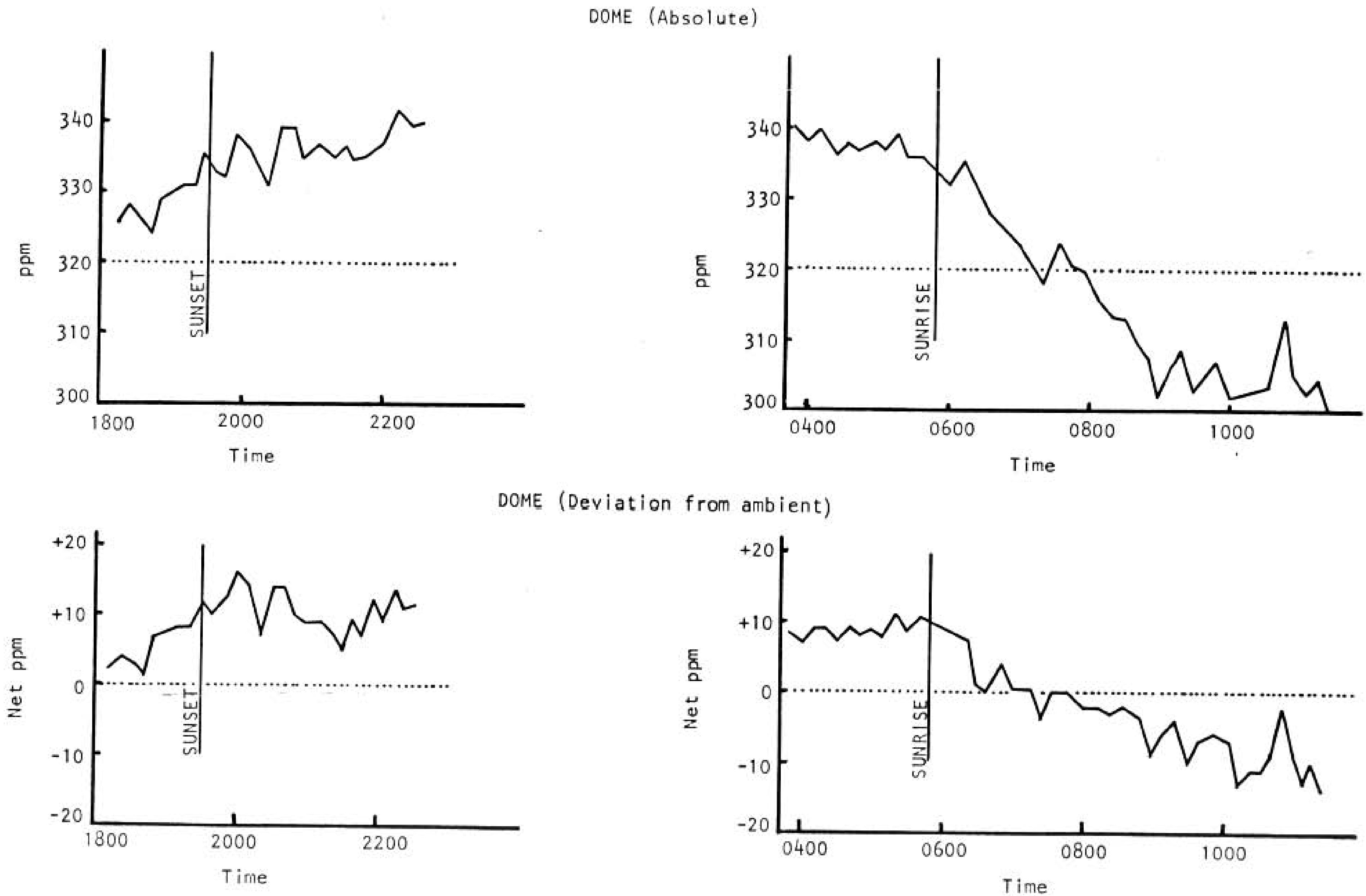

Fig. 3. Diurnal trend of carbon dioxide levels in dome environment containing shortgrass vegetation at the Pawnee Site on 26-27 July 1969.

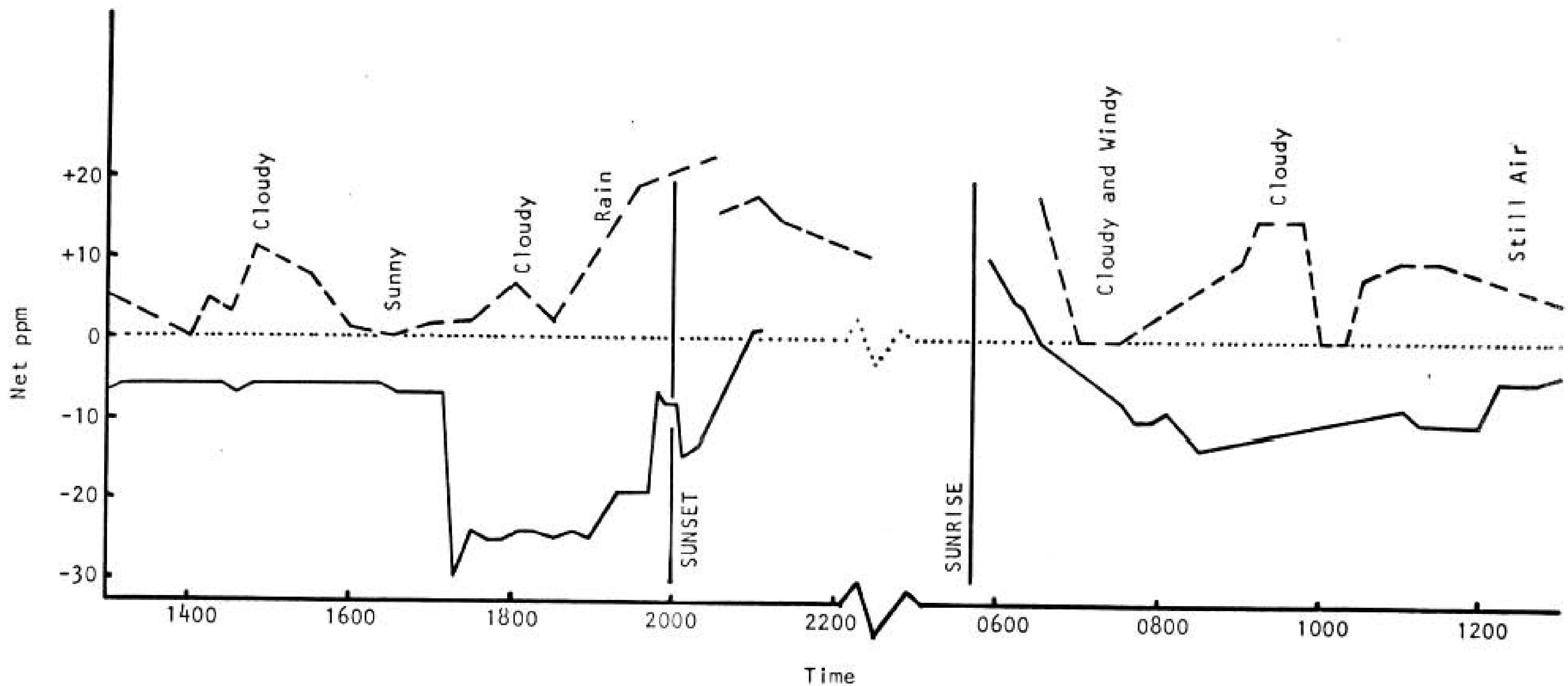

Fig. 4. Diurnal trends of carbon dioxide levels measured aerodynamically near the end of the shortgrass growing season at the Pawnee Site on 9-10 August 1969 (solid line) and on 16-17 August 1969 (dashed line).