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PHOTOSYNTHESIS OF TWO IMPORTANT GRASSES OF THE SHORTGRASS PRAIRIE AS AFFECTED BY SEVERAL ECOLOGICAL VARIABLES

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ABSTRACT

Two studies were conducted during 1971 and 1972 in the greenhouse and in the field to determine the photosynthetic and aboveground respiration rates of blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) as affected by several ecological variables. The major objective was to provide carbon dioxide (CO_2) exchange rates for these two species for use in the ecosystem modeling efforts of the U.S.-IBP Grassland Biome. The variables chosen for consideration for their effects on the CO_2 exchange rates of both species were soil water potential, temperature and irradiance, with phenological stage added as a fourth variable affecting the CO_2 exchange rates of blue grama. Carbon dioxide exchange rates were determined by infrared gas analysis using separate systems in both the greenhouse and in the field.

The CO_2 exchange rates of both species were significantly affected ($p < 0.01$) by each of the variables considered. Light saturation of the C_4 species, blue grama, was evident only at very high irradiances accompanied by high temperatures and soil water stress. The C_3 species, western wheatgrass, was light saturated at relatively low irradiances. The optimum photosynthetic temperature for blue grama ranged from about 26°C to 33°C. Optimum conditions of soil water potential and irradiance resulted in an optimum temperature near 33°C, while soil water stress and low irradiance resulted in

lower optimum temperatures for photosynthesis of blue grama. The optimum temperature for photosynthesis of western wheatgrass was lower than the lowest temperature of 20°C included in the experimental design. Increasing soil water stress resulted in significant decreases in the photosynthetic rates of both species. Aboveground dark respiration for both species increased with increasing temperature and decreased with increasing soil water stress.

Four 24-hour ambient simulations of abiotic conditions for in situ blue grama sods in the field during the 1972 growing season provided integrated net photosynthetic rates of from 1.7 to 14.3 g $CH_2O \cdot m^{-2}$ ground area$\cdot day^{-1}$. The greater photosynthetic rates were noted during near optimum conditions of soil water potential, visible irradiance, and temperature.

A dynamic seasonal primary productivity model for blue grama was constructed utilizing the CO_2 exchange data set determined in the field study. The model predicted a total net primary production for blue grama of 714 g $CH_2O \cdot m^{-2}$ ground area$\cdot year^{-1}$, which compared favorably with 809 $g \cdot m^{-2}$ ground area$\cdot year^{-1}$ determined through harvesting techniques by Lauenroth (1973) for the same growing season (1972) and which included other species on the shortgrass prairie site.

INTRODUCTION

Photosynthesis is the basic process determining primary production, which, in sequence, determines all secondary production. Photosynthesis, through the fixation of carbon dioxide (CO_2) from the atmosphere, is usually considered to be the first step in the process of the flow of carbon through the ecosystem. The importance of photosynthesis in nature makes an understanding of the process essential for any ecosystem analysis and modeling endeavor.

The primary objective of this study was to determine the effects of several abiotic driving variables on photosynthetic rates of two important shortgrass species. Additional objectives included monitoring of CO_2 exchange of the shortgrass dominant in the field as influenced by plant phenological development and abiotic variables, and terminally, to utilize the data in a primary productivity simulation model.

Two species of the shortgrass prairie were chosen for consideration in the study. The first, and most important species, was blue grama (*Bouteloua gracilis* (H.B.K.) Lag.). According to Weaver and Albertson (1956) blue grama is the dominant species of the shortgrass prairie, which is the largest grassland association on the North American continent. Blue grama is also the major native forage species on the continent and, according to Uresk (1971), comprises about three-fourths of the graminous vegetation of the Pawnee Intensive Study Site of the Grassland Biome of the U.S. International Biological Program. Blue grama is a warm season grass which exhibits the C_4, dicarboxylic acid biochemical pathway

of CO_2 fixation (Williams and Markley, 1973). The second species chosen for study was western wheatgrass (*Agropyron smithii* Rydb.). Western wheatgrass is a sub-dominant of the shortgrass prairie and is a cool season grass exhibiting the C_3, Calvin-Benson pathway of CO_2 fixation (Williams and Markley, 1973).

Although blue grama and western wheatgrass have different pathways of CO_2 fixation, both species are well adapted to the semi-arid shortgrass prairie in eastern Colorado. Therefore, an extensive comparison of the CO_2 exchange rates of the two species will be made in terms of C_3 and C_4 ecophysiological characteristics.

Four variables deemed most important in influencing the photosynthetic rates of plants were chosen for consideration in the present study. They were soil water potential, temperature, visible irradiance, and phenology. The effects of these variables on photosynthetic rates for several species have been documented in the literature, but most of the species previously studied have been single stem crop varieties. Photosynthetic rates of single stem plants are much more easily measured utilizing CO_2 exchange systems because an assimilation chamber can easily be sealed around a stem. Multi-stem species, such as forage grasses, have been little studied to date because of the complexities involved in eliminating CO_2 evolution from the soil. It is necessary to either seal the soil surface to prevent CO_2 diffusion from the soil, or to subtract out the CO_2 enrichment from the soil by making various supplemental measurements.

Carbon dioxide exchange studies were carried out in both the greenhouse and in the field with two separate CO_2 exchange systems.

The greenhouse study involved both blue grama and western wheatgrass. The field study was conducted on in situ blue grama vegetation only.

The greenhouse CO_2 exchange system allowed photosynthetic determinations to be made at a constant phenological stage of development for each species. The study provided data on CO_2 exchange rates for steady state conditions of abiotic variables, but more importantly, it provided direct determinations of net photosynthetic and aboveground respiration rates for each species. Net photosynthetic and aboveground respiration rates were impossible to measure directly in the field.

A portable CO_2 exchange system was utilized during the 1972 growing season at the Pawnee Site to determine CO_2 exchange rates of in situ blue grama vegetation. Two types of experiments concerning CO_2 exchange rates of blue grama in the field were made. The first experiment involved collecting data for steady state conditions. This required the manual recording of CO_2 exchange rates, and all values of other variables, when all environmental conditions were constant. Both greenhouse and field steady state determinations provided information on photosynthetic rates of blue grama for various levels of each variable and for a variety of combinations of the variables, and should, therefore, be of greatest value for modeling purposes.

The second type of field experiment was the determination of CO_2 exchange rates of in situ blue grama sods for 24-hour periods during several times throughout the 1972 growing season. These determinations allowed integration of photosynthetic values for

24-hour periods, thereby providing illustrative daily production values for the shortgrass prairie.

The greenhouse experiments were used to supplement the field experiments. A combination of both field and greenhouse experiments gave a thorough understanding of CO_2 exchange characteristics of two major grasses of the shortgrass prairie.

REVIEW OF LITERATURE

Biotic Factors Affecting Carbon Dioxide Exchange Rates

The C_3 Pathway

Benson and Calvin (1947), and many subsequent publications by them and their co-workers, determined the basic cycle of CO_2 fixation by plants. The cycle is variously referred to as the photosynthetic carbon reduction cycle, the Calvin-Benson cycle, or the C_3 cycle (because the initial product is a three-carbon compound). The entire cycle of reactions was reported by Zelitch (1971) and is too complex for the purposes of this paper. Suffice it to say that the initial reaction is the catalysis of ribulose-1,5-diphosphate with CO_2, forming two molecules of 3-phosphoglyceric acid. The C_3 cycle can be thought of as the common denominator of all photosynthetic pathways.

The C_4 Pathway

The C_4 cycle, termed the C_4 dicarboxylic acid cycle by Hatch and Slack (1966, 1968 and 1970) enhances the C_3 cycle by acting as a mechanism for concentrating CO_2 for the carboxylation step in the C_3 pathway. The initial reaction is the catalysis of phosphoenolpyruvic acid with CO_2 forming an intermediate four-carbon compound, oxaloacetate, which immediately goes to either malate or aspartate. Both malate and aspartate form CO_2 in subsequent reactions in the thick-walled bundle sheath cells of C_4 plants. This CO_2 is not lost because of the thick walls that act as physical barriers to CO_2 diffusion. Therefore, CO_2 is concentrated for the initial reaction of the C_3 cycle. This results in high rates of CO_2

fixation at high light intensities and temperatures. In addition, reductions in the detrimental effects of high plant water stress are often observed for C_4 plants (Downton, 1971).

The C_3 cycle requires three adenosine triphosphate molecules (ATP) and two nicotinamide adenine dinucleotide phosphate molecules (NADPH) from the light reaction of photosynthesis for the energy source and reducing power to reduce one molecule of CO_2. In contrast, the C_4 cycle requires five ATP's and three NADPH's for reduction of each molecule of CO_2. Superficially, the additional energy requirement for the C_4 cycle implies that the C_3 cycle is more efficient than the C_4 cycle. This is not the case because C_4 plants are capable of utilizing higher light intensities than C_3 plants. Although C_4 plants require more energy to facilitate their reactions, they are capable of utilizing the energy available to them at higher light intensities.

Morphology, Anatomy and Evolution

Some of the morphological characteristics of plants affect the photosynthetic rates by serving to dampen the effects of some abiotic driving variables such as temperature. Morphology will be discussed in each subsequent section where appropriate.

Grass leaves have been divided into two major anatomical groups by Prat (1936) and Brown (1958). The two groups are referred to as the Panicoid and Festucoid groups. The chlorenchyma cells of the Panicoids are radially arranged around the vascular bundles. This radial arrangement is termed "Kranz" anatomy, and is directly associated with the C_4 pathway of CO_2 fixation (Downton, 1971). In

addition, the bundle sheath cells of Panicoids have numerous chloroplasts. The chlorenchyma cells of the Festucoids are irregularly arranged between adjacent vascular bundles. This irregular arrangement is associated with the C_3 pathway (Downton, 1971).

There has been much disagreement as to the value of leaf anatomy as a tool for determining which photosynthetic pathway a plant possesses. Downton (1971) was a strong proponent of the use of leaf anatomy as the most rapid and unambiguous means of photosynthetic pathway identification. Even with such a positive statement, it is still generally felt that the most reliable method for pathway determination is the analysis of products of the initial photosynthetic reaction (Williams and Markley, 1973). Williams and Markley (1973) developed a technique for rapid identification of the initial products which was used for determining the photosynthetic pathways of western wheatgrass, blue grama, and four other shortgrass prairie species.

The C_4 dicarboxylic acid synthesis initially occurs in the mesophyll layer. From there the acids malate and aspartate are actively translocated to the bundle sheath where they are decarboxylated providing CO_2 for the initial C_3 reactions (Hatch, 1971). The C_3 plants lack the highly evolved parenchyma bundle sheath cells containing specialized chloroplasts which facilitate the fixation of CO_2 from both the atmosphere and respiration (Downton, 1971).

Downton (1971) speculated that the C_4 system in grasses first evolved from the Festucoid (C_3) leaf type to a leaf type something similar to that of the Bambusoid of today. Bambusoids possess thin-walled bundle sheaths containing unspecialized chloroplasts.

Next, Downton (1971) speculated that the cell walls could have thickened causing a concomitant reduction in mesophyll air space and a consequent radial arrangement of the mesophyll cells.

Another indication that C_4 species might have evolved from C_3 species comes from the findings of Downton, Barry and Tregunna (1969) that members of the *Dichanthelium* sub-genus of *Panicum* behaved as C_3 plants even though they belong to a predominantly C_4 group.

Troughton (1971) took advantage of the fact that higher plants discriminate against the heavier isotope of carbon, ^{13}C. He studied numerous species of plants and found the extent of discrimination to be directly correlated with the photosynthetic pathway, C_4 species being less discriminatory than C_3 species. Analysis of coal samples taken from America and Australia dating back to the Cambrian Period indicated that C_3 plants formed the coal.

Evans (1971) in a thorough assessment of the taxonomic distribution of plants, also concluded that the C_3 cycle was the more primitive photosynthetic pathway.

Certainly one of the most important considerations involved in determining the evolution of C_4 plants must be the fact that all plants today rely on the C_3 mechanism for the ultimate steps in CO_2 fixation. The greater CO_2 fixation rates of C_4 plants are probably important in terms of survival and adaptation, but more importantly, the performance of these plants under extreme conditions of stress is definitely of selective advantage in many parts of the world (Bjorkman, 1971). The C_4 species survive and may be better

adapted than many C_3 species under conditions of high water stress, high temperature, high oxygen concentrations, low CO_2 concentrations and high irradiances (Bjorkman, 1971). These conditions were probably not typical during the evolution of higher plant life on this planet. The C_3 plants must have been the first higher plants to evolve in the low oxygen, high CO_2 atmosphere of the earth at that time. The C_4 pathway probably evolved as an adaptive mechanism of plants originally native to moist tropical regions and climates, which immigrated to temperate regions and more temperate climates in tropical regions. Because of the evolutionary trends, grasses possessing the C_4 cycle are commonly referred to as warm season or tropical grasses, whereas those exhibiting the C_3 cycle are referred to as cool season or temperate grasses (Downton, 1971).

Originally, the C_4 pathway was shown by Hatch and Slack (1966) to be present in a few tropical grasses. To date, the C_4 pathway is known to exist in hundreds of monocotyledous and dicotyledous species comprising nearly 100 genera and at least ten plant families (Bjorkman and Berry, 1973).

Photorespiration

Photorespiration is light-stimulated respiration. Photorespiration differs biochemically from normal dark respiration (which also occurs in light) and is specifically associated with the oxidation of immediate photosynthetic products. It is variously defined as either the total amount of respiration occurring in light, or as the amount of respiration due only to light. According to Zelitch (1971) photorespiration rates can be three to five times greater

than dark respiration rates. The significance of photorespiration becomes more clear when it is realized that the decrease in dry weight gain because of dark respiration alone can be very high. Respiration is probably the single most important factor limiting the dry weight gain of plants.

Respiration rates of both C_3 and C_4 species are usually greater in light than in darkness, but photorespiration cannot be measured directly by conventional CO_2 exchange apparatus under normal conditions. The biochemical source of photorespiratory CO_2 is not definitely known, but according to Zelitch (1968), the source is probably glycolate which has been synthesized from ribulose-1,5-diphosphate (RuDP). Light is necessary for the regeneration of RuDP in all plants, thus light leads to the production of photorespiratory CO_2. Plants possessing the C_4 photosynthetic pathway are capable of immediately reassimilating this CO_2 because the bundle sheath cells of C_4 plants have thicker walls which provide a barrier to CO_2 diffusion. Therefore, the C_4 plants probably possess, but do not exhibit, photorespiration.

According to Samish and Koller (1968) the lack of measurable photorespiration for C_4 plants is also caused by a low mesophyll resistance to CO_2 diffusion. Low mesophyll resistance of C_4 plants is associated with the greater amount of energy available to them for CO_2 fixation. The lack of apparent photorespiration in C_4 plants might account for the greater net photosynthetic rates observed in these species.

The limiting effect of normal atmospheric oxygen concentrations on the net photosynthetic rates of C_3 plants is directly associated with photorespiration. The C_4 plants are not limited by oxygen concentrations normally found in the environment (Mulchi, Volk and Jackson, 1971). Gauhl and Bjorkman (1969) determined the photosynthetic rates of *Solanum duleamora* and *Atriplex patula* spp. *hastata* (both lacking the C_4 pathway) to be approximately 50 percent greater at 1.5 percent oxygen than at 21 percent oxygen. The photosynthetic rate of *Atriplex rosea*, a C_4 species, was not significantly greater at the lower oxygen concentration.

The inhibitory effect of oxygen on photosynthetic rates of C_3 plants varies with both light intensity and temperature. Bjorkman (1966) determined that the net photosynthetic rate of *Pantago lanceolata* was inhibited by normal oxygen concentrations at a very low light intensity, and that the inhibitory effect increased with increasing light intensity. Increasing temperatures also caused increases in photorespiration.

The lack of apparent photorespiration in C_4 species along with the trait that they do not release measurable CO_2 into a CO_2-free atmosphere has been associated with very low CO_2 compensation points in these species (El-Sharkawy and Hesketh, 1965). The CO_2 compensation point is considered to be the CO_2 concentration below which a plant can no longer take up CO_2 from the atmosphere. Downton and Tregunna (1968) pointed out that plants with high photosynthetic rates, 40-60 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, had CO_2 compensation points very near zero parts per million (ppm), while plants with low photosynthetic

rates, 20-30 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, had CO_2 compensation points of 39 ppm or greater.

Kruger and Moss (1969) determined low CO_2 compensation points for eight species of the genus *Panicum*, and high CO_2 compensation points for two other species of the same genus. The genus *Atriplex* exhibits a similar variation in photosynthetic pathway. Wallace et al. (1971) reported on variations in photosynthetic pathway within the same species and Caldwell et al. (1972) determined a very broad range of optimum photosynthetic temperature over a growing season for *Atriplex confertifolia*. This might at first be construed to indicate a transition from the C_3 to the C_4 photosynthetic pathway during the growing season for the same plant. However, *Atriplex confertifolia* is a C_4 species.

Another variation among C_3 and C_4 plants in relation to photorespiration is the observation by Moss (1966) that C_3 plants exhibited a post-illumination burst of CO_2 upon both illumination and darkening. He found that the rate of CO_2 released from the leaves of five species of C_3 plants decreased when they were first illuminated, then passed through a minimum, and then increased to a higher rate than the original dark rate. Upon darkening, the rate of CO_2 evolution rapidly increased to a rate greater than that when under illumination. The evolution rate then gradually decayed to the original steady dark respiration rate. Light probably enhanced a reaction which produced more CO_2 than normal dark respiration. A further explanation for the post-illumination burst of CO_2 was proposed by Tregunna, Krotkov, and Nelson (1964). They theorized that either CO_2 trapped in the

stomate was immediately rejected and released upon darkening or that there was an immediate breakdown of a recent photosynthate. The C_4 species do not exhibit a burst of CO_2 because they form less glycolate and do not photorespire as much, which is directly related to the greater photosynthetic efficiency observed in C_4 species.

Ageing

Jewiss and Woledge (1967) studied the effect of age on the rate of apparent photosynthesis of leaves of tall fescue (*Festuca arundinacea*). Their results showed a progressive decline in the photosynthetic rates of leaves as the leaves aged. Woledge and Jewiss (1969) discussed the temperature-age interaction effect on tall fescue. They reported that plants grown at the higher temperatures aged faster, with a concomitant decrease in photosynthetic activity, than plants grown at cooler temperatures.

Treharne, Cooper and Taylor (1968) determined that the photosynthetic rates of orchardgrass (*Dactylis glomerata*) increased for 15 to 20 days and then declined sharply. Further examination showed that the photosynthetic rates per unit of chlorophyll changed very little throughout the life of the leaf which indicated that fluctuating chlorophyll content was the cause of the change in photosynthetic rates.

Wright and Lemon (1966) calculated the vertical distribution of photosynthetic CO_2 fixation at different levels within corn (*Zea mays*) crop. Their results demonstrated both the importance of the younger upper leaves and the increased fixation by the lower leaves during periods of high light penetration. Tripathy, Eastin

and Schrader (1972) compared photosynthate export from two leaf positions in a corn canopy. They determined that the rate of export of photosynthate from older leaves was slower than from younger leaves, but that the direction of export from a given leaf position changed as phenology changed. Transport from upper leaves was predominantly downward, whereas direction of export from lower leaves changed from downward to upward as the ear became the dominant sink.

Geronimo and Beevers (1964) determined the effects of ageing on the respiration of pea (*Pisum sativum*) leaves. They found that respiration rates were greatest in the youngest leaves, and decreased 40 to 60 percent as the leaves aged about ten days. Hadley and Bliss (1964) reported that the respiration rates of *Carex bigelowii* early in the season were approximately double the rates later in the growing season. They attributed much of this reduction in respiration with advancement of season to a completion of leaf expansion and reduction of terminal growth. Consequently, *Carex bigelowii* showed no positive net photosynthesis until spring growth, flowering, and fruiting were completed.

Abiotic Factors Affecting Carbon Dioxide Exchange Rates

Light

Not all of the incident solar radiation is available for photosynthetic capture. It is generally agreed that only the total solar radiation within the 400 to 700 nm wave band should be considered as photosynthetically active irradiance (Botkin and Malone, 1968; Loomis and Williams, 1963).

Voskresenskaya et al. (1970) experimented with the effect of light quality on the photosynthetic rates of tobacco and three other C_3 species. They found that the photosynthetic rate in blue light was greater than or equal to that in red light. They also found that low intensities of blue light sometimes inhibited photosynthesis, but by adding red light, allowing prolonged exposure to blue light, or by lowering the oxygen concentration, inhibition was avoided. Balegh and Biddulph (1970) determined the action spectrum for bean (*Phaseolus vulgaris*) leaves and found great similarity between it and the absorption spectrum for six species determined by Moss and Loomis (1952).

Many C_4 plants show no light saturation while most C_3 plants generally saturate at 20 to 30 percent of full sunlight. Hesketh and Moss (1963) determined that the photosynthetic rate of corn, a C_4 species, increased 20 to 60 percent as the light intensity was raised from 0.5 to 1.0 langley$\cdot$min^{-1}. Sunflower, an exceptional C_3 plant in this respect, responded similarly.

Bjorkman and Holmgren (1963) and Bjorkman (1968) studied the adaptability of the photosynthetic apparatus to light intensity of ecotypes of *Solidago virgaurea* from exposed and shaded habitats. They found that strong light actually decreased the photosynthetic rate of the shade ecotype. Low light intensities decreased the photosynthetic rates of the sun ecotype, but the shade ecotype had higher rates of photosynthesis than the sun ecotype at low light intensities. However, each ecotype exhibited adaptability to the new light regime in which it was placed.

The quantity and quality of light absorbed by a single leaf is very important in determining the photosynthetic rate of the leaf. However, when productivity is considered, the amount of light available for photosynthesis is also dependent upon the leaf area index (LAI). The LAI is defined as the ratio between the amount of leaf area (one side of the leaf) and the amount of ground surface area (Knight, 1973). Brown, Blaser and Dunton (1966) found that apparent photosynthesis of individual leaves of three forage species was light saturated at lower intensities than were intact swards.

Pearce, Brown and Blaser (1967a) found that an increase in LAI resulted in an exponential decrease in light penetration in swards of barley. Net photosynthesis increased with increasing LAI until the optimum LAI was reached, after which net photosynthesis decreased.

Leaf angle also becomes an important factor for production because the quantity of light intercepted is dependent upon the angle of the leaf in relation to the angle of incident radiation. Leaf angle interacts with LAI in its effects on productivity. Pearce, Brown and Blaser (1967b) found that leaf angle had little effect on the net photosynthetic rate of barley up to an LAI of 2.5, but as the LAI increased above 2.5 the net photosynthetic rate was higher for more vertically-oriented leaves.

Knight (1973) reported maximum LAI's of 0.55 and 0.37 for the Pawnee Site during 1970 and 1971, respectively. He attributed this difference to the mid-summer drought of 1971, and indicated that water was the primary limiting factor for LAI on the shortgrass

prairie. He also indicated that nitrogen fertilization was required to obtain an LAI much greater than 0.5. It is improbable that photosynthetic rates of shortgrass species based upon leaf area are greatly affected by changes in LAI, since LAI is usually less than one.

Temperature

Different plant species demonstrate a wide range of optimum photosynthetic temperatures. Wolf (1969), in a study on the effects of temperature and light intensity on 30 species, found that one or more of the species demonstrated greatest rates of photosynthesis at each of the three temperatures of 23°C, 30°C, and 35°C. General optimum temperatures for C_3 and C_4 species are 10°C to 25°C and 30°C to 40°C, respectively. Most C_3 plants become chlorotic and die around 35°C, while many C_4 species can withstand temperatures as high as 50°C (Downton, 1971). Conversely, some C_3 species are quite active at 5°C, while most C_4 species are generally inactive at that temperature (Downton, 1971).

Woledge and Jewiss (1969) found that tall fescue adapted to the temperature regime in which it was grown. Plants grown in high temperatures had high optimum temperatures for photosynthesis and those grown at low temperatures had low optimum temperatures. When plants grown in high temperatures were transferred to cooler growing conditions, the optimum temperature decreased as the plants adapted to the cooler environment.

Bjorkman et al. (1972) determined an optimum photosynthetic temperature of 47°C for *Tidestromia oblongifolia* growing in Death

Valley, California. They attributed this very high optimum photosynthetic temperature to the C_4 photosynthetic pathway and a high thermal stability of the biochemical photosynthetic apparatus. This is the highest reported optimum photosynthetic temperature recorded to date for a higher plant, and is very high even for C_4 plants.

Taylor and Rowley (1971) measured the effects of chilling stress under various light and time treatments of assorted C_3 and C_4 species. The photosynthetic rates of all species decreased when subjected to the chilling stress of 10°C, but the photosynthetic rates of the C_4 species declined to negligible levels after two to three days. The photosynthetic rates of the C_3 species studied decreased more slowly and maintained a positive net photosynthesis at the 10°C temperature.

Mooney and Billings (1961) compared the physiological ecology of arctic and alpine populations of *Oxyria digyra*. They found that plants from northern populations had higher respiratory rates at all temperatures than plants from southern alpine populations. The northern plants also had higher photosynthetic rates at low temperatures and a lower optimum photosynthetic temperature than the southern plants.

Water

All vital chemical reactions and all life processes take place in water. Soil acts as an absorbent and reservoir for the water necessary to maintain plant life. Water in an unsaturated soil exists as films around the soil particles and as vapor in the gas-filled spaces between the particles. The thinner the film of water

around the soil particles, the more tightly the water is held, and the less available it is for plant uptake and use. The plant must provide energy to remove water from the soil and the amount of energy required is partially dependent upon the thickness of the layer of water around the soil particles. The total energy required for uptake is a function of the free energy status of the soil water, often referred to as the soil water potential.

According to Brown (1970), the most important forces affecting water potential are the additive forces of matric, osmotic and pressure potentials. Matric potential is the term applied to the adsorption of the water film on the soil particle. Osmotic potential is a function of the presence of dissolved substances in the solution, while pressure potential is the effect of pressure on the total water potential. Temperature and gravity also affect soil water potential.

The free energy, or potential, of pure water is zero. Matric and osmotic components of soil water potential additively decrease the potential of the water. The pressure component can act only to raise the total water potential since at normal atmospheric pressure (considered zero) there is a balance of pressures canceling each other out. Positive pressures will increase the water potential and should be considered for plants only when such things as turgor pressure in cells will have an effect. Considering these relative values, soil and plant water potentials will always be negative.

The driving force for water movement in the soil-plant-atmosphere continuum is the decreasing energy gradient of water in the system.

The most important biotic and abiotic factors responsible for maintenance of the decreasing energy gradient (and therefore the dynamics of water in the system) are transpiration, evaporation, temperature, and atmospheric vapor pressure gradients. Each factor serves to create a type of energy vacuum which is filled by the dynamics of high energy soil water flowing toward an area of low energy. According to Wiebe et al. (1971), water in the soil-plant continuum is rarely, if ever, in equilibrium with surrounding water.

According to Black (1968), the traditional values given for soil water potential at field capacity and permanent wilting percentage are -0.3 and -15.0 bars, respectively. These values were considered soil water constants identifying the upper and lower limits of soil water available to plants. According to Kozlowski (1964) these values were first questioned by Taylor, Blaney and McLanghlin (1934) who visualized a "wilting range" rather than a wilting point, and later by Slatyer (1957) when he indicated that the permanent wilting point is determined by the osmotic characteristics of the plant rather than the soil.

The most commonly observed effect of water stress on plants is the general decrease in growth or size because of a reduction in cell elongation and cell turgor (Kramer, 1969). Size reduction can easily be measured for trees and shrubs and can be observed in grasses when the leaves involute under water stress. Water stress directly or indirectly affects all physiological processes.

The effect of water stress on photosynthesis is very complex. Perhaps the most important single effect of low soil water potentials

is low cell turgor which leads to stomatal closure and eventually to reduced leaf area. Stomates must be open for the rapid exchange of CO_2 and oxygen. Water stress, therefore, reduces the capacity of the plant to carry on photosynthesis. Translocation is also affected by water stress as it is related to transpiration which is highly correlated with photosynthetic rate (Zelitch and Waggoner, 1962). It appears that much water lost through transpiration is not necessary. Most of the water lost through transpiration is a compromise for the necessary CO_2 diffusion into the stomates (Kozlowski, 1964). The relative humidity inside the leaf is essentially 100 percent and when the stomates open for gaseous exchange, water vapor diffuses out.

According to Stalfelt (1959), the size of the stomatal aperture is regulated by both photoactive and hydroactive processes. The photoactive process is stomatal closure at sundown and opening at dawn. Most research conducted on the effect of soil water on photosynthesis is related to stomatal response to stress caused by low soil water. Brown and Rosenberg (1970) found a linear relationship between decreasing soil water potential from -0.35 bars to -0.52 bars and stomatal resistance to gaseous diffusion in the C_3 plant sugar beets (*Beta vulgaris*). A significantly detrimental effect of high temperatures on plants often results from increased evapotranspiration demand. According to Kramer (1969), when two climates with similar amounts of precipitation are compared, the cool climate might support a forest, whereas the hot climate might result in a grassland. The most striking adaptation of grasses to xeric conditions

is their ability to roll or involute their leaves, thus reducing the transpiration surface to a minimum. The resultant high humidity within the leaf roll reduces the amount of transpiration within the roll (Shields, 1950). Convolutions of the leaf surface are a particular adaptation of the cool season grass, western wheatgrass, to xeric conditions. Cannon (1921) pointed out that strong parallel veination of the leaf surface formed convolutions which reduced the effect of wind on the boundary layer resistance.

The gray, rough-textured leaf surface of western wheatgrass also prevented some transpiration loss by decreasing light absorption and increased boundary layer resistances to transpiration. These morphologic characteristics of the C_3 species western wheatgrass help explain its survival on the shortgrass prairie (Cannon, 1921).

Ghorashy et al. (1971) studied the effect of leaf pubescence on transpiration, photosynthetic rate and seed yield of three near-isogenic lines of soybeans (*Glycine max*). They found that the seed yields and the photosynthetic rates were not significantly affected by dense pubescence but that the transpiration rate was significantly lower. Their data suggested that breeding for pubescence would increase the water use efficiency of soybeans. Very small decreases of only -0.5 bars lead to partial stomatal closure and caused a decrease in photosynthetic activity indicating not only a linear response, but also an extremely sensitive response to increasing soil water stress.

Bielorai and Mendel (1969) found that the rate of both photosynthesis and transpiration gradually decreased as the soil water

potential was reduced from -0.2 bars to -3.0 bars, but rapidly decreased as soil water decreased from -3.0 to -15.0 bars. Very low soil water potentials have a greater effect on photosynthesis than on transpiration. Bierhuizen, Nunes and Ploegman (1969) found that net photosynthesis was almost negligible at a soil water potential where transpiration was still 45 percent of the amount of transpiration at field capacity. Hellmuth (1970) determined an approximate average decrease because of water stress of 60 percent in net photosynthetic rate in arid and semi-arid species in Australia. The water stress was not measured, but only stated as late summer, as opposed to optimal water in the spring.

Iljin (1957) found that potassium caused breakdown of starch accumulated in guard cells, thus inducing stomatal opening. The loss of water by the plant when the wilting point was passed resulted in the hydrolysis of the starch in the guard cells. After the starch was hydrolyzed, sugars accumulated. These are some of the biochemical effects caused by soil water stress. Photosynthetic activity can thus be decreased by chemical effects causing physical change of the stomates. In addition, chemical changes of the photosynthetic tissues because of low soil water potential cause a decrease in the photosynthetic rate. Plants respond to a history of water stress due to biochemical disruptions. It is not uncommon for five to seven days to elapse before net photosynthesis is restored to pre-drought rates (Brown, 1968).

Growth is more affected by soil water stress than is photosynthesis. Wardlaw (1969) found that while growth of *Lolium temulentum*

had almost ceased at a relative turgidity of 75 percent (-25 bars), photosynthetic activity was still about one-third of the maximum rate. According to Kozlowski (1964), Staple and Lehane (1941) found that although growth of wheat (*Triticum aestivum*) had ceased and the plant had been desiccated beyond the ability to respond to watering at the permanent wilting point of approximately -15 bars, the plant continued to take up water from the soil to tensions exceeding -26 bars. This continued uptake of water increased both the yield and quality of the grain.

Wind also has an interaction effect on photosynthesis during water stress. If the soil water potential is not optimal during a period of potential fast growth, dry wind can cause an increase in stomatal resistance by causing a greater water vapor pressure deficit (Kramer, 1969). If the humidity of the air is high, wind can increase diffusion by breaking down the boundary layer of gasses that surround the leaf.

The effect of low soil water potential on plant respiration is less complicated than on photosynthesis. Kaul (1966) found that slight water deficits increased respiration of wheat by about 20 percent, while greater water stress decreased respiration up to approximately 50 percent.

Soil water potential also affects leaf water potential. Boyer (1970a) found that leaf enlargement was inhibited earlier and more severely than was photosynthesis or respiration as the leaf water potential decreased in corn, soybean, and sunflower (*Helianthus annus*). Dark respiration was directly proportional to

leaf water potential to -16 bars where it leveled off. Boyer (1970b) found that photosynthesis in soybean was not reduced until leaf water potential dropped below -11 bars, while photosynthesis of corn was affected anywhere below -3.5 bars. Therefore, corn, which has the C_4 pathway, was more sensitive to desiccation than the C_3 plant soybean. This is contrary to the hypothesis that C_4 pathway plants have greater drought resistance than C_3 plants.

Boyer (1971) found that two factors inhibited recovery of photosynthetic rates of sunflower after a period of low leaf water potential: 1) incomplete recovery of leaf water potential, and 2) incomplete return to full stomatal opening in the light. Desiccation at -10 to -12 bars permitted full recovery of photosynthesis within six hours after rewatering under both high and low light intensities. After desiccation to -16 bars, photosynthesis under high light intensity did not return to pre-desiccation levels of photosynthesis, even though the leaves did return to the original water potential.

Chen, Mederski and Carry (1971) determined that the rate of decrease for photosynthesis of soybeans appeared to be greater when the relative leaf water content decreased from 90 to 75 percent than when the relative leaf water content was less than 70 percent. This was again attributed to stomatal closure.

Generally, C_4 plants require approximately one-half as much water per gram of dry matter produced as C_3 plants (Downton, 1971). The low mesophyll resistance of C_4 plants permits relatively high stomatal resistance to CO_2 and water vapor diffusion. The two-staged

anatomical and biochemical apparatus of C_4 plants for CO_2 reduction in first the mesophyll and next the bundle sheath cells maintains a very large partial pressure gradient of CO_2 from the atmosphere to the bundle sheath. Therefore, many C_4 plants require less stomatal area than C_3 plants to permit the same volume of water vapor diffusion out of the leaf.

Shearman et al. (1972) determined that the net photosynthetic rate of the C_4 plant sorghum (*Sorghum bicolor*) was not significantly decreased until soil water stress was increased below about -20 bars. The soil water stress resistance was attributed more to leaf resistance than to a decrease in enzyme activity.

Wuenscher and Kozlowski (1971) determined that stomatal resistance and water-use efficiencies increased along an ecological gradient from mesophytic to xerophytic types of deciduous trees.

Computer Simulation Models of Biological Systems

There are many different types and levels of models for biological systems. Some models encompass large areas of land such as the forest productivity model prepared by Botkin, Woodwell and Tempel (1970). They monitored net photosynthetic rates of the three dominant tree species of an oak-pine forest of central Long Island. Incorporation of the results into a model predicted a gross primary production of 2950 $g \cdot m^{-2}$ for one growing season which was 10 to 22 percent higher than previous estimates based on harvest techniques.

Another modeling effort that covered a large geographical area was the ELM model of Innis et al. (1972) prepared for the Grassland Biome, U.S. International Biological Program. The ELM model was far more complex than the one prepared by Botkin, Woodwell and Tempel (1970) because it incorporated more species and many more processes and state variables of the grassland ecosystems it described.

In contrast to the models referred to above, some models have been constructed of very specific parts of biological systems such as a model of the mesophyll resistance of a leaf. The degree of complexity of these models can be just as high as the degree of complexity of an ecosystem model. The ultimate model of a biological system might be one which would express each of the specific chemical, physical and biological components of all of the compartments and sub-compartments of an ecosystem or biome. This would be the ideal model, and probably cannot be attained because of the lack of quantitative data and inability of present day computers to handle such a tremendous task.

Waggoner (1969a) developed a single leaf model utilizing an electrical resistance analogy for the various resistances encountered by CO_2 during photosynthesis. This model was then expanded (Waggoner, 1969b) to simulate the activities of plants in stands. Radiation and crop extinction coefficients, temperature, humidity, wind speed, canopy architecture, leaf angle, plant physiology, biochemistry, boundry layer, and stomatal resistance were all included in this later model (Waggoner, 1969b) along with the resultant interactions. Among other things, the model predicted that greatest photosynthetic

rates occurred with an LAI (leaf area index) of near 4.0 for horizontal leaves and 8.0 for more erect leaves. Photorespiration was also accounted for in the biochemical components of the model and illustrated the different photosynthetic rates expected between C_3 and C_4 species.

The effect on crop growth rate caused by the angle of incident solar radiation was modelled by de Wit (1965). The model assessed the distribution of light within a canopy of leaves and predicted 28, 40, or 44 $g \cdot m^{-2} \cdot day^{-1}$ for a grass or small grain crop with the angle of the sun held at 30, 60, or 90 degrees from the horizontal.

Connor, Brown and Trlica (1974) utilized the basic approach to stand structure and light penetration developed by Warren-Wilson (1967) to develop a functional primary productivity model of the shortgrass prairie. The model described the relationship between community photosynthesis, leaf area index, irradiance, ambient temperature and soil water potential and was compared with several statistical models of the photosynthetic rates of blue grama. The statistical models were not accurate when environmental conditions were introduced which were beyond the range of conditions used to determine the equations. The functional model provided biologically-reasonable predictions of the productivity of blue grama. Proportionality factors were used to delineate the effects of temperature and soil water stress on the photosynthetic rates of blue grama.

Stephens and Waggoner (1970) characterized the photosynthetic nature of components of a Costa Rican tropical rainforest by measuring the relation between illumination and photosynthesis. A

companion study by Lemon, Allen and Muller (1970) utilized the data reported by Stephens and Waggoner (1970) to determine typical diurnal CO_2 budgets of the forest. They found photosynthetic and respiration rates to be about one-tenth of the peak rates of temperate region forests and agricultural crops. The resultant low productivity was not typical of other tropical forests (Hesketh and Baker, 1967) and they theorized that the forest might have been at maturity.

Brown (1969) developed a model for the relationship between net photosynthetic rate and light intensity at a given concentration of CO_2 in the air. He used compatible photosynthetic data from many sources in the literature for 11 different species, most of which were crops. The model provided a prediction of the sum of the diffusion resistances, the capacity of the leaf to fix CO_2, the concentration of CO_2 at the photosynthesis sites and the respiration rate. The resultant rates of photorespiration of wheat were twice the dark respiration rates at the same temperature. The sum of the diffusion resistances was inversely related to the maximum rate of photosynthesis for all species investigated.

Curry (1971) developed a model of plant growth utilizing the simulation language CSMP (Continuous System Modeling Program). The model predicted photosynthesis, respiration and transpiration from driving variable inputs of light, CO_2, wind, temperature and soil moisture. The model was tested against data collected by Williams et al. (1968) for corn and proved to be biologically reasonable. This model was later expanded and modified to utilize actual daily

weather data (Curry and Chen, 1971). Among other things, this later model was a good predictor of the effects of season, competition and plant density on the productivity of corn.

Stapleton and Meyers (1971) modelled the growth of cotton (*Gossypium hirsutum*) in relation to the total production and marketing system of the commercial product. In addition to the normal environmental inputs, they incorporated such things as human intervention with growth, and the grower's decision process, experience and resources.

Duncan and Barfield (1971) improved on an earlier community photosynthesis model by Duncan et al. (1967) to compute the effects of CO_2 concentration variations on photosynthesis of stratified crop canopies. Of particular interest was the investigation of the possible effect of CO_2 fertilization from substantial soil block CO_2 evolution. A two-percent increase in photosynthetic rates caused by this CO_2 fertilization was calculated. This indicated little contribution of additional CO_2 to enhanced yields observed on highly organic soil. Leaf orientation to the sun (phototropism) was also investigated in the model.

METHODS AND MATERIALS

Units for Expressing CO_2 Exchange Rates

Carbon dioxide exchange rates reported in the literature are based on a wide variety of units. A quantity of carbon, CO_2, or even oxygen per unit of leaf weight or area, or soil surface area, per unit of time are usually the basic units reported. However, the units for each component have not been internationally standardized. Carbon has been reported as grams, milligrams, or micrograms; CO_2 and oxygen have been reported as grams, milligrams, micrograms, microliters or millimoles; and time ranges from seconds to days. Most of the quantity and time components are easily interconvertible, but the units of leaf weight or area, or soil surface area, present a somewhat more complicated problem. Typical measurements have been grams dry weight green (DWG) plant material, grams dry weight total aboveground (DWT) plant material, ground area (GA) and leaf area (LA). These measurements can all be interconverted if the relationships are known among weight, leaf area, and ground area, but there is disagreement as to which unit provides the most accurate representation of CO_2 exchange rates.

Carbon dioxide exchange rates based on GA are desirable for many reasons. First, they can be easily compared to other productivity determinations such as clipping data. Also, when the exchange rate of an actual GA is determined, it intrinsically incorporates the integration of the variability among such factors as sun and shade leaves, young and old leaves, stem and leaf CO_2

exchange, and the effects of mutual shading of leaves. The main problem encountered in attempting to base CO_2 exchange rates on a GA basis has been the physical limitation of the size of CO_2 assimilation chambers. For example, it is very difficult to place an assimilation chamber over an entire shrub or tree; therefore, a branch or two is usually measured and the values obtained must be extrapolated to the entire shrub or tree. The same analogy can be used when considering smaller plants. It is much easier to place a portion of a leaf or a whole leaf in an assimilation chamber than the entire plant. This process is desirable because it eliminates the necessity of contending with any belowground contribution of CO_2 to the assimilation chamber and requires a smaller air conditioning subsystem. For these reasons, CO_2 exchange rates of most plants have been reported on a leaf area basis.

At times it is necessary to base CO_2 exchange rates on a foliage weight, or even a volume basis. For example, the leaf areas of such species as *Artemisia tridentata*, *Eurotia lanata* and *Atriplex confertifolia* are very difficult to determine. For this reason, Caldwell et al. (1972) reported their findings on these species on a weight basis. Ronco (1970) reported CO_2 exchange rates of *Picea engelmannii* and *Pinus contorta* on a foliage volume basis.

In an effort to further explore the units controversy, I calculated many CO_2 exchange determinations on the basis of DWT. This was done because it eliminated the tedious and uncertain process of separating dead from live plant material. It was hoped that CO_2 exchange rates based on DWT would be consistent with CO_2

exchange rates based on leaf area or soil surface area. This did not prove to be the case. Carbon dioxide exchange rates based on DWT proved to be far too variable and were not analyzed further. Although CO_2 exchange rates on the basis of DWG were consistent with data based on leaf area, they were of less value for herbaceous species because most values found in the literature have been reported on the basis of leaf area.

The Greenhouse Study

Sod Collection and Greenhouse Procedures

Approximately 20 undisturbed sods of both blue grama and western wheatgrass were cut at the Pawnee Site, potted in no. 10 cans, and brought into the Range Science greenhouse on the Colorado State University campus. The sods of each species were collected at the Pawnee Site in the same afternoon from an area of Ascalon sandy loam soil of approximately 100 m^2. The collection area was purposely kept small so that soil type and water content of each sod would be similar. Blue grama sods were collected during late summer, 1971, and western wheatgrass during January, 1972. These collection dates provided sods of each species that were in a state of quiescence. Both species were grown for approximately four weeks in the greenhouse to an early reproduction stage of phenology.

One calibrated thermocouple psychrometer was installed in the spacial center of each sod for measurement of soil water potential. The potted sods with thermocouple psychrometers are shown in Figure 1 along with the microvoltmeter used for reading

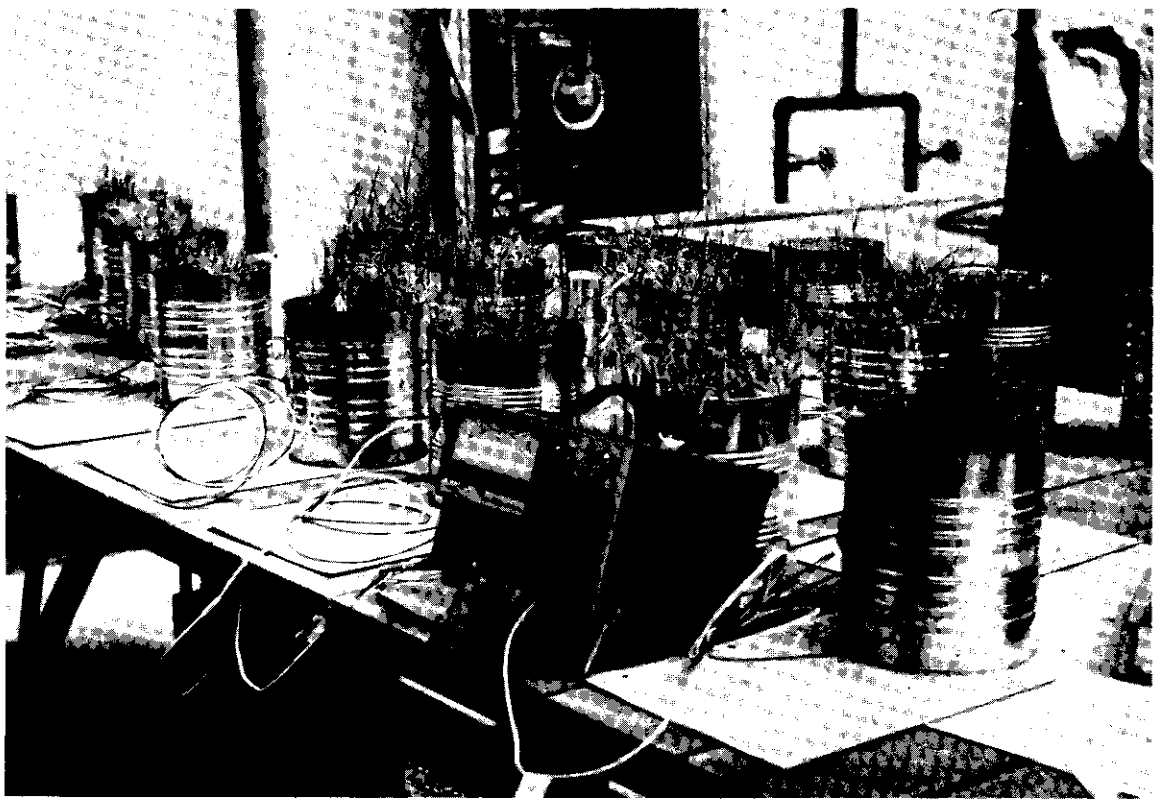

Figure 1. Potted sods of blue grama (*Bouteloua gracilis*) in the greenhouse with thermocouple psychrometers installed in the spacial center of each sod. The instrument shown in the foreground is a microvoltmeter used for reading the psychrometers to determine soil water potential.

the psychrometers. The sods were then weighed and watered. The original weight of each sod was used throughout the growth period 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 the thermocouple psychrometers. The thermocouple psychrometers were read twice daily and plotted against the relative water content of the sod for conformity. The sods were allowed to dry to about -30 bars, then rewatered to zero bars soil water potential to provide the cycling of soil water normally encountered on the shortgrass prairie. Thermocouple psychrometer readings were not recorded until the third day after each watering, thus allowing even distribution of water throughout the sod and insuring an accurate representation of the soil water potential of the sod. Each sod was watered three to four times before gas exchange measurements were made.

Greenhouse CO_2 Exchange System Description

The CO_2 exchange system utilized for photosynthetic and respiration rate determinations in the greenhouse studies was developed by Ronco (1969). Basically, it was a closed CO_2 exchange system consisting of three components: (1) an assimilation chamber with very sensitive temperature control that allowed maintenance of constant temperatures from approximately 15.0°C to 45.0°C, $\pm$ 2°C, (2) a bank of seven 300 W reflector spotlights capable of producing irradiances of up to 1.54 langleys per minute between 400 and 700 nm after being filtered through an eight-centimeter deep continuous flow

water bath for removal of much of the infrared radiation, and (3) an infrared analyzer (IRGA) and a gas injection unit allowing the operator to reestablish CO_2 concentrations without opening the system to the surrounding atmosphere.

The closed CO_2 exchange system is diagrammed in Figure 2 and is pictured in operation in Figure 3. A fan provided continuous internal air circulation within the assimilation chamber. This air circulation eliminated variations in rate determinations that were observed by Decker (1947) to have been caused by fluctuations in air flow rates. The temperature control system utilized a modified drinking fountain cooler as a coolant reservoir. A three-way valve regulated the amount of coolant circulated through 12 m of copper tubing between the walls of the assimilation chamber, thus maintaining the desired air temperature within the chamber. The three-way valve was electronically controlled by both an air temperature thermistor in the chamber and a water temperature thermistor in the coolant line. This dual temperature control provided a high degree of temperature sensitivity to the system.

The light bank was the main source of heat for the assimilation chamber; however, the heat given off by the lights was not sufficient to maintain the chamber temperature above 35°C. Therefore, the system was modified so that the coolant liquid could be heated to obtain the desired 40°C temperatures during part of the experiments. For a more detailed description of the system refer to Ronco (1967 and 1969).

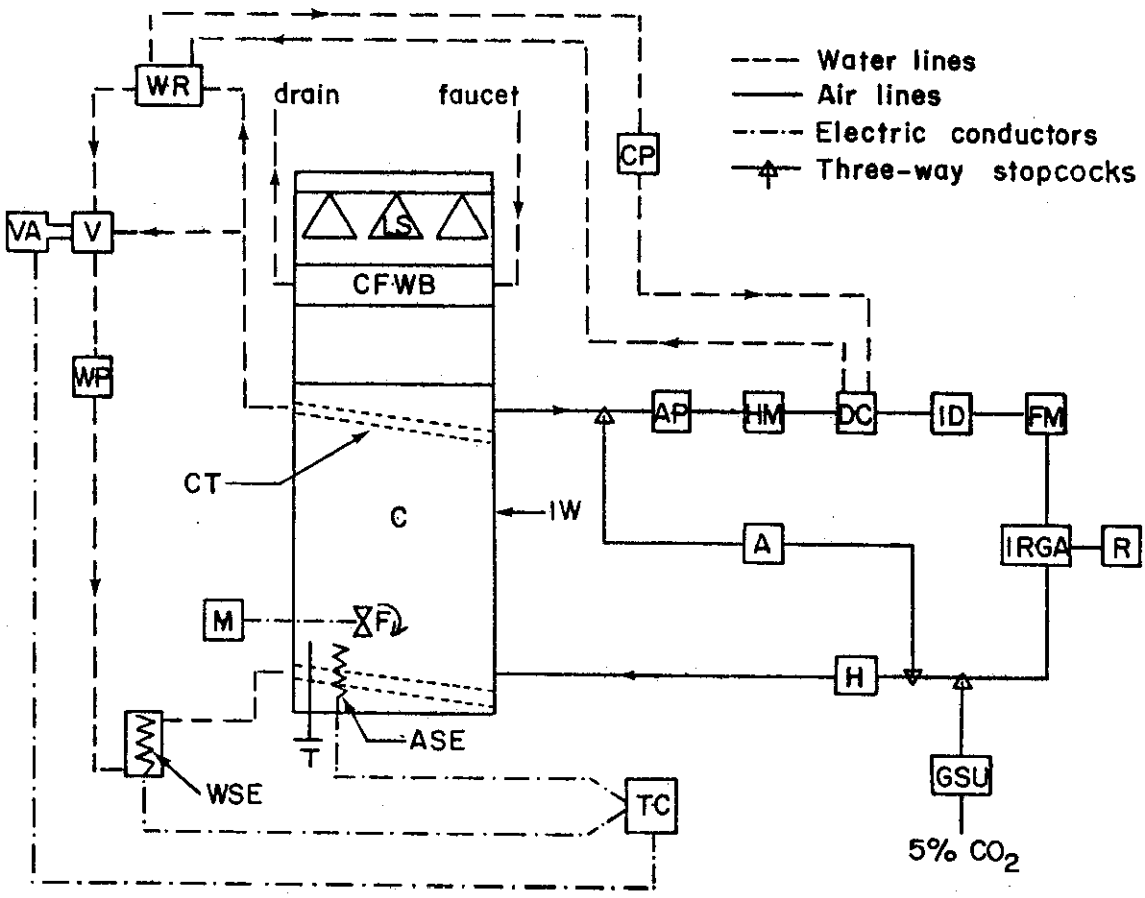

Figure 2. Schematic diagram of CO_2 exchange system developed by Ronco (1969) for measuring photosynthetic and respiration rates.

A - ascarite column
AP - air pump
ASE - air temperature sensing element
C - assimilation chamber
CFWB - continuous flow water bath
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 (double sealed shaft)
R - strip chart recorder
T - thermometer
TC - temperature controller
V - three-way valve
VA - valve actuator
WP - water pump
WR - water reservoir, cooler-heater
WSE - water temperature sensing element

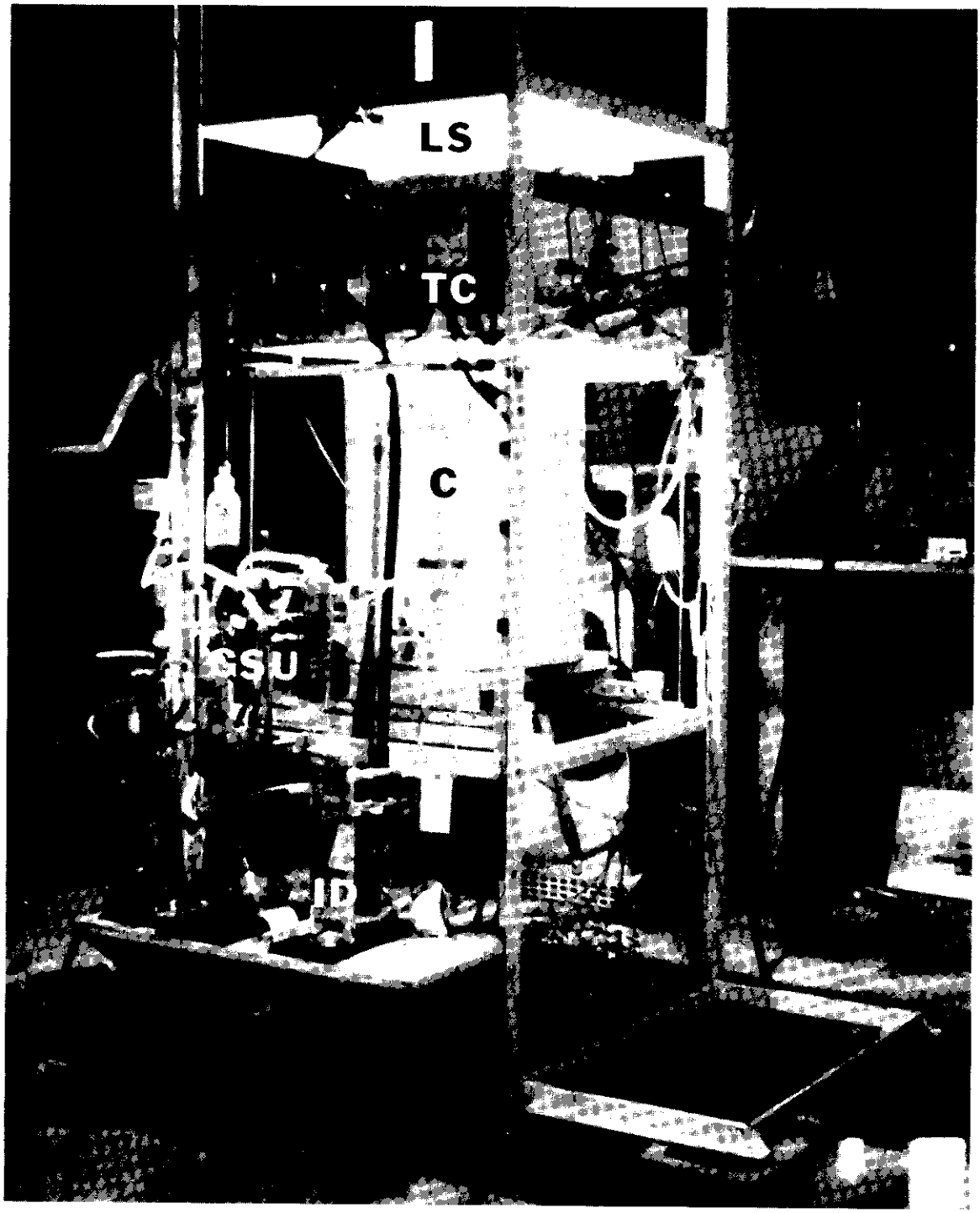

Figure 3. The closed system of CO_2 exchange used to measure photosynthesis and respiration rates of blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) in the greenhouse study. The various discernible components are the light source (LS), temperature controller (TC), assimilation chamber (C), gas injection unit (GSU), and indicating drierite column (ID).

Carbon dioxide concentrations were measured with a differential infrared gas analyzer (IRGA). The CO_2 exchange rates were recorded on a single point strip chart recorder.

Experimental Procedures

The CO_2 exchange system used in the greenhouse was a closed system; therefore, the CO_2 concentration in the system could not be maintained at one level. Photosynthesis caused a decrease in the CO_2 concentration of the system, and conversely, the CO_2 concentration of the system was enhanced by respiration. Therefore, steady states of photosynthesis and respiration were measured by steady rates of CO_2 concentration decreases or increases, respectively. The rate was recorded as a diagonal straight line on the strip chart recorder paper.

Prior to initiation of experiments with both blue grama and western wheatgrass, pre-trial determinations showed the photosynthetic rates of both species to be essentially unaffected by CO_2 concentrations between 370 and 190 parts per million (ppm). This was in direct contradiction to the findings of some other researchers. Hesketh (1963) demonstrated approximately a two-fold increase in net photosynthesis of both a C_3 and C_4 species with an increase in CO_2 concentration from 150 to 300 ppm. He observed similar rate increases when the CO_2 concentration was raised to 600 ppm. Hesketh and Moss (1963) showed that the net photosynthetic rate of maize in full sunlight was 50 percent greater at 500 ppm of CO_2 than at 300 ppm. This response by plants to CO_2 concentration was thoroughly

discussed by Wittwer and Robb (1964) and is the basis for CO_2 fertilization used by many commercial greenhouse operators.

Brown (1968) criticized closed CO_2 exchange systems for their continuously changing CO_2 concentrations. Conversely, Hew, Krotkov and Canvin (1969) obtained similar results from both an open and a closed system. Decker (1957) determined net photosynthetic responses of tobacco (*Nictotiana langsdorfii*) to CO_2 concentrations to be nearly linear up to about 400 ppm.

Assuming a totally linear response in net photosynthesis between 280 and 360 ppm CO_2, with an average net photosynthetic rate of 15.0 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, the net photosynthetic rate would be about 3.0 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ greater at 360 ppm CO_2 than at 280 ppm. This range of CO_2 concentrations (280 to 360 ppm) was the greatest differential between which any of the greenhouse CO_2 exchange rate determinations were made. This example might leave one with the impression that there must have been a 20 percent error involved in the greenhouse determinations. However, the error could not have been this great because the photosynthetic rate determinations were begun at about 360 ppm CO_2, which is about 40 ppm above ambient concentrations, and were terminated at no less than 280 ppm, which is about 40 ppm below ambient CO_2 concentrations. This procedure provided a cancelling effect for the recorded rate of CO_2 exchange because the rate recorded was the average over the entire range of CO_2 concentration. This approach to measurement of CO_2 exchange rates with a closed system should have provided results with negligible error.

The determination of photosynthetic rates of plants requires that only the CO_2 exchange of the aboveground portions of the plant be taken into consideration. This provides the net photosynthetic rate (in light) and requires the exclusion of the belowground contribution of CO_2. According to Zelitch (1971), net CO_2 assimilation (sometimes called "apparent" photosynthesis) is equal to the gross photosynthesis (sometimes referred to as "true" photosynthesis) minus the loss resulting from respiration. More commonly, net photosynthesis (Pn) equals gross photosynthesis (Pg) minus aboveground respiration (AGR). Net photosynthesis was measured as a CO_2 assimilation rate in light, and foliage respiration was measured as a CO_2 production rate in total darkness. Gross photosynthesis (Pg) was determined by the addition of these two rates (Pn + AGR).

Contribution of CO_2 to the system from the soil was excluded by sealing the sods at the soil-atmosphere interface with heavy mineral oil. Previous experimentation showed mineral oil to be impervious to CO_2 diffusion and to be nontoxic to either species. Mineral oil had no detectable influence on CO_2 assimilation rates for up to 15 hours after application.

Polyethylene glycols (carbowax) of different molecular weights (and consequently, different melting points) have been used by Lawlor (1970) and others in an attempt to seal the soil surface. However, it was found in this study that carbowax acted as a desiccant, absorbed water from the plants and thereby affected the physiology of the plants. For this reason, mineral oil was used as a sealant instead of carbowax.

Normal photoperiods were allowed and no artificial lighting was used during the growth period in the greenhouse. Day and night temperatures within the greenhouse were maintained at about 40°C/15°C for blue grama and 25°C/5°C for western wheatgrass. These temperature regimes were representative of the respective growing season for each species.

At the end of the growth period, a sod was randomly selected which was at one of the three desired soil water potentials (0, -15, or -30 bars, $\pm$ 2 bars), the soil surface was sealed with heavy mineral oil, and a sequence of net photosynthetic and respiration rate determinations were made for the aboveground foliage. The sequence of determinations consisted of measuring the net photosynthetic rate of the foliage of one sod (at one of the three soil water potentials) at the three levels of irradiance (0.30, 1.12, and 1.54 $ly \cdot min^{-1}$) and at three levels of temperature (20°C, 30°C, and 40°C). In an experimental determination, irradiance was varied first while temperature was held constant. Dark respiration rates were concurrently determined in the sequence at each temperature. Thus a total of 12 CO_2 exchange rate determinations were recorded for each sod. Three sods at each of the three soil water potentials provided the triple replication to the statistical design. A split-plot factorial design was utilized for data analysis.

All determinations were made at night to eliminate variations in irradiance caused by sunlight. A physiological equilibration period of approximately 15 minutes was allowed between each change in

irradiance, while 30 minutes equilibration was allowed between changes in temperatures.

Leaf water potential was determined as an external variable at the beginning and at the end of each set of 12 rate determinations. The cans in which the sods were potted had only 186 cm^2 soil surface area, thereby making it impractical to make more leaf water potential measurements.

The foliage of each sod was clipped at the conclusion of each set of determinations. The foliage was hand separated into green and nongreen material and the leaf area (LA) of the green (photosynthetically-active) grass blades and sheaths was determined. The samples were then oven dried at 60°C and weighed. Both net and gross photosynthetic rates were calculated on the basis of square decimeters of leaf area (one side), dry weight of green photosynthetically-active material (DWG), and dry weight of total aboveground biomass of both photosynthetic and nonphotosynthetic plant material (DWT).

Leaf areas for western wheatgrass were carefully calculated from manual measurements. One-way analysis of variance of the leaf areas showed non-significant differences ($p > 0.10$) among the nine sods.

The determination of the LA for blue grama sods was more difficult because of the smaller, more numerous leaves. An air flow planimeter was constructed similar to that described by Mayland (1969) in an attempt to provide LA determinations. The air flow planimeter proved to be unsatisfactory for measurement of LA for

the grasses, therefore, a correlation between LA and DWG was determined by linear regression on measurements taken in the field throughout the 1972 growing season at the Pawnee Site. The LA was determined using the inclined point quadrant method developed by Warren-Wilson (1963) and adapted to the shortgrass prairie by Knight (1973). The regression analysis provided the prediction equation:

$$LA = 0.0 + 0.527\ (DWG) \qquad (r^2 = .82)$$

where: LA = leaf area of one side (dm^2)
DWG = dry weight of green photosynthetically-active material (g).

This coefficient was used to convert the dry weights of the blue grama foliage in the greenhouse study to square decimeters of LA (0.527 dm^2 LA/g DWG). One-way analysis of variance was then performed on the resultant LA data and indicated no significant differences ($p > 0.10$) among LA of the blue grama sods used in the greenhouse study.

Irradiance produced by the variable light source of the CO_2 exchange system was measured at plant height using an Eppley pyranometer equipped with a KG-3 filter which provided values in the visible spectrum only. One 300 W spotlight provided 0.30 $ly \cdot min^{-1}$, while all seven 300 W spotlights produced 1.54 $ly \cdot min^{-1}$. The high intensities were used for the purpose of demonstrating the presence or absence of light saturation of the species studied.

All photosynthetic and respiratory rates determined in the greenhouse study were computed by the equation:

$$\text{Pn or AGR} = [(MVT_1P/LT\ P_1)(\Delta\text{ppm/hr} \times 10^{-6})] \ / \ \text{DWG or DWT or LA,}$$

where:
- Pn = net photosynthesis (mg $CO_2 \cdot g^{-1} \cdot hr^{-1}$) on dry weight green (DWG) or total aboveground biomass basis (DWT), or on leaf area (LA) basis (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)
- AGR = aboveground dark respiration (mg $CO_2 \cdot g^{-1} \cdot hr^{-1}$ or mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)
- M = mole weight of CO_2 (44,010 mg)
- V = volume of closed system (34.48 ℓ)
- T_1 = 273°K
- P = average barometric pressure (635 mm Hg)
- L = mole volume of CO_2 (22.414 ℓ)
- T = chamber air temperature (°K)
- P_1 = standard barometric pressure (760 mm Hg)
- Δppm/hr = CO_2 exchange rate in parts per million per hour converted to the volume fraction of CO_2 by multiplying by 10^{-6}
- DWG = dry weight green aboveground biomass (g)
- DWT = dry weight total green and non-green aboveground biomass (g)
- LA = leaf area of one side (dm^2).

The method of determining gross photosynthetic rates by addition of Pn and AGR for plants possessing the C_3 pathway of CO_2 fixation (western wheatgrass) is probably in error because photorespiration was probably occurring. However, the net photosynthetic rate determinations for western wheatgrass should not be in error because all aboveground respiration was automatically accounted for in the determinations of net photosynthetic rates. Both net and gross photosynthetic rate determinations on blue grama are believed to be accurate and valid since blue grama is a species that exhibits negligible photorespiration (C_4 species).

The Field Study

Site Description

The field study was conducted at the Pawnee Site, which is part of the Pawnee National Grasslands, administered by the Forest Service and Agriculture Research Service, U.S. Department of Agriculture. It is located in northeastern Colorado, near the town of Nunn, Colorado, in Weld County. The Pawnee Site is approximately 40 km west of the Rocky Mountains and is, therefore, a part of the western edge of the Central Great Plains. The average annual precipitation is 30 cm, but it varies between 10 and 50 cm with about 75 percent occurring between May and September (Jameson, 1969). Most of the summer precipitation is in the form of afternoon thundershowers with occasional intense thunderstorms. Winter precipitation is usually in the form of snow. The climate is semi-arid with warm summers and cold winters. Wind blows almost contiuously throughout the year, and is especially prevalent during the spring. The highest temperatures generally occur in July and August, and lowest temperatures during December, January, and February. The average frost free period is about 135 days. The mean maximum temperature during July is 29.5°C. According to Lauenroth (1973), the major species of the Pawnee Site are: blue grama, fringed sagewort (*Artemisia frigida*), scarlet globemallow (*Sphaeralcea coccinea*), plains pricklypear (*Opuntia polyacantha*), broom snakeweed (*Gutierrezia sarothrae*) and needleleaf sedge (*Carex eleocharis*). A more detailed description of the Pawnee Site is given by Jameson (1969).

Field CO_2 Exchange System Description

Moir et al. (1969), Dye and Moir (1971), and Dye (1972) developed the basic field CO_2 exchange system and pioneered the first measurements of CO_2 exchange of shortgrass in the field. Those studies had little control of temperature, no control of irradiance, no soil water potential measurements, and no phenological observations and analysis. The studies were done almost entirely on blue grama, and were essentially continuous monitoring of CO_2 exchange rates of blue grama sods under natural conditions on the shortgrass prairie. They had relatively inadequate instrumentation for measurement of irradiance and air flow rates.

Instrumentation of the field CO_2 exchange system was expanded in the present study to provide instantaneous irradiance monitoring, better temperature control, and accurate, continuous recording of air flow rates. The system was made more mobile, a resistance heater was added to the heat exchanger unit, automatic and manual gas switching systems were installed, phenological determinations were made, and soil water potentials were determined daily. In addition, a 16-channel automatic analog-digital data acquisition system was constructed which recorded all electronically-measured observations on cassette tape for conversion to computer-compatable magnetic tape.

Field CO_2 exchange determinations for this study were made for pure in situ blue grama sods at the Pawnee Site utilizing the improved CO_2 exchange system described in detail by Trlica et al. (1973). The basic design of a transparent dome situated over a

graminous sod was similar to the CO_2 exchange system used by Redmann (1973), but that was the only similarity between the two systems. The system used at the Pawnee Site was an open system of CO_2 exchange. An open system differs from a closed system (utilized for photosynthetic determinations in the greenhouse) in that air is continuously flowing into and out of the assimilation chamber from the atmosphere. The entire system consisting of the dome assimilation chamber, a heat exchanger, a refrigeration unit and a modified trailer house housing the instrumentation is shown in Figure 4. The dome enclosed .2919 m^2 of vegetation. The heat exchanger, the dome and some of the abiotic sensors are shown in operation in Figure 5. A schematic diagram of the entire system is shown in Figure 6. Figures 7 and 8 show the instrument panel within the trailer and the automatic data acquisition system, respectively.

Ambient air was pumped into the system from the atmosphere at six meters above the soil surface. A sample of this air was routed through the reference cell of the IRGA for the determination of a base line (zero differential) CO_2 concentration. The remainder of the air, an amount varying from about 40 to 75 $\ell \cdot min^{-1}$, was routed to the dome assimilation chamber. An air sample was then withdrawn from the dome by a separate pump at a lesser flow rate to insure only outward air leakage from the system. The sample from the dome was routed through the sample cell of the IRGA. The IRGA was used to determine the differential CO_2 concentration (Δppm CO_2), between ambient and dome CO_2 concentrations. This Δppm CO_2,

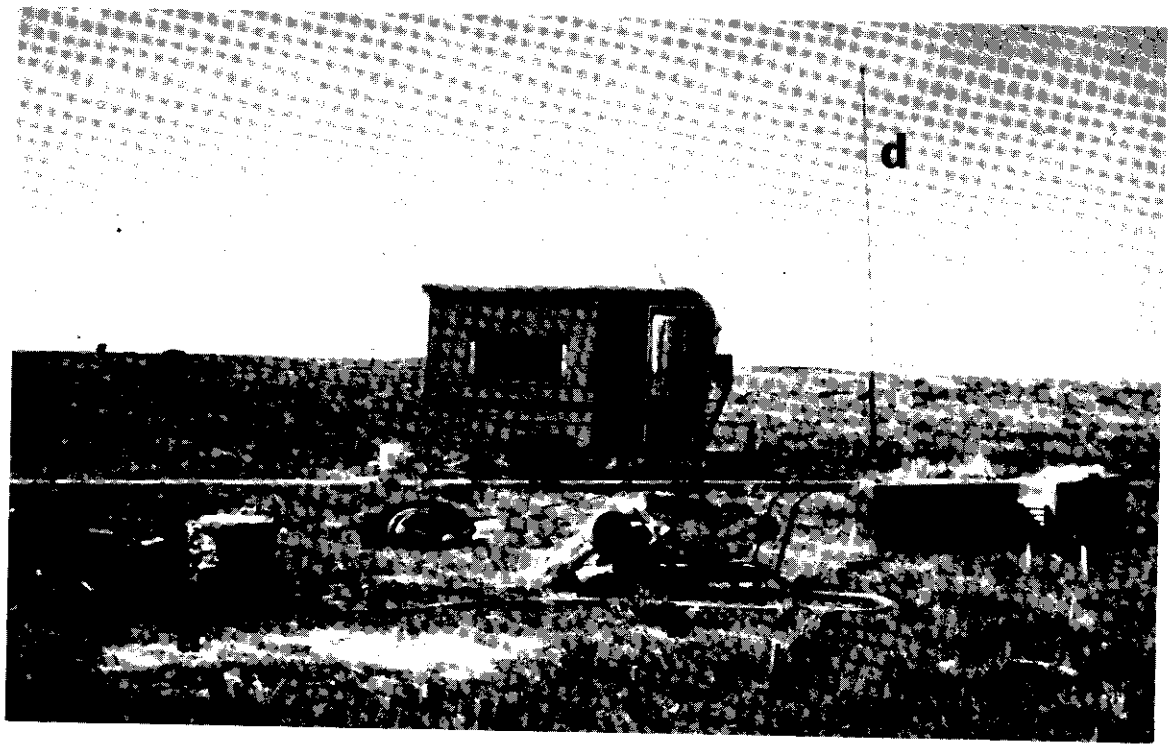

Figure 4. The open CO_2 exchange system utilized for measuring gas exchange in the field. The photograph shows the refrigeration unit (a), the heat exchanger (b), and their metal covers (c). The ambient air intake (d) is at the top of a 6-m mast to the right of the trailer. The dome assimilation chamber cannot be seen in this photograph.

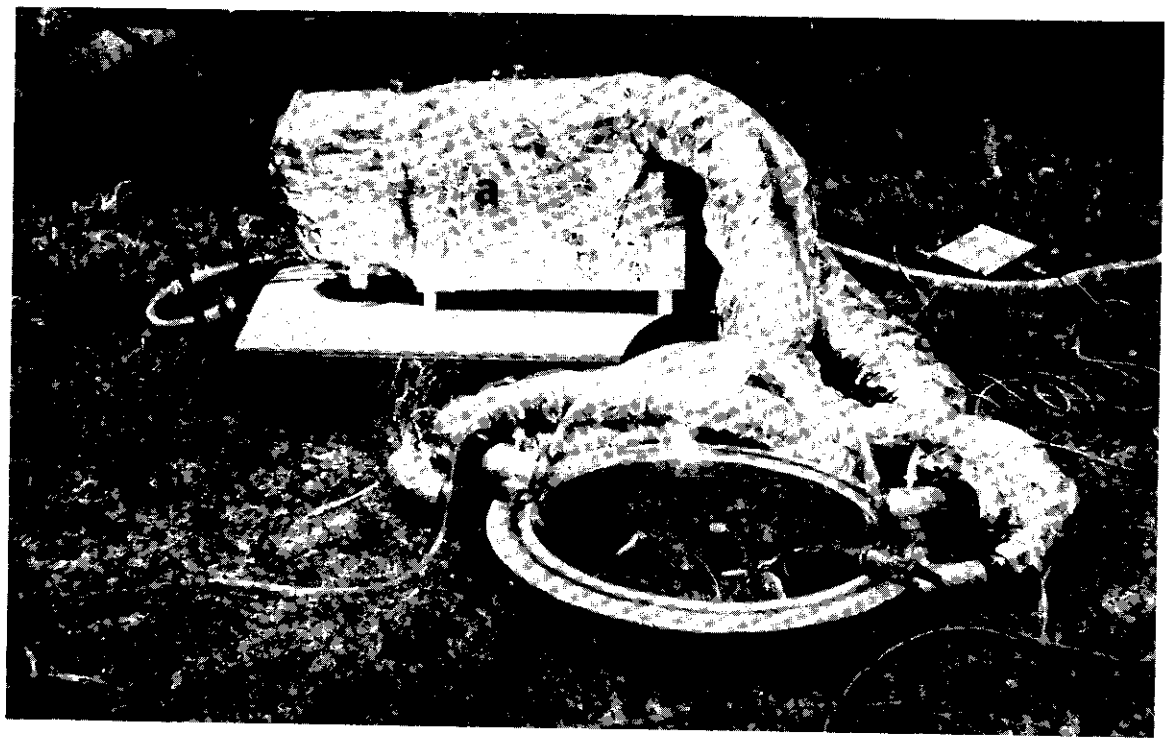

Figure 5. The heat exchanger (a) connected to the dome assimilation chamber. The silicon cell and thermistors are visible underneath the dome. The large hose on the right of the heat exchanger is the coolant line from the refrigeration system. The other hoses connected to the dome are incoming and outgoing air lines. Electrical umbilical cords from trailer can also be seen in the foreground.

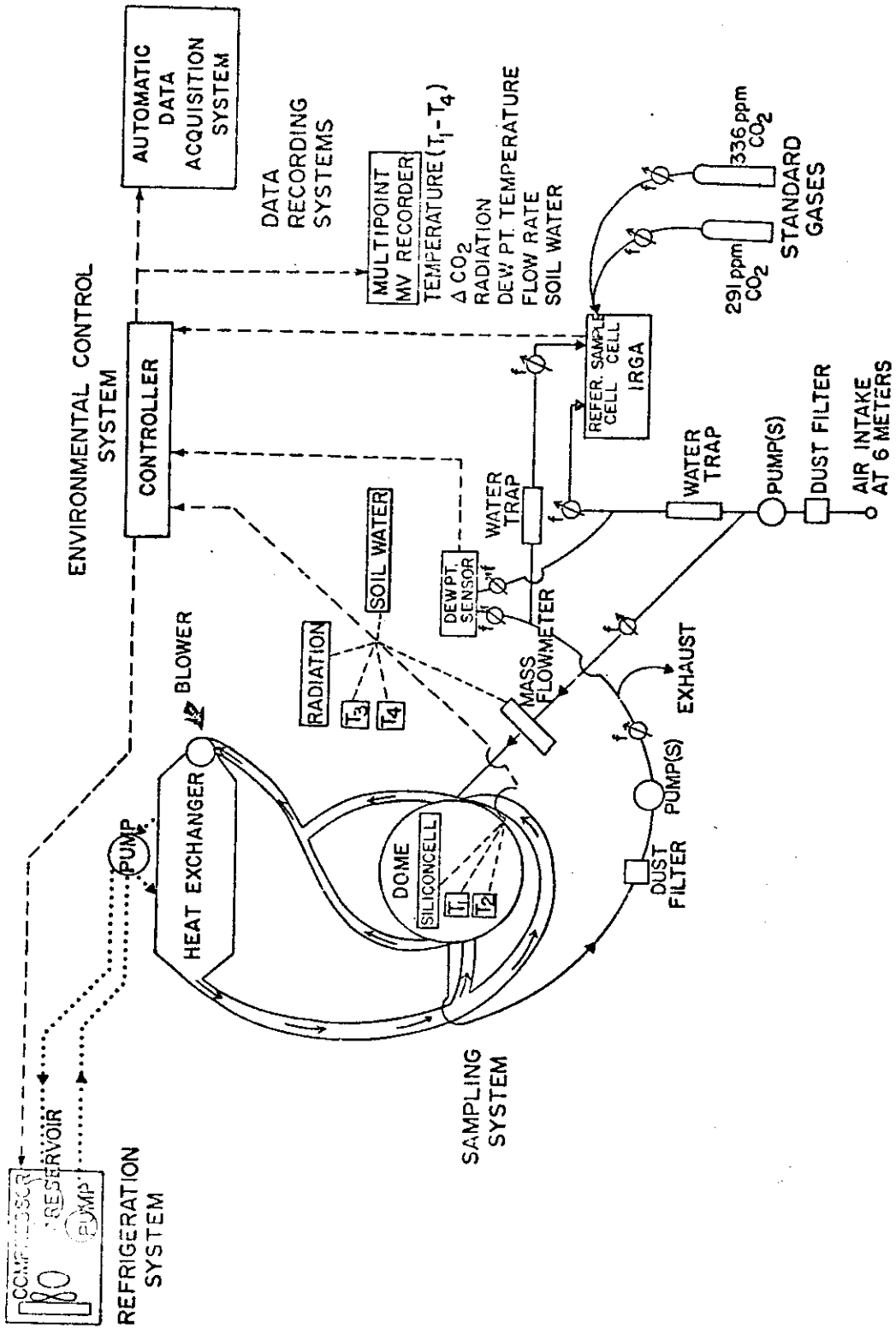

Figure 6. Schematic diagram taken from Trlica et al. (1973) of the open system of CO_2 exchange used in the field for measuring rates of CO_2 exchange of in situ blue grama swards. Dashed lines represent electrical lines connecting sensors and controller unit. Solid lines depict the air flow in the system, while dotted lines illustrate the flow of the coolant between the heat exchanger and the refrigeration unit.

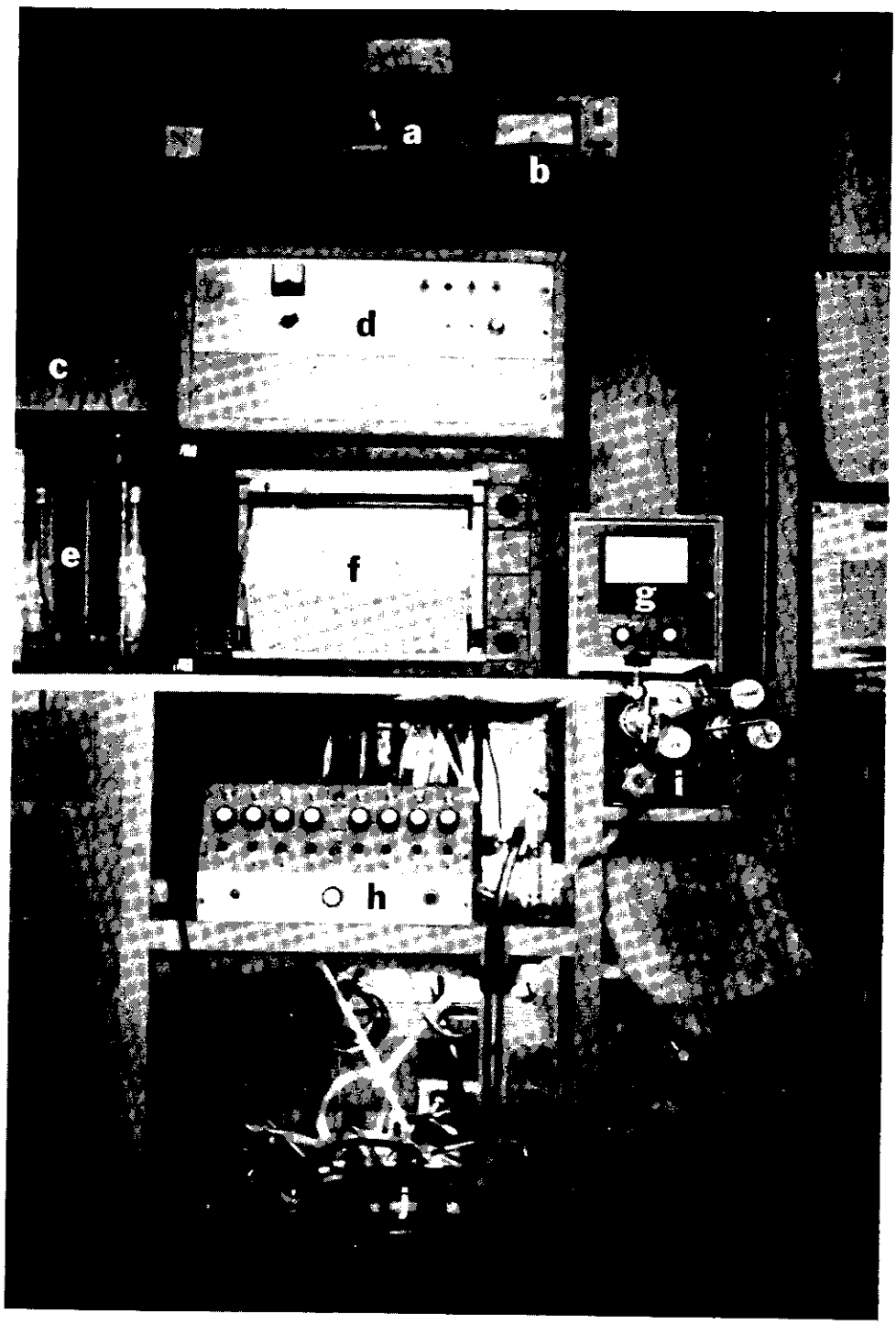

Figure 7. Photograph of equipment and instrumentation housed within the trailer including dew point hygrometer (a), mass flow meter (b), manual gas switches (c), temperature controller unit (d), gas sample flow meters (e), 24-channel strip chart recorder (f), IRGA amplifier control section (g), automatic gas switch (h), standard gasses (i), and air pumps (j).

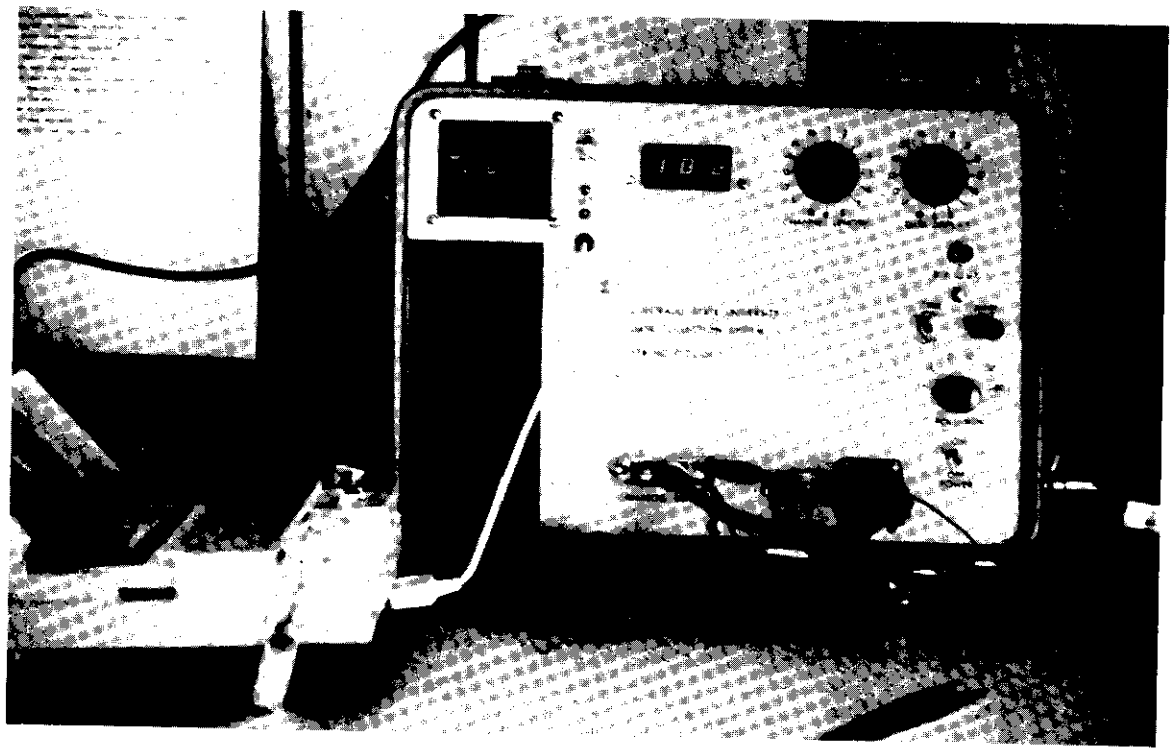

Figure 8. The 16-channel automatic data acquisition system with attached cassette tape recorder for recording incoming data plus date and time.

along with the flow rate of ambient air entering the dome, was used to calculate the CO_2 exchange rate of the sod under the dome.

Experimental Procedures

The method for determining photosynthetic rates from field measurements of CO_2 exchange was fairly intricate because of enrichment of CO_2 within the dome environment contributed by belowground respiration. During a normal daylight photosynthetic rate determination in the field, only two CO_2 exchange values could be measured utilizing this system. The first value was a differential in CO_2 concentration between incoming ambient air and a sample of air withdrawn from the dome environment. This value was arbitrarily labelled net carbon dioxide exchange (NCE). The NCE value was not the net photosynthetic rate (Pn) because of the belowground contribution of CO_2 to the dome environment from belowground root and soil microbial respiration (BGR). The second value determined was dark respiration (RESP) which was obtained by covering the dome to exclude all irradiance and allowing the system to reach a steady state of CO_2 exchange. This value was the sum of BGR and aboveground foliage respiration (AGR). Steady state conditions were reached when all abiotic variables and CO_2 exchange rates remained constant for 10 to 15 minutes.

The NCE values could have been positive, negative or zero depending upon the rate of gross photosynthesis (Pg) in relation to RESP. That is, NCE would have been zero if Pg = RESP. The NCE values were recorded as negative if Pg was greater than RESP. All

RESP rates were recorded as positive. Thus, Pg was determined by:

$$Pg = - (NCE) + RESP, \text{ or } Pg = - (NCE) + AGR + BGR.$$

Gross photosynthetic rates are not as meaningful as Pn values because Pg is not as directly related to net primary productivity as is Pn. The AGR could not be measured with the field system because it was not possible to seal the large soil surface. Consequently, Pn could not be directly determined in the field study.

To obtain Pn data from the field Pg data, a two-way interaction graph of soil water potential and temperature effects on photosynthetic rates of blue grama was prepared utilizing the CO_2 exchange rates determined in the greenhouse study. The ordinate of the graph was the percentage of Pg accounted for by Pn. It was believed that this relationship between Pg and Pn in the greenhouse could provide a direct conversion for CO_2 exchange in the greenhouse study to the CO_2 exchange in the field study. It was possible to test this relationship in the field by measurements of CO_2 exchange of sods before and after clipping at different soil water potentials and temperatures. These measurements separated the AGR and BGR components in the field. It was found that the percentage relationship between Pg and Pn under field conditions was similar, but not identical, to the relationship determined in the greenhouse study. Therefore, the original percentage graph determined for the greenhouse study was adjusted by using data from the field study for field conditions. The graph was also enlarged to the temperature range (15°C to 45°C) encountered in the field. The final adjusted graph is shown as Figure 9, and

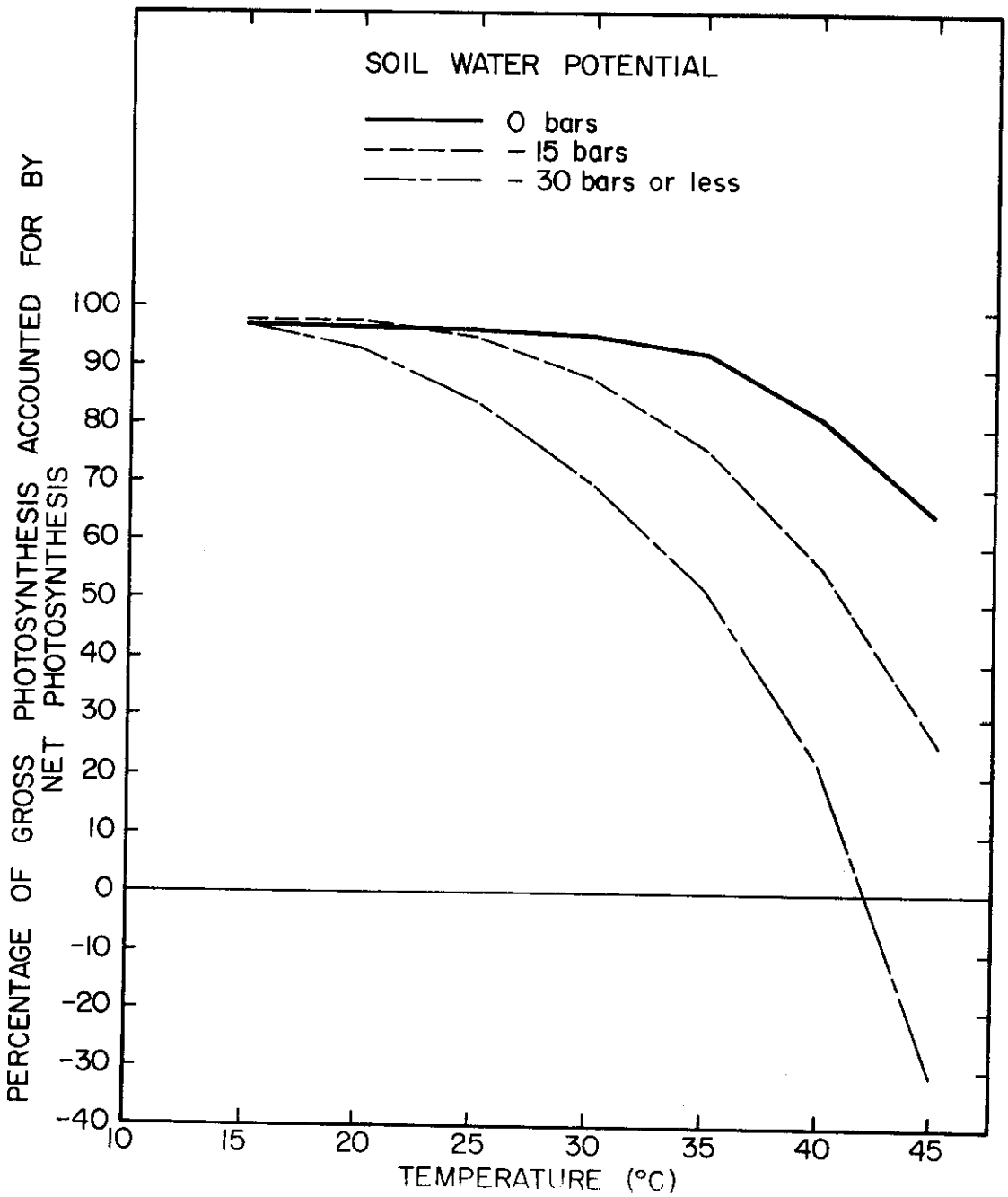

Figure 9. The two-way interaction graph of the effects of temperature and soil water potential on net photosynthesis as a percentage of gross photosynthesis. The basic curves (20°C-40°C) were determined from greenhouse data. Carbon dioxide exchange determinations on clipped sods in the field allowed the curves to be enlarged to the 15°C to 45°C temperature range and corrected for field conditions.

was used to convert field Pg determinations to what has been termed calculated net photosynthesis of blue grama in the field. Calculated net photosynthetic rates are, therefore, the Pn rates reported for the field study. This conversion also allowed for further reduction of the data into the BGR and AGR components by using the following assumptions:

if Pg = Pn + AGR with Pg measured and Pn calculated,

then AGR = Pg - Pn,

and since RESP = AGR + BGR with RESP measured and AGR calculated, then BGR = RESP - AGR.

All Pg and NCE rates were calculated by the following equation:

$$Pg \text{ or } NCE = (MF/L)(\Delta ppm \times 10^{-6}) \; / \; DWG \text{ or } DWT \text{ or } LA,$$

where: M = mole weight of CO_2 (44,010 mg)
F = ambient air flow rate into the dome assimilation chamber ($\ell \cdot hr^{-1}$)
L = mole volume of CO_2 (22,414 ℓ).

This equation and all the symbols and units used are similar to the equation used for calculating CO_2 exchange rates in the greenhouse study with the exception that ambient air flow rate (F) replaced the known volume (V) of the closed system used in the greenhouse study. No temperature and pressure corrections were necessary in the calculation of CO_2 exchange rates in the field because the flow rates were automatically corrected for temperature and pressure by the flow meter used.

Temperatures in the field were measured by using linear thermistors. Temperatures were controlled by the heat exchanger

and refrigeration unit of the system. Air temperatures within the plant canopy both inside and outside the dome were continuously recorded. The temperature within the dome environment could be either manually controlled, or made to simulate the ambient temperature ($\pm$ 2°C) by the electromechanical feedback system of the temperature controller located inside the trailer. As with the closed system utilized in the greenhouse, radiant energy was the main source of heat, with the source being the sun in the field study. Therefore, cooling of the dome environment was required almost continuously when the sun was shining because of the greenhouse effect within the dome environment. If ambient temperature simulation was desired, the controller electronically activated cooling by pumping a mixture of water and ethylene-glycol from the refrigerated coolant reservoir through radiator cores in the heat exchanger unit. Air within the dome system was continuously circulated by a squirrel cage fan through the heat exchanger and across the radiator cores in a closed circuit, thereby providing cooling when required.

Dark respiration rates were obtained by covering the dome with a thick dacron sleeping bag to eliminate incoming shortwave radiation. This would normally cause the air temperature within the dome to decrease 4°C to 5°C. This decrease in temperature was compensated for by the addition of an electrical resistance heater located in the closed air stream as part of the heat exchanger unit. Switching the heater on prior to covering the dome allowed dark respiration rates to be determined at the same temperature

that NCE rates had been determined a few minutes before. It usually took only about 15 minutes to reach steady state conditions of CO_2 exchange for dark respiration, indicating almost immediate stomatal closure in response to darkness. Resumption of a steady state NCE rate when the dome was again uncovered required about 30 minutes, indicating a relatively slower stomatal opening in response to light. Similar stomatal responses were reported by Kuiper (1961).

Solar irradiance was continuously monitored with two instruments: (1) a silicon solar cell placed under the dome, and (2) an Eppley pyranometer placed on top of the trailer which housed the instrumentation. No attempt was made to obtain accurate measures of irradiance with the solar cell. It was used only to indicate complete darkness under the dome, thereby delineating dark respiration determinations.

The Eppley pyranometer with a KG-3 filter provided a measurement of irradiance in the 400-700 nm range in units of langleys $\cdot$ minute^{-1}. Solar irradiance under the dome was controlled in some experiments by shading the dome with a variable number of layers of aluminum window screening. The average percent transmittance of visible irradiance into the dome at various times of the day and with varying layers of screening had been previously determined with the Eppley pyranometer. These values were then used to convert solar irradiance measured on the roof of the trailer to irradiance under the dome with one, two, or three layers of screening.

Soil water potentials were manually recorded each day within a few meters of the sod being measured on that day. Calibrated thermocouple psychrometers were placed at 5-, 10- and 20-cm depths in the soil very early in the growing season with minimum disturbance to the soil. The psychrometers were generally read only once a day; however they were read more often if the soil was drying rapidly from -10 to -50 bars. The psychrometers were found to be inaccurate at soil water potentials of less than -50 bars. Regression analysis indicated that soil water potentials at the 10-cm depth were best for predicting photosynthetic rates, therefore only these values were used throughout the analyses. Figure 10 illustrates the influence of rainfall on soil water potentials at 5-cm and 10-cm depths through the 1972 growing season at the Pawnee Site.

Phenological development of blue grama was determined by visual observation throughout the growing season. Phenology was coded according to the following descriptions:

Code Number	Phenology
1	1st leaf stage
2	2nd leaf stage
3	3rd leaf stage
4	4th leaf stage
5	5th leaf stage
6	seed stalk elongation
7	anthesis
8	seed development
9	seed shatter-fall regrowth.

Code numbers 1 through 5 and 9 were pooled and termed vegetative phenological status for the final statistical analysis, while code numbers 6 through 8 were termed reproductive phenological status.

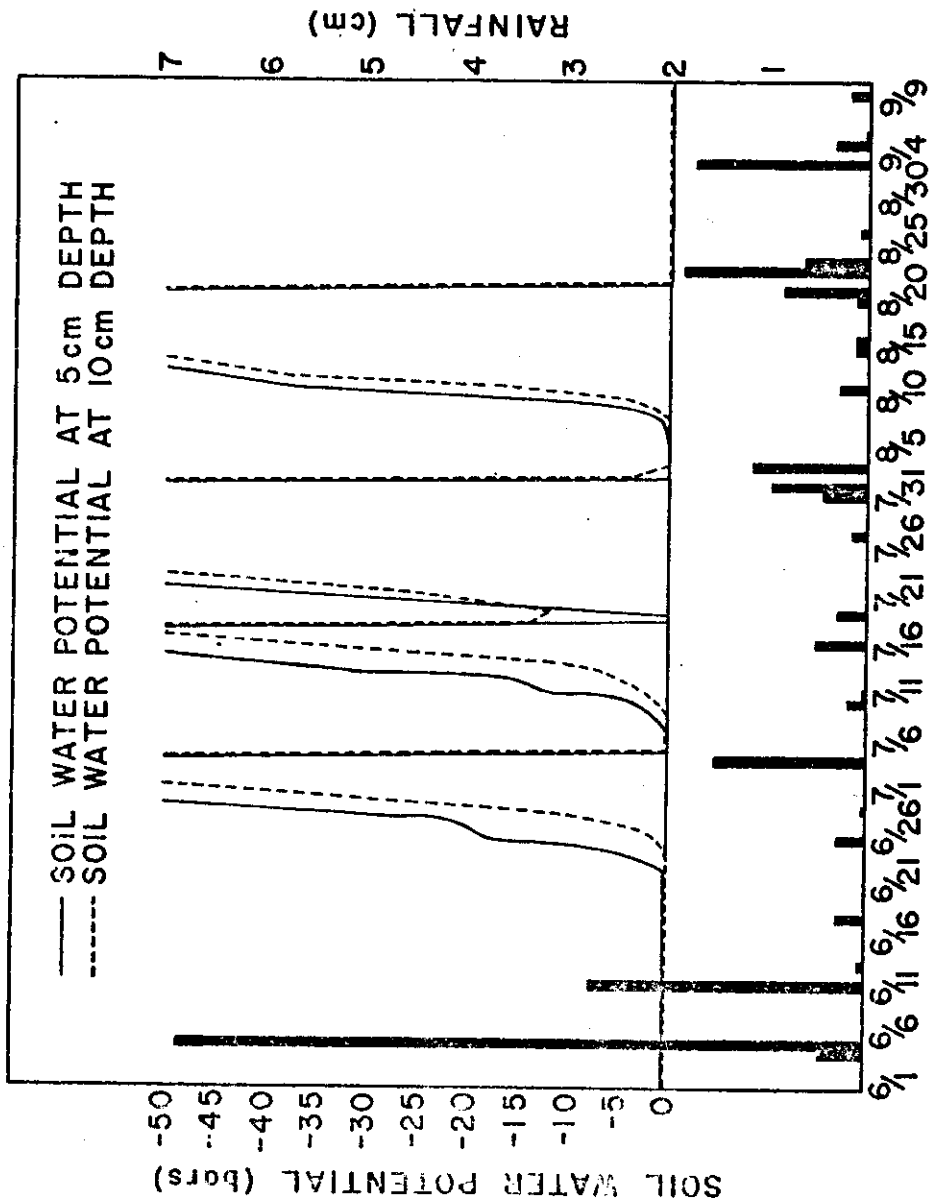

Figure 10. Rainfall and soil water potentials at 5- and 10-cm depths throughout most of the 1972 growing season at the Pawnee Site. No values of less than -50 bars were recorded because thermocouple psychrometers were not accurate beyond that point.

Combining phenological stages into two categories was done to reduce the degrees of freedom to a reasonable level for statistical analysis.

Leaf area indices of green foliage were determined by the non-destructive inclined point quadrat technique described by Warren-Wilson (1963) (Figure 11). The technique was adapted to the shortgrass prairie by Knight (1971, 1972, and 1973). Leaf area indices of sods under consideration were determined at about weekly intervals. In addition, the aboveground foliage of six sods was clipped during the 1972 growing season for determination of foliage dry weights and for measurements of belowground respiration. The clipping procedure allowed CO_2 exchange rates of blue grama to be based on either dry weights or leaf area and provided the indirect method for obtaining calculated net photosynthetic rates in the field. Figure 12 shows the leaf area indices of each sod until clipped throughout the growing season at the study site. Sod number 1 was never clipped, and is an example of the leaf area dynamics of blue grama throughout the 1972 growing season.

Two kinds of field experiments on CO_2 exchange rates of blue grama were made during the 1972 growing season. The first experiment was somewhat similar to the greenhouse experiment where the effects of varying levels of soil water potential, temperature and irradiance on CO_2 exchange rates of blue grama were examined. However, phenological status was added as the fourth variable in the field experiment. The major effort during the 1972 growing season was expended on collecting CO_2 exchange data for steady state conditions of the

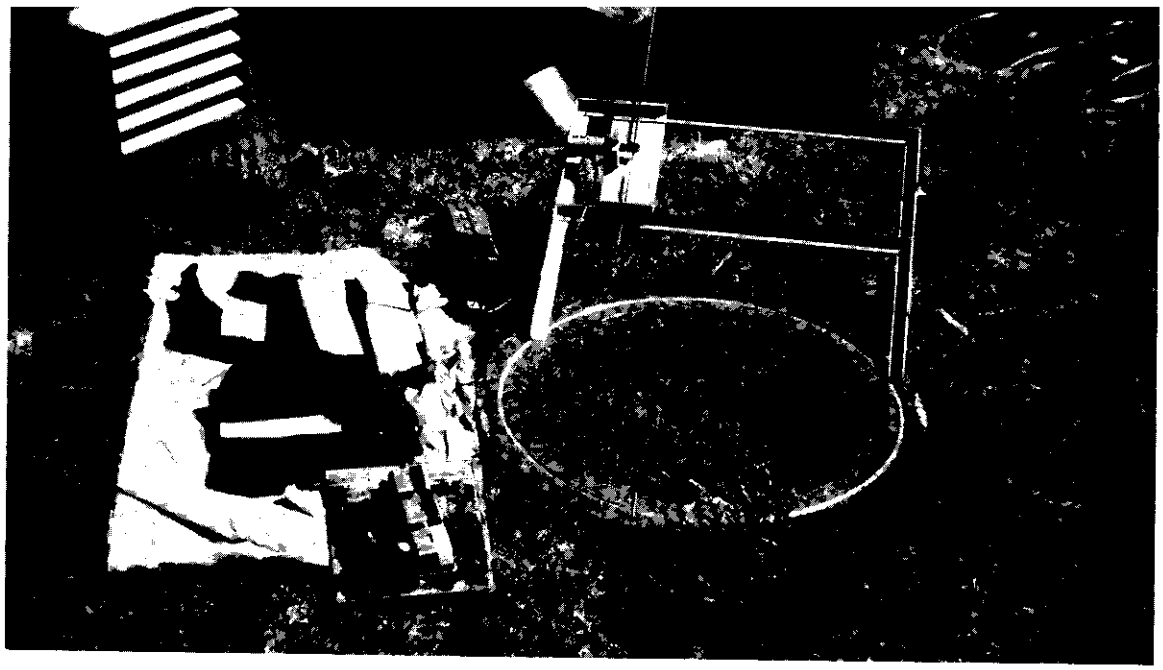

Figure 11. The inclined point quadrat used for nondestructive determinations of leaf area index (LAI) at the Pawnee Site. The point frame is shown in position over one of the 0.29 m^2 blue grama sods used in the field experiments. The metal covers in the background were used as a wind break while measuring LAI. To the left of the sod are three counters used for recording the number of hits encountered by the pin.

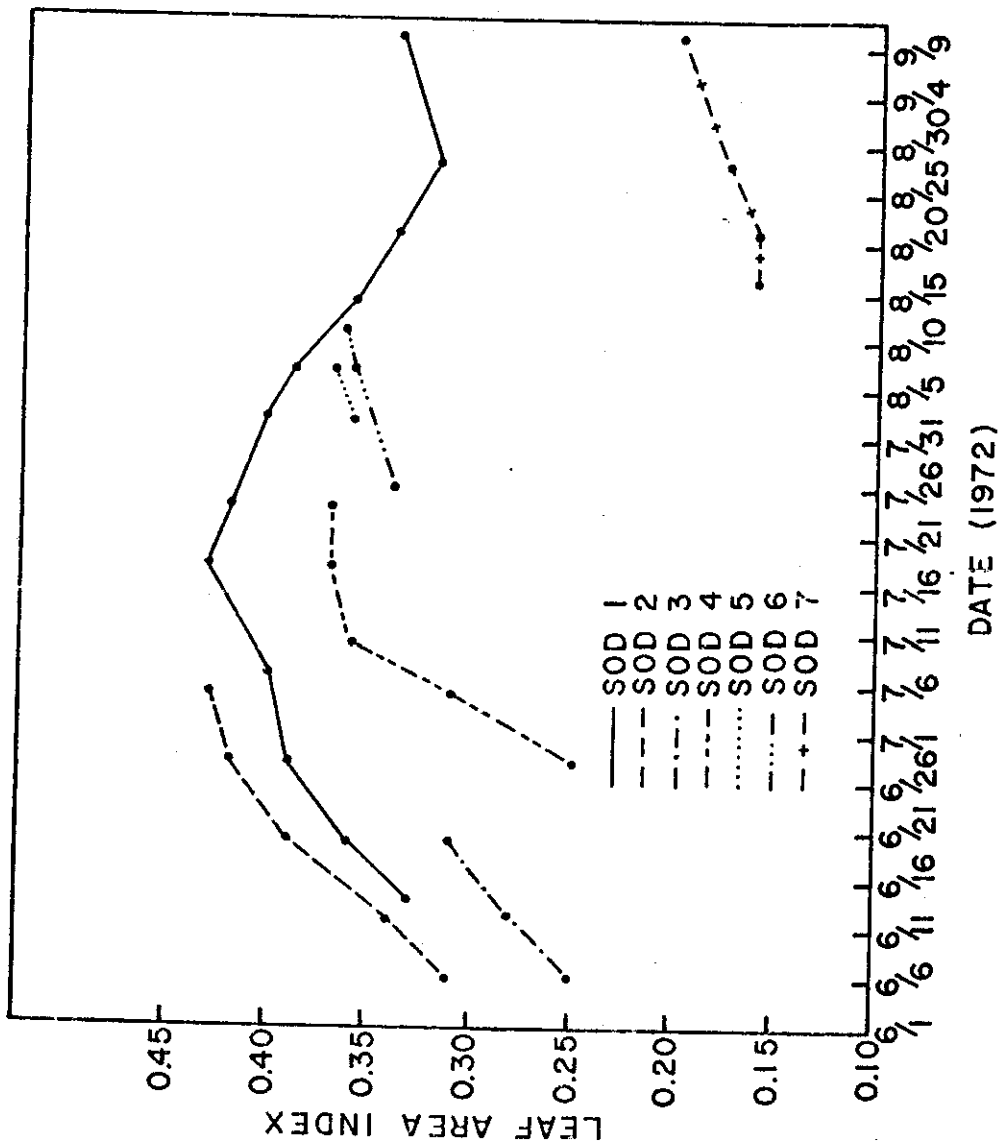

Figure 12. Leaf area indices for various blue grama (*Bouteloua gracilis*) sods at the study site throughout the 1972 growing season.

above variables. This was done because this type of data was believed to be of great value in modeling and understanding primary productivity of the shortgrass prairie. The procedure was to obtain NCE and RESP rates of blue grama sods when each of the four variables was held relatively constant. Phenology and soil water potential were constant over short time periods, but temperature and irradiance were sometimes very difficult to maintain at one level for 20 to 30 minutes. Scattered cloudiness caused irradiance and temperature to vary rapidly. A small cloud could reduce the irradiance to one-half the original value, and in turn, cause the temperature of the air within the folaige to decrease by perhaps 5°C within one to two minutes. Perfectly clear conditions allowed data on steady state conditions of CO_2 exchange to be collected at the rate of approximately three determinations per hour.

At the beginning of the 1972 growing season it was hoped that a sample size of 400 to 500 steady state conditions could be attained. However, because of unusually cloudy conditions on the shortgrass prairie during the 1972 growing season, only about 250 steady state rates were actually recorded.

The second type of field CO_2 exchange experiments conducted during the 1972 season was continuous 24-hour ambient simulations. The naturally fluctuating levels of temperature and irradiance encountered on the shortgrass prairie were simulated within the dome environment. These experiments were repeated periodically throughout the growing season at various constant levels of

phenological development and soil water potential. All the components of photosynthesis (Pg, Pn, and NCE) and respiration (AGR and BGR) were calculated, plotted, and integrated over each 24-hour period. These experiments provided typical examples of daily production for the dominant species of the shortgrass prairie throughout the growing season.

RESULTS AND DISCUSSION

Comparison of Results of Photosynthetic Rates of Blue Grama and Western Wheatgrass on the Basis of Dry Weight and Leaf Area

All CO_2 exchange rates determined in the greenhouse study for blue grama on a DWG basis were reported by Dye, Brown, and Trlica (1972). Similar analysis was done (but not reported) on the exchange rates for western wheatgrass. All statistical relationships of each species based on both LA and DWG were similar.

On the basis of LA, the grand means of blue grama and western wheatgrass in the greenhouse study were 9.6 and 4.5 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, respectively, while on the basis of DWG, the grand means were 5.1 and 6.1 mg $CO_2 \cdot g^{-1} \cdot hr^{-1}$, respectively. Therefore, on the basis of DWG, the photosynthetic rates of western wheatgrass were slightly greater than the photosynthetic rates of blue grama over the ranges of the variables considered. This was surprising because photosynthesis of blue grama, a C_4 species, would be expected to far exceed the photosynthetic rates of most C_3 species. However, blue grama photosynthetic rates were definitely greater than western wheatgrass photosynthetic rates when based on LA. The reason for this difference was found in the relationship between LA and DWG for each species. As previously mentioned, the ratio of LA to DWG for blue grama was 0.53 $dm^2 \cdot g^{-1}$. The ratio of LA to DWG for western wheatgrass was 1.43 $dm^2 \cdot g^{-1}$. Thus, western wheatgrass leaves exhibited more LA per unit of dry weight than did blue grama leaves, and consequently, photosynthetic rates based on DWG were proportionately greater for western wheatgrass as compared with blue grama.

The Greenhouse Study

All CO_2 exchange rates will be discussed in units of mg $CO_2 \cdot dm^{-2}$ $LA \cdot hr^{-1}$. The three-way interaction means and standard errors of net and gross photosynthetic rates and aboveground dark respiration rates for blue grama and western wheatgrass in the greenhouse study are shown in Appendix A, Table 1. All CO_2 exchange measurements were replicated three times at three levels each of soil water potential, irradiance and temperature. A reproductive stage of phenology was constant throughout all determinations for both species.

It should be stressed that the irradiances used in the greenhouse study (0.30 $ly \cdot min^{-1}$ = low, 1.12 $ly \cdot min^{-1}$ = medium, and 1.54 $ly \cdot min^{-1}$ = high) were not actually low, medium, and high in terms of normal ambient conditions of irradiance. The highest ambient visible irradiance recorded in the field during the 1972 growing season was about 0.82 $ly \cdot min^{-1}$. This occurred during partly cloudy conditions when reflections from clouds resulted in a significant increase in irradiance for short periods of time.

Net Photosynthesis (Pn)

The analyses of variance of Pn rates of both blue grama and western wheatgrass at three levels each of soil water potential, irradiance and temperature are shown in Appendix A, Table 2. The analyses showed that each of the three main treatments significantly affected ($p < 0.01$) the Pn rates of both species (Appendix A, Table 2). Each species was also significantly affected ($p < 0.01$) by the two-way interactions of soil water potential and irradiance, and soil

water potential and temperature (Appendix A, Table 2). An irradiance and temperature interaction affected Pn for both blue grama ($p < 0.10$) and western wheatgrass ($p < 0.05$) (Appendix A, Table 2). The three-way interaction of soil water potential, irradiance and temperature significantly affected blue grama ($p < 0.01$) Pn, but had no significant affect on Pn of western wheatgrass (Appendix A, Table 2).

Interaction Effects of Soil Water Potential and Irradiance on Net Photosynthesis of Blue Grama and Western Wheatgrass.

The Pn rates of blue grama at the medium and high irradiances decreased almost linearly with increasing soil water stress from zero to -30 bars (Figure 13). The Pn rates at the highest irradiance were greater than the Pn rates at the medium irradiance until soil water stress of -30 bars was reached. This indicated that blue grama had not reached light saturation at the medium irradiance of 1.12 $ly \cdot min^{-1}$. The Pn rates of blue grama were similar at both high and medium irradiances at -30 bars soil water potential, indicating that this species was probably light saturated at 1.12 $ly \cdot min^{-1}$ when subjected to high water stress. There was very little effect on the Pn rates of blue grama when the soil water stress was increased from zero to -15 bars at the low light intensity (Figure 13). However, further water stress, from -15 to -30 bars resulted in a sharp decrease in the Pn rates of blue grama.

The effects of increasing the soil water stress from zero to -30 bars on the Pn rates of western wheatgrass were almost identical at the medium and high irradiances (Figure 13). This indicated that

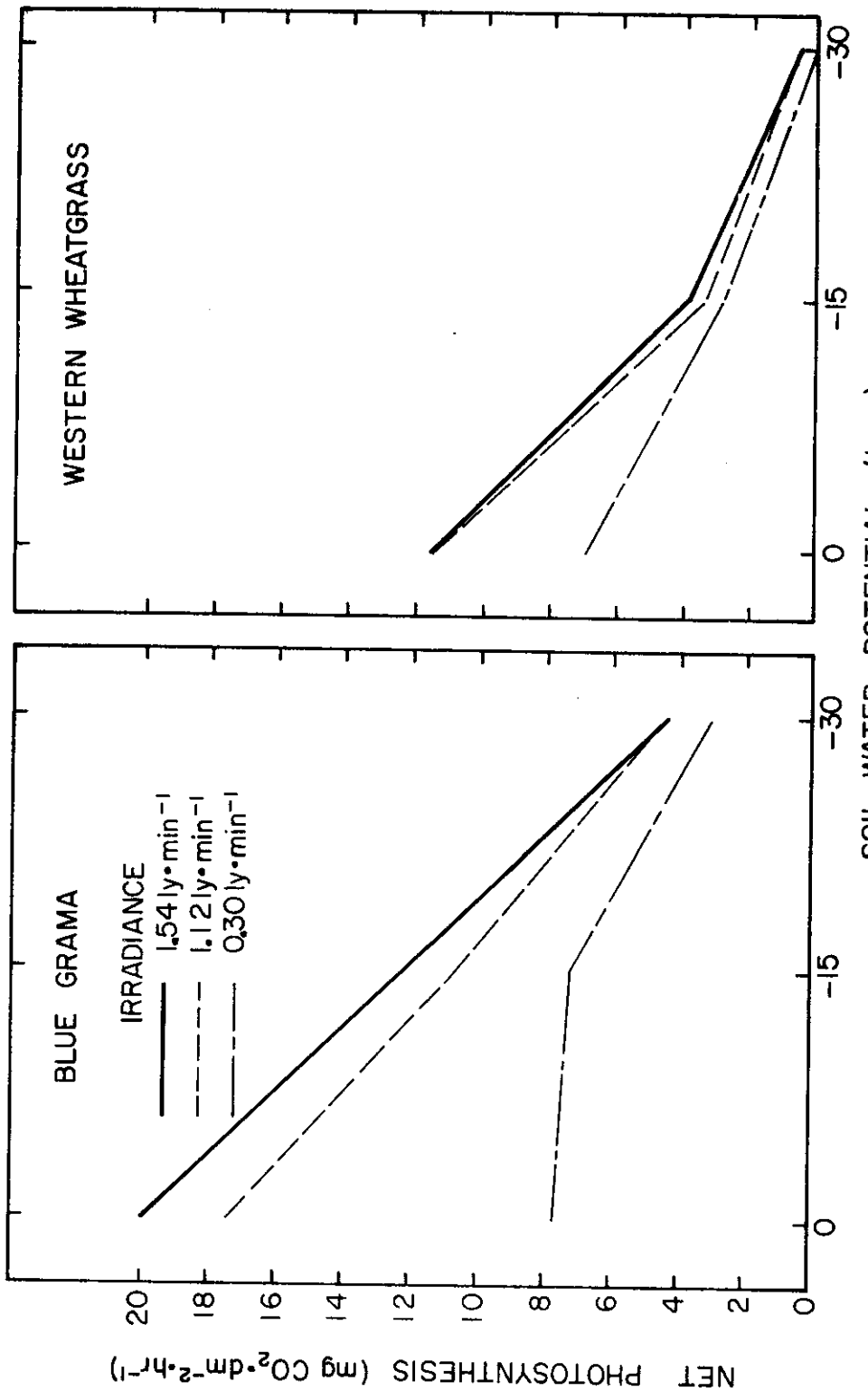

Figure 13. Two-way interaction effects of soil water potential and irradiance on the net photosynthetic rates of blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) as determined in the greenhouse study.

this C_3 species had reached light saturation at 1.12 ly·min^{-1} or lower. The Pn rates at all three irradiances were similar from -15 to -30 bars, indicating probable light saturation of western wheatgrass very near the low irradiance of 0.30 ly·min^{-1} at these water stresses. The effect of increasing soil water stress from zero to -30 bars resulted in a nearly linear decrease in the Pn rate of western wheatgrass at the low irradiance.

Increasing soil water stress generally caused sharp decreases in the Pn rates of both blue grama and western wheatgrass at all irradiances. The large differences among Pn rates of the C_3 and the C_4 species were probably caused by the ability of the blue grama to utilize the higher irradiances more fully at all of the soil water stresses considered (Figure 13). Also, blue grama demonstrated less response to increasing soil water stress at the low irradiance than did western wheatgrass.

Interaction Effects of Soil Water Potential and Temperature on Net Photosynthesis of Blue Grama and Western Wheatgrass

Generally, the Pn rates of blue grama decreased with increasing soil water stress at all temperatures (Figure 14). The initial soil water stress increment from zero to -15 bars caused greater decreases in the Pn rates of blue grama with each increase in temperature. The effects of increasing soil water stress were less at 20°C than at the two higher temperatures of 30°C and 40°C. The Pn rates of this C_4 species were greatest at 30°C until the high soil water stress of -30 bars was attained. At -30 bars soil water potential the Pn rates were greatest at 20°C. This illustrated the

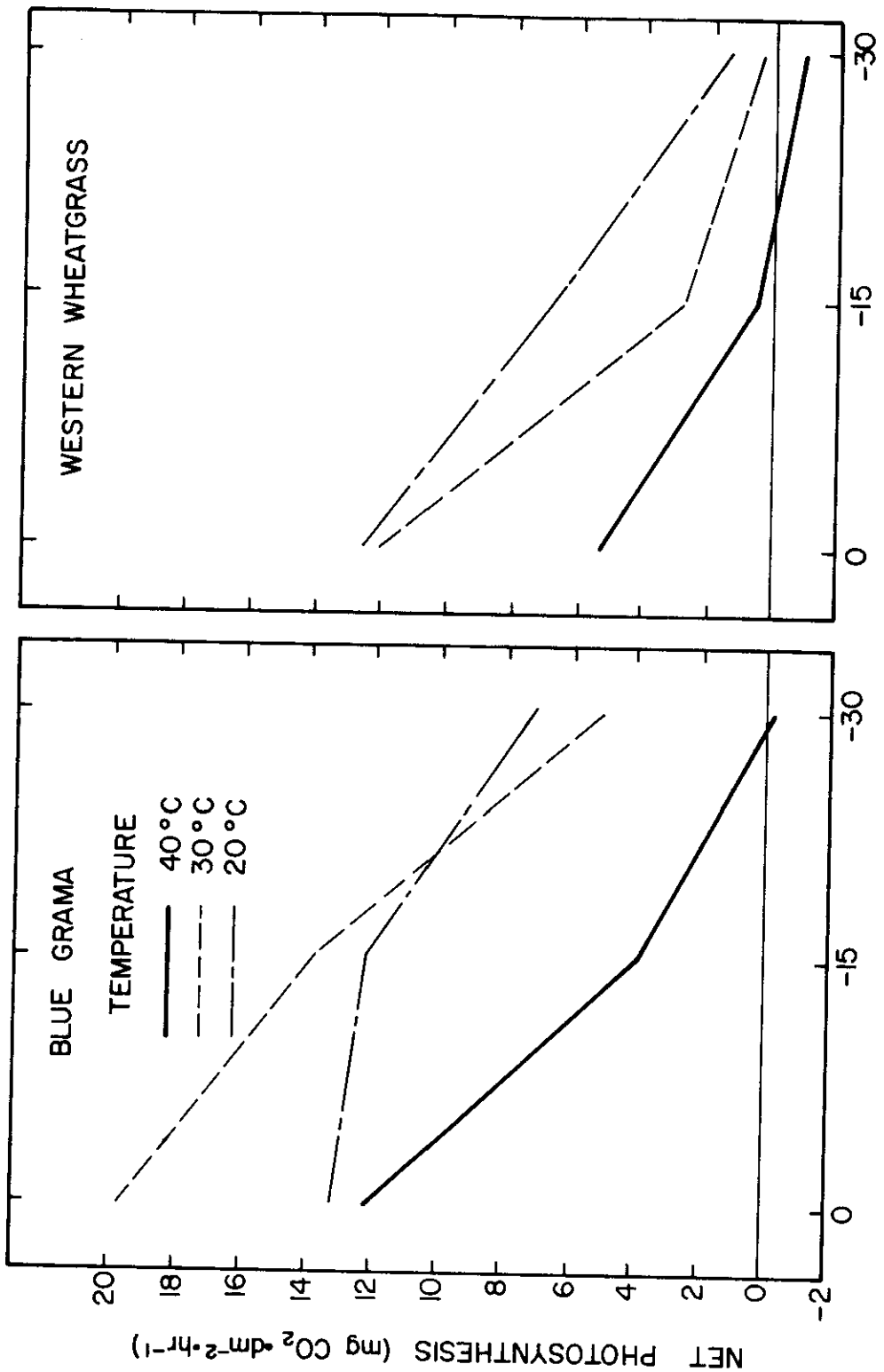

Figure 14. Two-way interaction effects of soil water potential and temperature on the net photosynthetic rates of blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) as determined in the greenhouse study.

variable range of optimum temperature for Pn of blue grama. The optimum temperature was nearest 30°C at the two lower levels of soil water stress, but decreased as the high soil water stress of -30 bars was approached. The Pn rates of blue grama at 40°C were lowest at all soil water stresses, indicating the increasing effect of aboveground dark respiration on Pn at higher temperatures.

The Pn rates of western wheatgrass also decreased with increasing soil water stress at all temperatures (Figure 14). The Pn rates of this C_3 species were greatest at 20°C at all levels of soil water, but decreased almost linearly with increasing soil water stress. At 30°C and 40°C the Pn rates of western wheatgrass were most affected by an increase in soil water stress from zero to -15 bars. Increasing the soil water stress further to -30 bars caused the Pn rates of western wheatgrass to be reduced to a lesser degree.

The effects of the interaction of soil water potential and temperature on the Pn rates of both blue grama and western wheatgrass clearly illustrated the detrimental effect of soil water stress (Figure 14). The large differences among the Pn rates of the C_3 and C_4 species at all respective levels of soil water potential reflected the greater resistance to water stress exhibited by C_4 species. The relative Pn rates of the two species at each temperature illustrated the different optimum Pn temperatures generally encountered among C_3 and C_4 species.

Interaction Effects of Irradiance and Temperature on Net Photosynthesis of Blue Grama and Western Wheatgrass

The optimum Pn temperature for blue grama at the medium and high levels of irradiance was obviously nearest 30°C (Figure 15). The Pn rates at the low irradiance were essentially unchanged between 20°C and 30°C, indicating the possibility that the optimum Pn temperature for blue grama might be between 20°C and 30°C at low irradiances. The Pn rates at 20°C under both the medium and high irradiances were essentially the same, indicating possible biochemical limitations of Pn for blue grama at the low temperature. The Pn rates decreased sharply at all irradiances with the temperature increase from 30°C to 40°C.

The Pn rates of western wheatgrass at all three levels of irradiance decreased almost linearly with increasing temperature, indicating the optimum temperature to be nearest 20°C (Figure 15). The Pn rates at both the medium and high irradiances and all temperatures were not significantly different, again indicating that western wheatgrass had reached light saturation at or below 1.12 $ly \cdot min^{-1}$.

The effects of both temperature and irradiance on the C_4 species, blue grama, were quite different from the effects of these variables on the C_3 species, western wheatgrass (Figure 15). The overall Pn rates for blue grama were greater than Pn rates for western wheatgrass because blue grama generally exhibited no light saturation.

As previously mentioned, the Pn grand means for blue grama and western wheatgrass were 9.6 and 4.5 mg $CO_2 \cdot dm^{-2}LA \cdot hr^{-1}$, respectively. Therefore, under the conditions of the experiments the Pn rates for western wheatgrass were only about 45 percent of the Pn rates

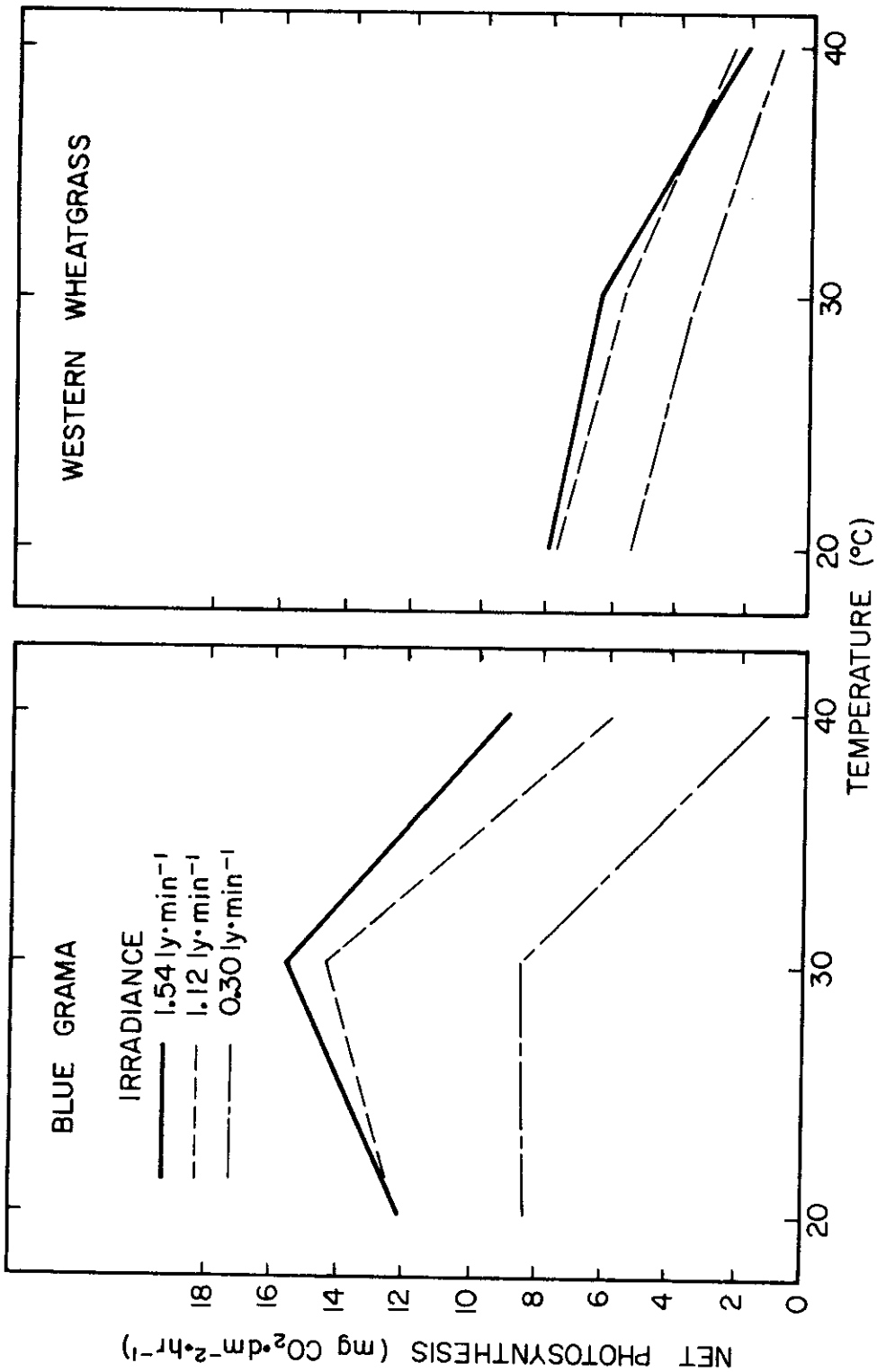

Figure 15. Two-way interaction effects of visible irradiance and temperature on the net photosynthetic rates of blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) as determined in the greenhouse study.

for blue grama. This overall relationship is reflected in each of the interaction comparisons.

It is estimated that the optimum Pn temperature for blue grama under optimum conditions of soil water potential and high irradiance was between 30°C and 36°C. Low irradiances and high soil water stress reduced the optimum Pn temperature to less than 30°C. Experimentation with western wheatgrass indicated its optimum Pn temperature to be less than 20°C.

Aboveground Dark Respiration (AGR)

The analyses of variance of AGR rates in the greenhouse study for both blue grama and western wheatgrass at three levels each of soil water potential and temperature are shown in Appendix A, Table 3. The analyses showed that both of the main treatments of soil water potential and temperature significantly affected ($p < 0.01$) AGR rates of blue grama (Appendix A, Table 3). The main treatments of soil water potential and temperature also significantly affected the AGR rates of western wheatgrass ($p < 0.05$ and $p < 0.01$, respectively)(Appendix A, Table 3). The AGR rate of each species was significantly affected ($p < 0.05$) by the two-way interaction of soil water potential and temperature (Appendix A, Table 3).

Interaction Effects of Soil Water Potential and Temperature on Aboveground Dark Respiration of Blue Grama and Western Wheatgrass

The AGR rates of blue grama generally decreased with increasing soil water stress, and increased with increasing temperature (Figure 16). At all three temperatures, the decrease in the AGR rates were rapid with the increase of soil water stress from zero to -15 bars.

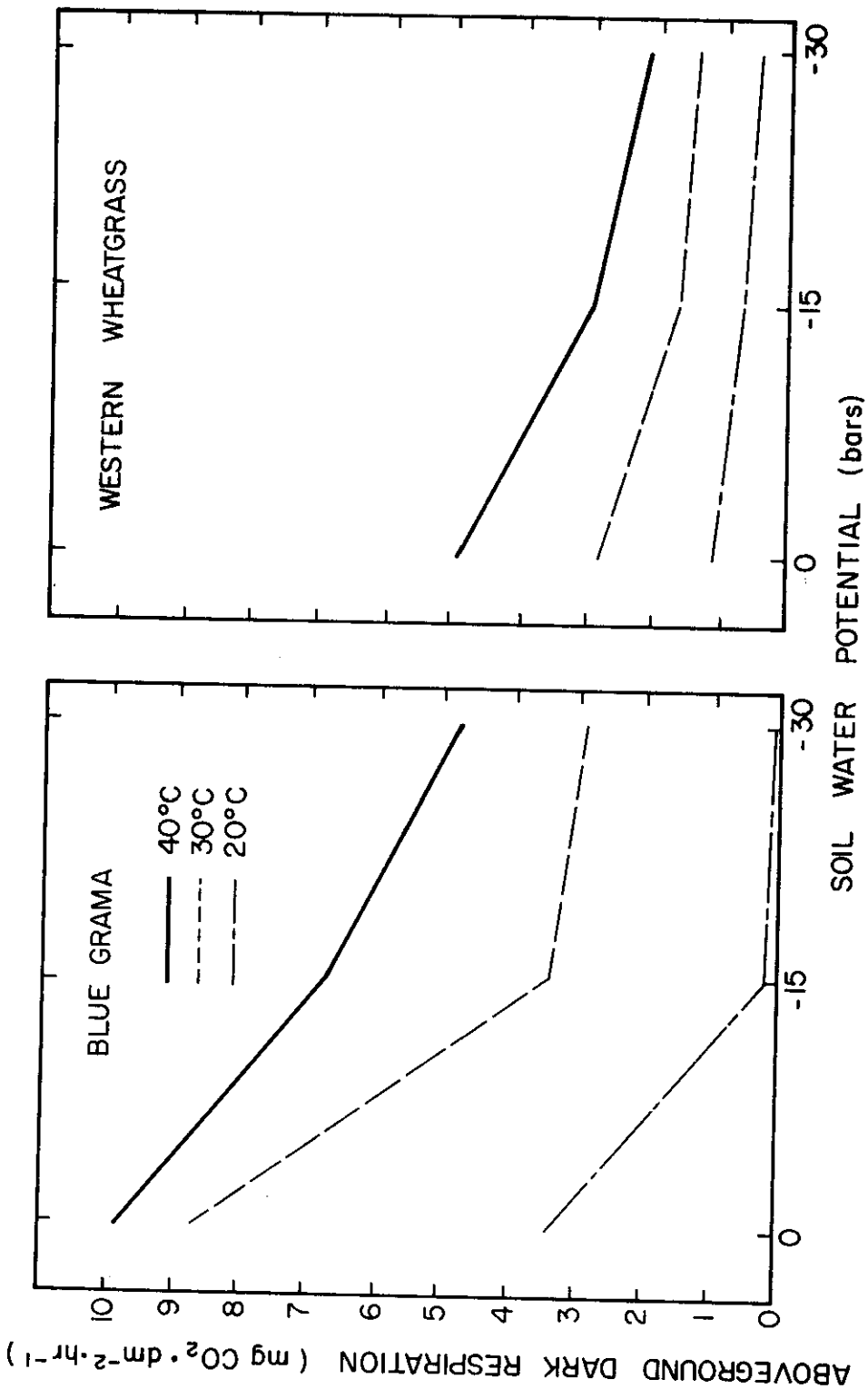

Figure 16. Two-way interaction effects of soil water potential and temperature on the aboveground dark respiration rates of blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) as determined in the greenhouse study.

Further increased water stress to -30 bars resulted in lesser decreases in the AGR rates of blue grama.

The overall response of the AGR rates for the C_3 species, western wheatgrass, to soil water stress and temperature were similar to the responses exhibited by blue grama (Figure 16). Increasing soil water stress and decreasing temperature resulted in decreasing AGR rates of western wheatgrass. The magnitude of the responses to these variables were less for western wheatgrass than for blue grama. In addition, the AGR rates of western wheatgrass were lower than those for blue grama at all soil water potentials at 30°C and 40°C. The AGR rates of western wheatgrass were also less than those of blue grama at zero soil water potential and 20°C. However, the AGR rates of western wheatgrass at 20°C were greater than the AGR rates for blue grama at -15 and -30 bars soil water potential.

The grand means of the AGR rates of blue grama and western wheatgrass were 4.5 and 2.0 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, respectively. Therefore, the AGR rates of western wheatgrass were only about 44 percent of the AGR rates of blue grama at the levels of variables chosen for study.

Hofstra and Hesketh (1969) determined the AGR rate of *Zea Mays*, a C_4 species, to be 3.0 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$. Osmond, Troughton and Goodchild (1969) reported AGR rates of 3.3 and 4.4 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ for *Atriplex spongiosa*, a C_4 species, and *Atriplex hastata*, a C_3 species, respectively. The AGR rate of sunflower, a C_3 species, was determined to be 2.1 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ by Hew, Krotkov and Canvin (1969).

Gross Photosynthesis (Pg)

As stated previously, Pg rates were calculated by combining (adding) Pn and AGR rates for each species. This approach was felt to be valid for the C_4 species, blue grama, but probably invalid for the C_3 species, western wheatgrass. Gross photosynthesis of blue grama is reported here because Pn was impossible to determine directly in the field study and it was important to be able to compare the Pg rates determined in the greenhouse study with the Pg rates determined in the field study for this species. Also, it is interesting to compare the Pg and Pn rates of blue grama in the greenhouse study to illustrate energy losses in the respiration process. The Pg rates of western wheatgrass are reported simply for C_3 - C_4 comparative purposes, realizing that the Pg rates of western wheatgrass should be greater by the amount of undetermined photorespiration occurring in this C_3 species. Because Pg is a combination of Pn and AGR, Pg will not be discussed in great detail for either species.

The analyses of variance of the Pg rates in the greenhouse study for both blue grama and western wheatgrass at three levels each of soil water potential, irradiance, and temperature are shown in Appendix A, Table 4. As with Pn rates, the Pg rates of both species were significantly affected ($p < 0.01$) by all three main treatments of soil water potential, irradiance and temperature. The two-way interaction effects of soil water potential and irradiance, and soil water potential and temperature were also highly significant ($p < 0.01$) for both species (Appendix A, Table 4). However, the irradiance and

temperature interaction did not significantly affect the Pg rates of blue grama and was of lesser significance ($p < 0.10$) for the Pg rates of western wheatgrass (Appendix A, Table 4). The three-way interaction effect of soil water potential, irradiance and temperature was highly significant ($p < 0.01$) for the Pg rates of blue grama, but did not significantly affect the Pg rates of western wheatgrass (Appendix A, Table 4).

Interaction Effects of Soil Water Potential and Irradiance on Gross Photosynthesis of Blue Grama and Western Wheatgrass

The interaction effects of soil water potential and irradiance on the Pg rates of blue grama (Figure 17) were generally similar to the effects of these variables on the Pn rates of blue grama (Figure 13). An exception was noted in that a linear decrease in the Pg rate of blue grama at the low irradiance with increasing soil water stress was found. The interaction effects of soil water potential and irradiance on the Pg rates of western wheatgrass (Figure 17) produced graphic results which were similar in shape to the Pn rates, but of course, of different magnitude (Figure 13). This indicated that the AGR rates of western wheatgrass were affected by the interaction to the same extent as the Pn rates throughout the various levels of the variables.

The grand means of the Pg rates of blue grama and western wheatgrass were 14.1 and 6.5 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, respectively. Therefore, the overall Pg rates for western wheatgrass were only about 46 percent of the Pg rates for blue grama, which of course compares favorably with the combined AGR and Pn relationships between the species.

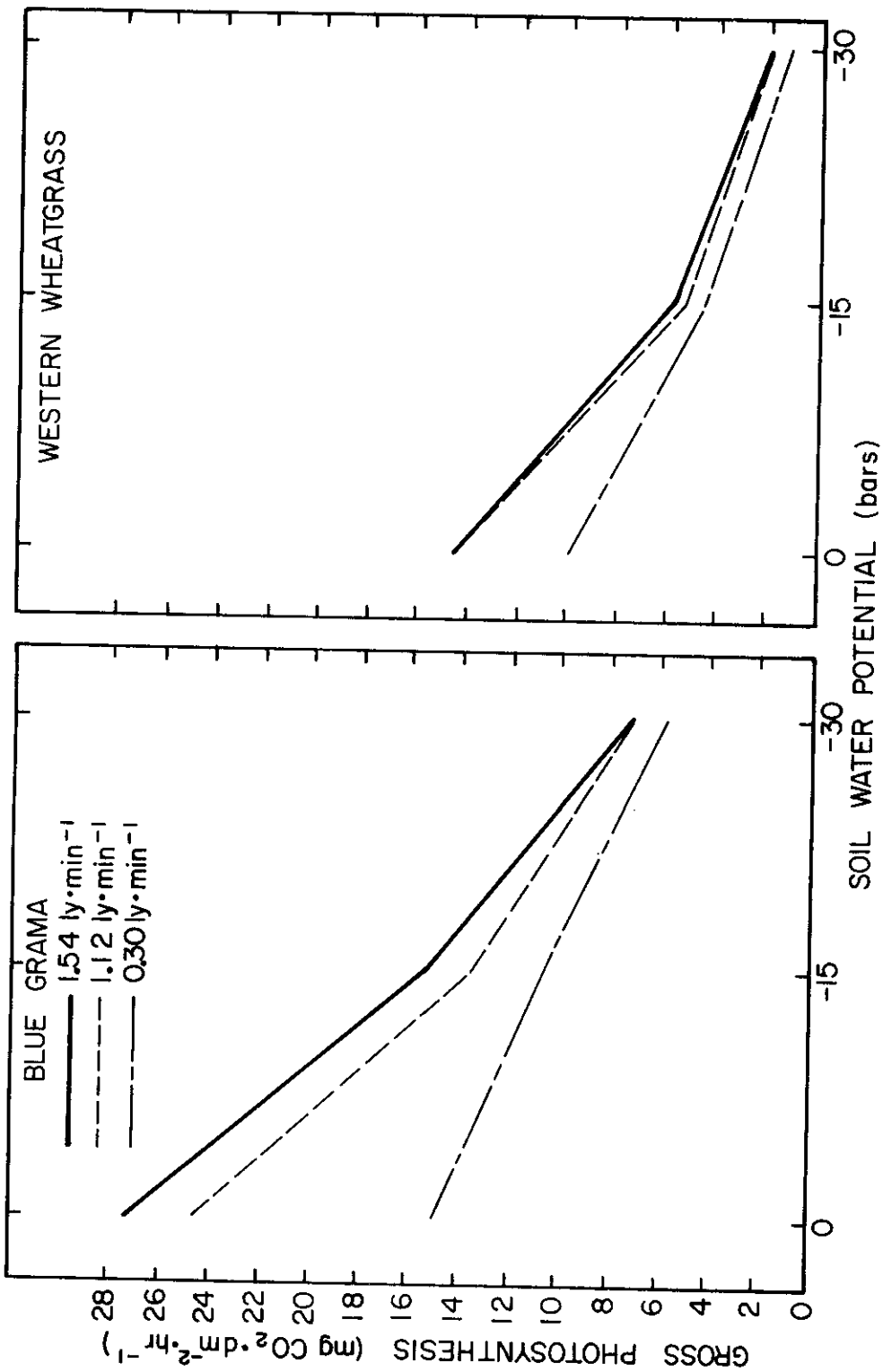

Figure 17. Two-way interaction effects of soil water potential and temperature on the gross photosynthetic rates of blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) as determined in the greenhouse study.

It is suspected that the actual Pg rates of western wheatgrass (inclusive of photorespiration) would in fact be much closer to the Pg rates determined for blue grama.

Interaction Effects of Soil Water Potential and Temperature on Gross Photosynthesis of Blue Grama and Western Wheatgrass

The Pg rates of blue grama (Figure 18) declined much the same as the Pn rates (Figure 14) with increasing soil water stress, but there was a change in the rates with respect to the various levels of temperature. The Pg rates of blue grama at 30°C were greatest at all levels of soil water stress. The Pg rates at 40°C were greater than the rates at 20°C at zero bars soil water potential. These changes in Pg rates of blue grama were all attributable to the significant effect ($p < 0.01$) of temperature on AGR rates of blue grama (Appendix A, Table 3).

Once again, the graphic representations of the Pg rates of western wheatgrass as affected by soil water potential and temperature (Figure 18) are nearly identical to the shapes of the curves representing Pn rates for this species as affected by the interaction (Figure 14). Any shifts in the estimated Pg rates are also attributable to the significant effect ($p < 0.01$) of temperature on the AGR rates of western wheatgrass (Appendix A, Table 3).

The Pg rates of blue grama were more sensitive to increasing soil water stress than the Pg rates of western wheatgrass. This is indicated by the relative slopes of the curves (Figure 18). However, this observation could be misleading because the Pg rates for blue grama remained greater than the Pg rates for western wheatgrass at all comparable levels of soil water potential and temperature.

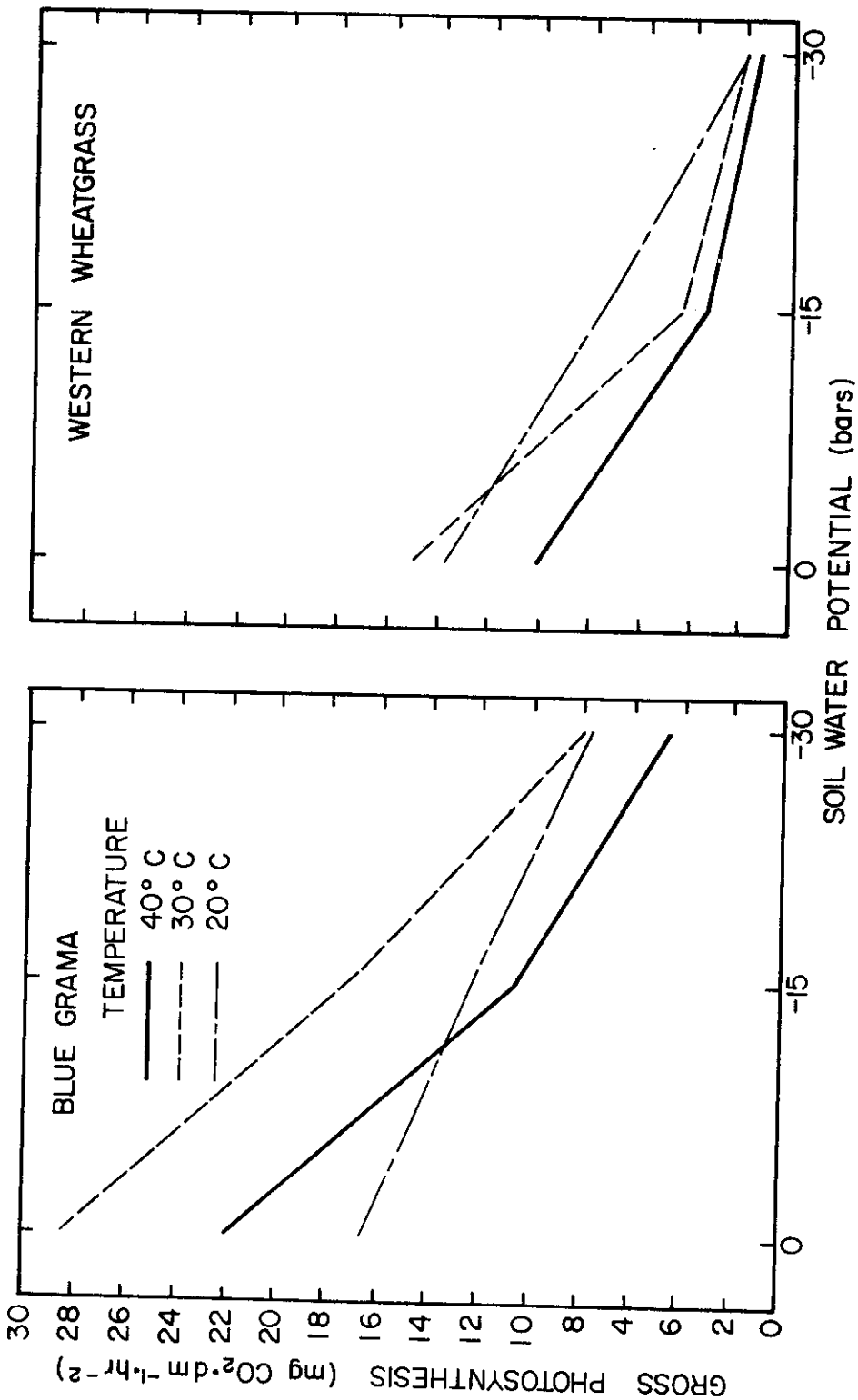

Figure 18. Two-way interaction effects of soil water potential and temperature on the gross photosynthetic rates of blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) as determined in the greenhouse study.

Interaction Effects of Visible Irradiance and Temperature on Gross Photosynthesis of Blue Grama and Western Wheatgrass

The two-way interaction effects of irradiance and temperature did not significantly affect the Pg rates of blue grama and only slightly affected ($p < 0.10$) the Pg rates of western wheatgrass (Appendix A, Table 4). Therefore, the effects will not be discussed, but are shown in graphic form in Figure 19 for the benefit of the reader.

The Field Study

Steady State Determinations

All steady state CO_2 exchange rates determined for in situ blue grama sods in the field were calculated in units of leaf area (LA) and ground area (GA), but will be discussed only in units of mg $CO_2 \cdot dm^{-2} LA \cdot hr^{-1}$. The approach to CO_2 exchange rate determinations in the field was unique in that an entire 0.29 m^2, in situ sod of blue grama grass was taken into consideration. Statistical analysis performed on the determinations provided similar relationships whether calculated in terms of GA or LA.

All field steady state CO_2 exchange rate determinations for blue grama for the various conditions of phenology, soil water potential, visible irradiance and temperature encountered throughout the 1972 growing season at the Pawnee Site are reported in Table 5 of Appendix A. The four-way interaction means and standard errors of the steady state Pg and calculated Pn determinations for in situ blue grama sods as influenced by phenology, soil water potential, irradiance and temperature throughout the growing season are reported

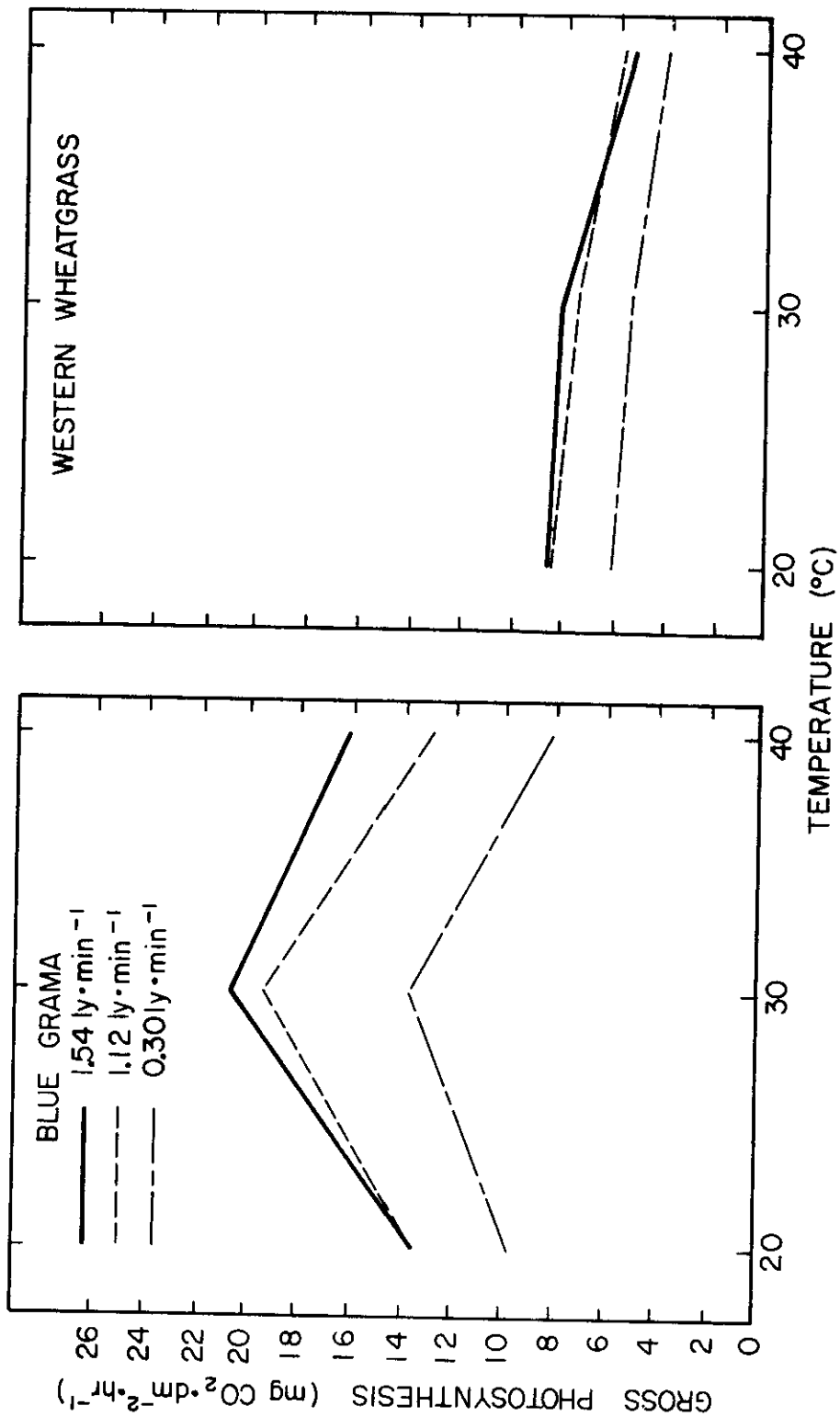

Figure 19. Two-way interaction effects of visible irradiance and temperature on the gross photosynthetic rates of blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) as determined in the greenhouse study.

in Appendix A, Table 6. The photosynthetic and respiratory rates reported (Appendix A, Table 5) in units of LA can be transformed to GA (m^2) by the following equation:

$$\text{mg } CO_2 \cdot m^{-2}GA \cdot hr^{-1} = (\text{mg } CO_2 \cdot dm^{-2}LA \cdot hr^{-1})(LAI \times 100),$$

where: LAI is the leaf area index.

Some measurements were also taken on clipped sods and are reported in Appendix A, Table 5, in units of mg $CO_2 \cdot m^{-2}GA \cdot hr^{-1}$.

Analyses of covariance of Pn and Pg rates of blue grama as affected by four levels each of irradiance and temperature, three levels of soil water potential, and two levels of phenology as the covariate are given in Appendix A, Table 7. All three of the main variables and the covariate were highly significant ($p < 0.01$) for both Pn and Pg rates except for the effect of temperature on Pg which was significant at the 0.05 level of probability (Appendix A, Table 7). As in the greenhouse study, the two-way interaction effect of soil water potential and temperature was highly significant ($p < 0.01$) on both Pn and Pg rates of blue grama (Appendix A, Table 7). Unlike the results of the greenhouse study, the interaction of soil water potential and irradiance did not significantly affect the Pn and Pg rates of blue grama in the field. The effect of the irradiance and temperature interaction on Pn and Pg rates of blue grama in the field study were similar to the effects of that interaction on blue grama in the greenhouse study. That is, there was no significant effect on Pg and a slightly significant ($p < 0.10$) effect on Pn rates caused by the interaction (Appendix A, Table 7).

Interaction Effects of Soil Water Potential and Temperature on Calculated Net Photosynthesis of Blue Grama

The two-way interaction effects of soil water potential and temperature on the Pn rates of blue grama are graphically illustrated in Figure 20. Increasing soil water stress produced nearly the same linear decreases in the Pn rates of blue grama in the field that were evident in the greenhouse study. A somewhat similar optimum Pn temperature range was also evident for blue grama when subjected to different soil water stresses. The optimum temperature range decreased with increasing soil water stress. Low soil water stress again resulted in optimum Pn temperatures near 30°C.

Interaction Effects of Irradiance and Temperature on Calculated Net Photosynthesis of Blue Grama

The two-way interaction effects of irradiance and temperature on the calculated Pn rates of blue grama in the field are illustrated in Figure 21. It was impossible to maintain a temperature in the 15.0°C-22.5°C range under high irradiance conditions, but the other data again illustrated a near 30°C optimum Pn temperature. Blue grama exhibited no light saturation.

Continuous 24-Hour Ambient Simulations

One 24-hour ambient simulation experiment was conducted each month on a different blue grama sod throughout four months of the 1972 growing season. The first experiment was conducted during June 28-29, 1972, and is illustrated in Figure 22. The figure clearly shows the combined effects of temperature and irradiance on the photosynthetic rates of blue grama. The effect of temperature on the aboveground dark respiration rate is also evident. Both Pn and Pg

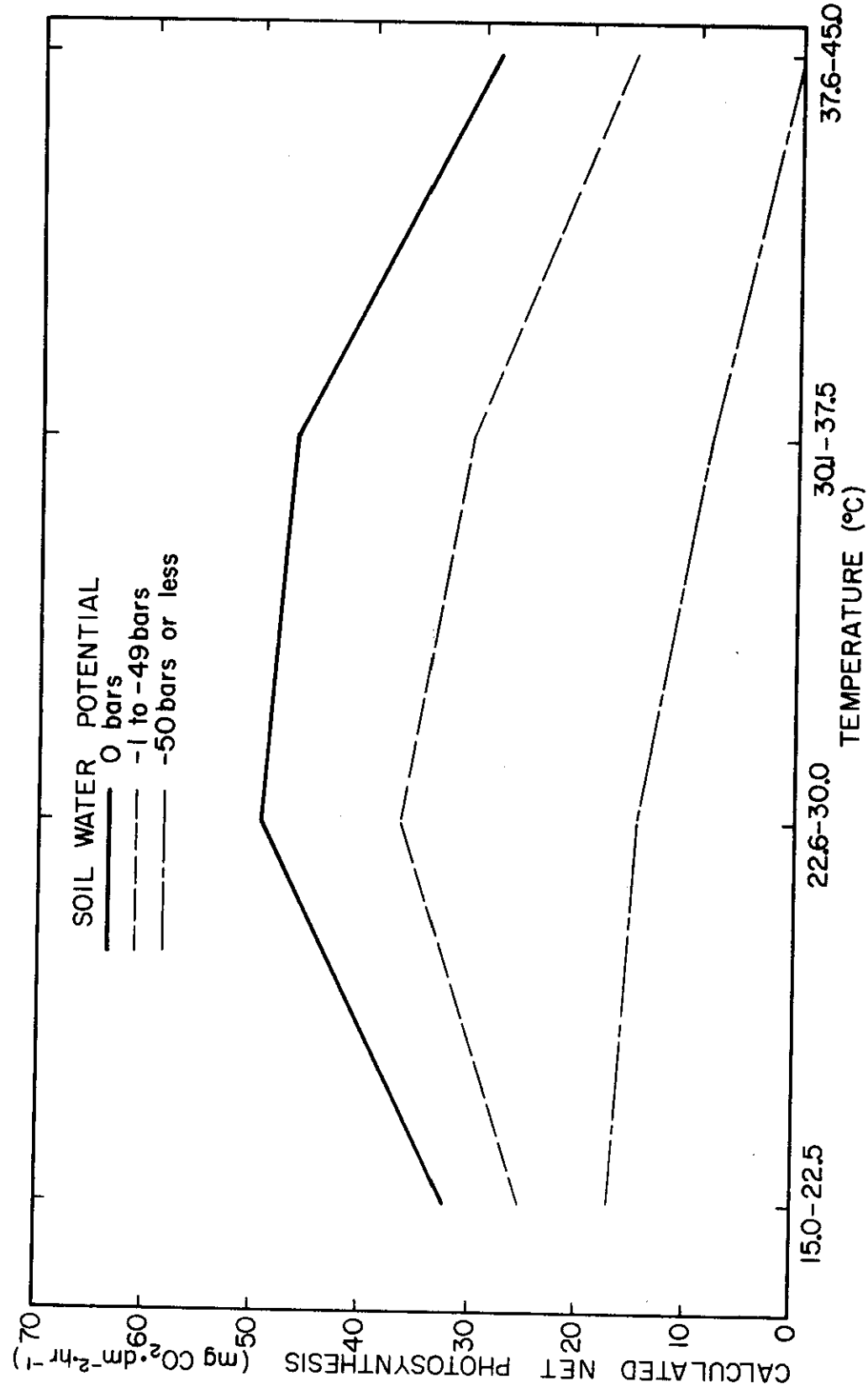

Figure 20. Two-way interaction effects of soil water potential and temperature on the net photosynthetic rate of blue grama (*Bouteloua gracilis*) as determined in the field study.

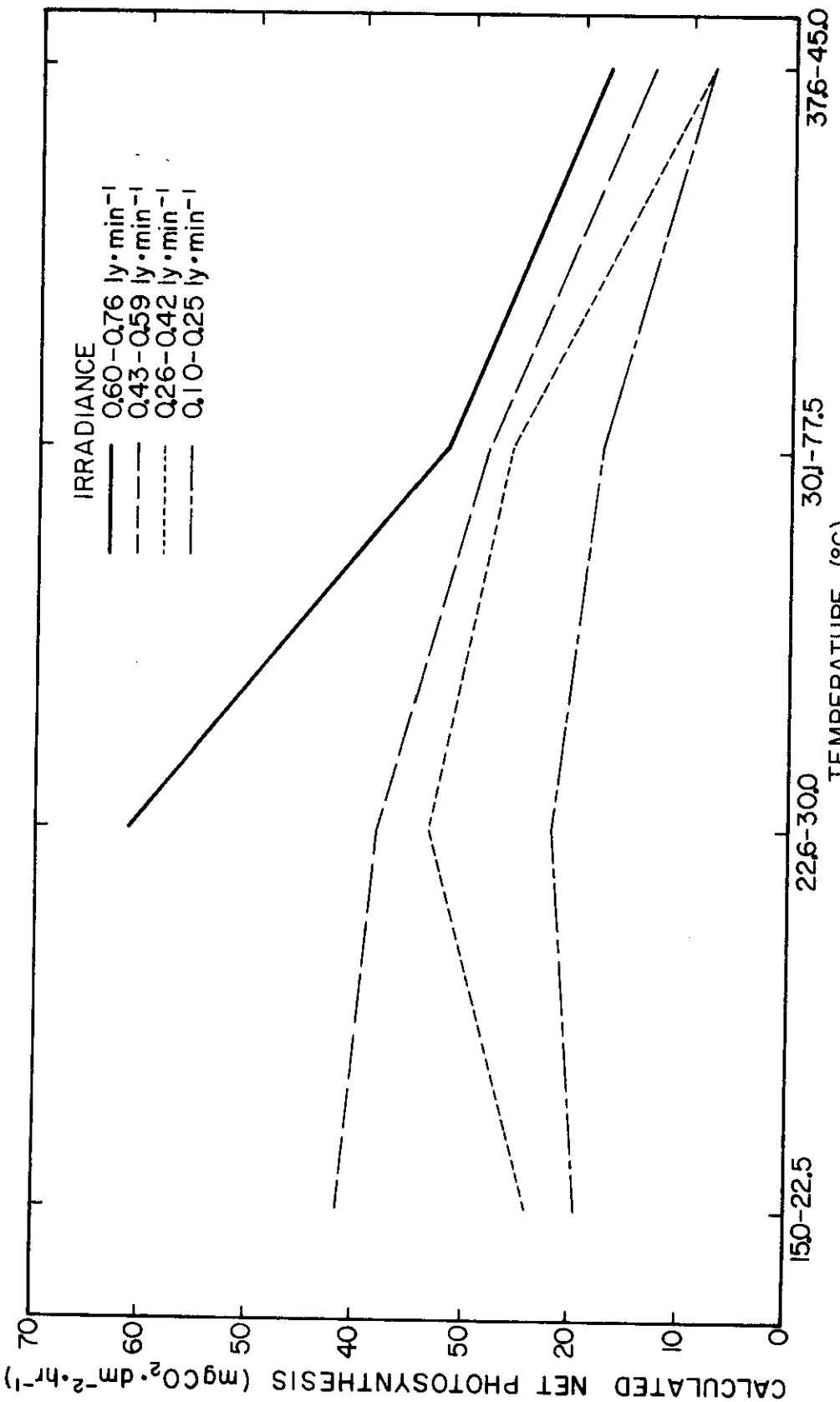

Figure 21. Two-way interaction effects of visible irradiance and temperature on the net photosynthetic rate of blue grama (*Bouteloua gracilis*) as determined in the field study.

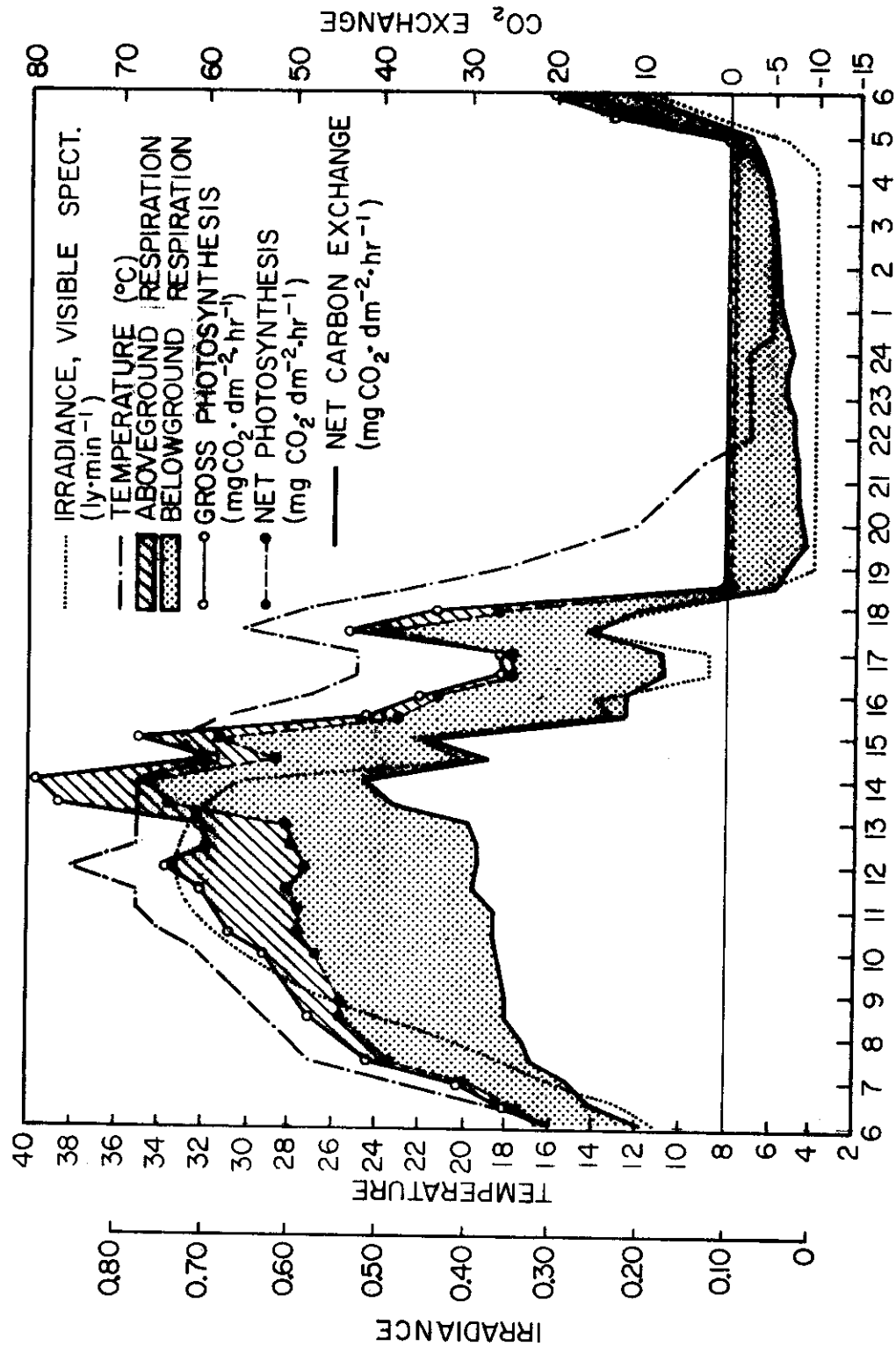

Figure 22. June 28-29, 1972, ambient track simulation for an in situ blue grama (*Bouteloua gracilis*) sod with an LAI of 0.39, vegetative phenological stage, and soil water potential of -8 bars decreasing to -14 bars at 10 cm depth.

rates increased from 06:00 Mountain Standard Time (MST) with increasing irradiance and temperature until temperature began to significantly increase AGR about 08:00 MST. The Pg rates continued to increase with increasing irradiance and temperature, but Pn rates began to level out. At 12:00 MST the sharp increase in temperature from 35°C to 38°C resulted in an increase in Pg, but a decrease in Pn rates because of the effect of greater AGR rates at the higher temperatures. At about 13:00 MST there was a sharp increase in both Pn and Pg rates because of a decrease in the temperature and continuing high irradiance. At 14:00 MST afternoon cloudiness increased which resulted in decreases in Pn, Pg and AGR rates. As visible irradiance approached zero at about 18:30 MST, Pn became negative because of the relationship of Pn with Pg and AGR rates (Pn = Pg - AGR). The AGR continued at a fairly constant rate through the nighttime hours.

The net carbon dioxide exchange (NCE) rates closely followed the photosynthetic rates throughout the 24-hour period, while below-ground respiration rates (BGR) were primarily dependent upon temperature (Figure 22). There was no way to ascertain root respiration from the CO_2 exchange measurements; therefore, net primary productivity of the continuous 24-hour ambient simulations could not be calculated.

Although all CO_2 exchange rates represented in Figure 22 through 25 are in terms of mg $CO_2 \cdot dm^{-2}LA \cdot hr^{-1}$, the curves were integrated in terms of g $CH_2O \cdot m^{-2}GA \cdot day^{-1}$. The Pg, Pn, and AGR daily values for June 28-29 were 16.4, 14.3, and 2.1 g $CH_2O \cdot m^{-2}GA \cdot day^{-1}$,

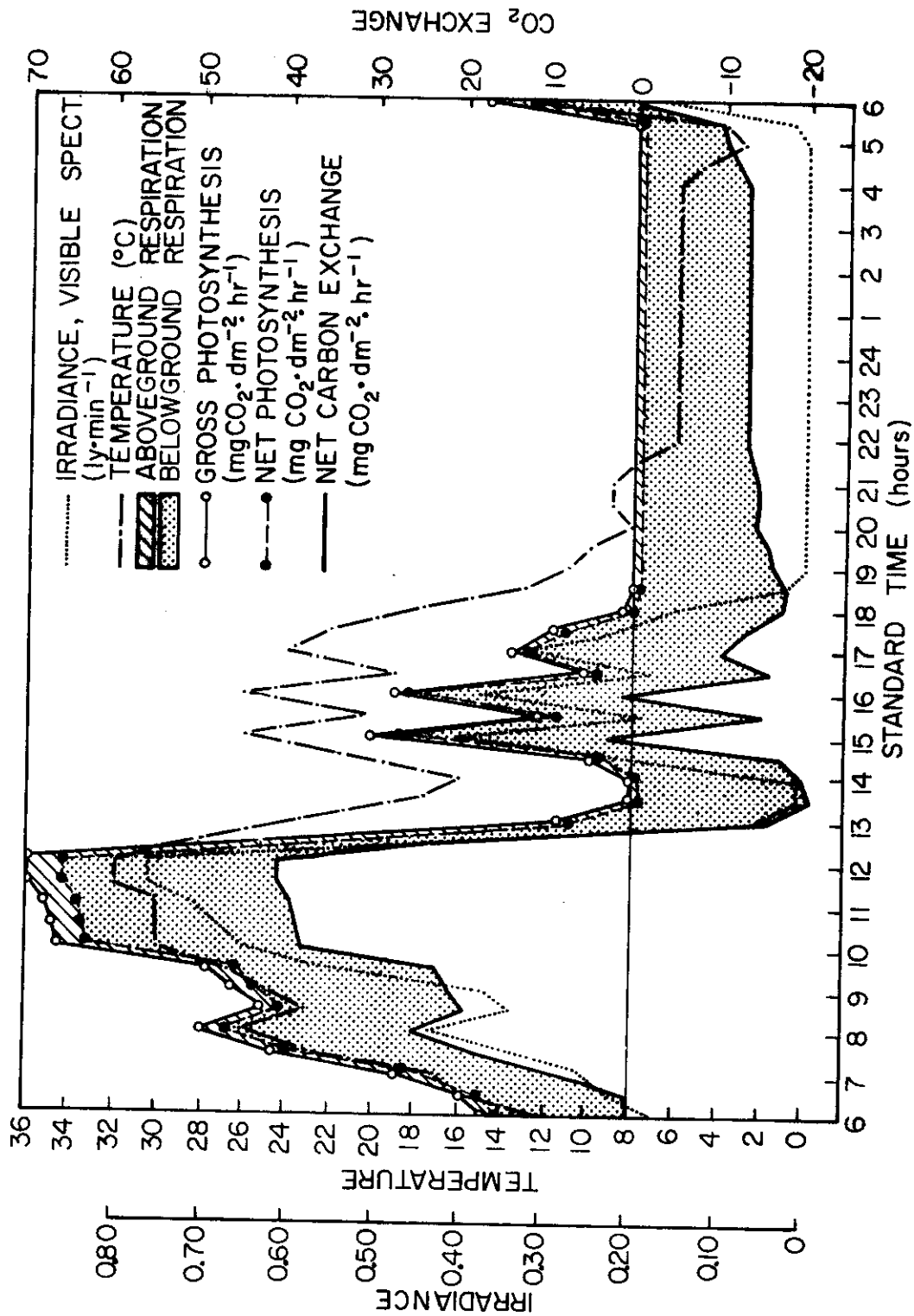

Figure 23. July 6-7, 1972, ambient track simulation for an in situ blue grama (*Bouteloua gracilis*) sod with an LAI of 0.43, vegetative phenological stage, and soil water potential of zero bars at 10 cm depth.

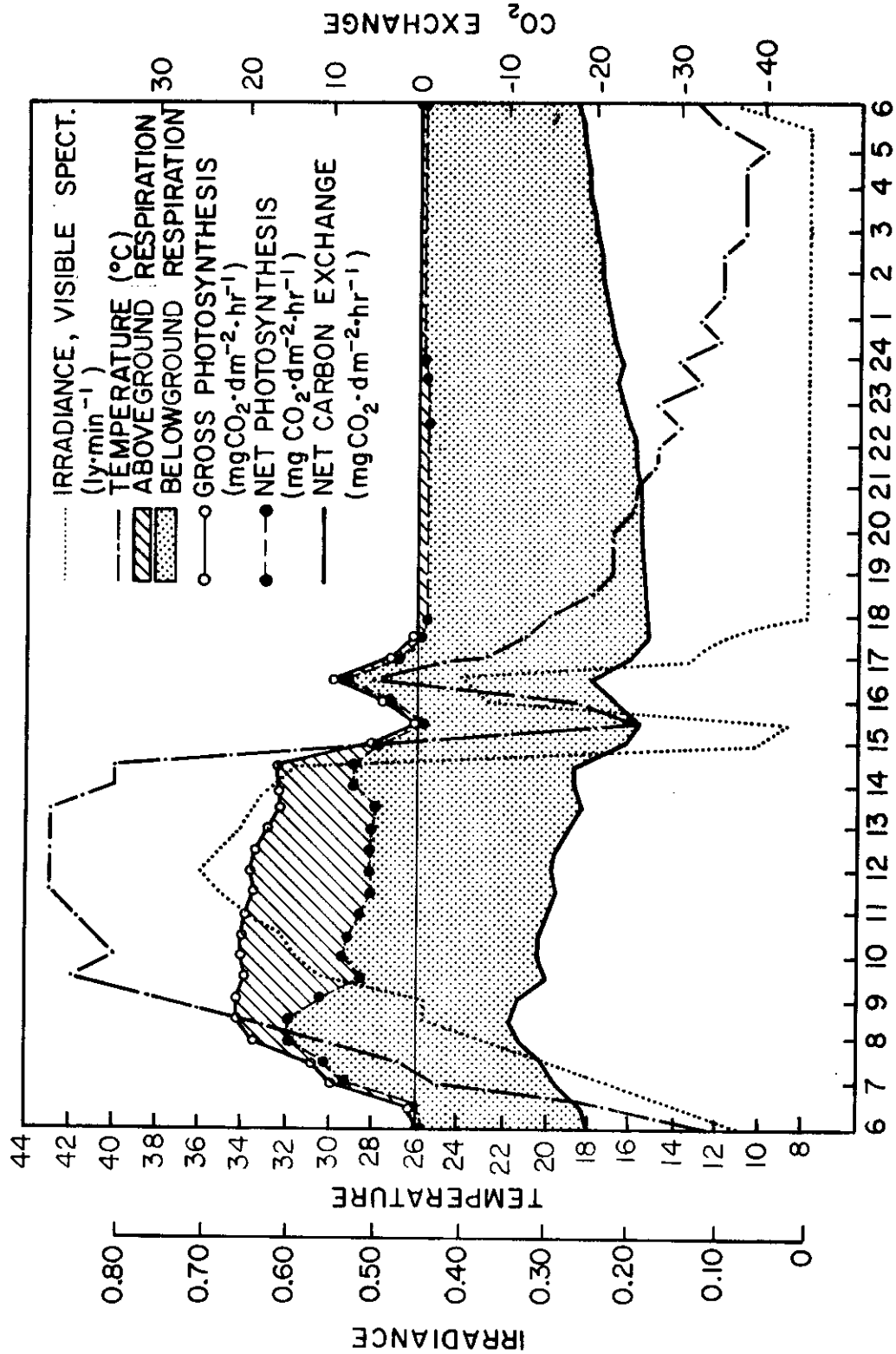

Figure 24. August 11-12, 1972 ambient track simulation for an in situ blue grama (*Bouteloua gracilis*) sod with LAI of 0.36, reproductive phenological stage, and soil water potential of -21 bars decreasing to -32 bars at 10 cm depth.

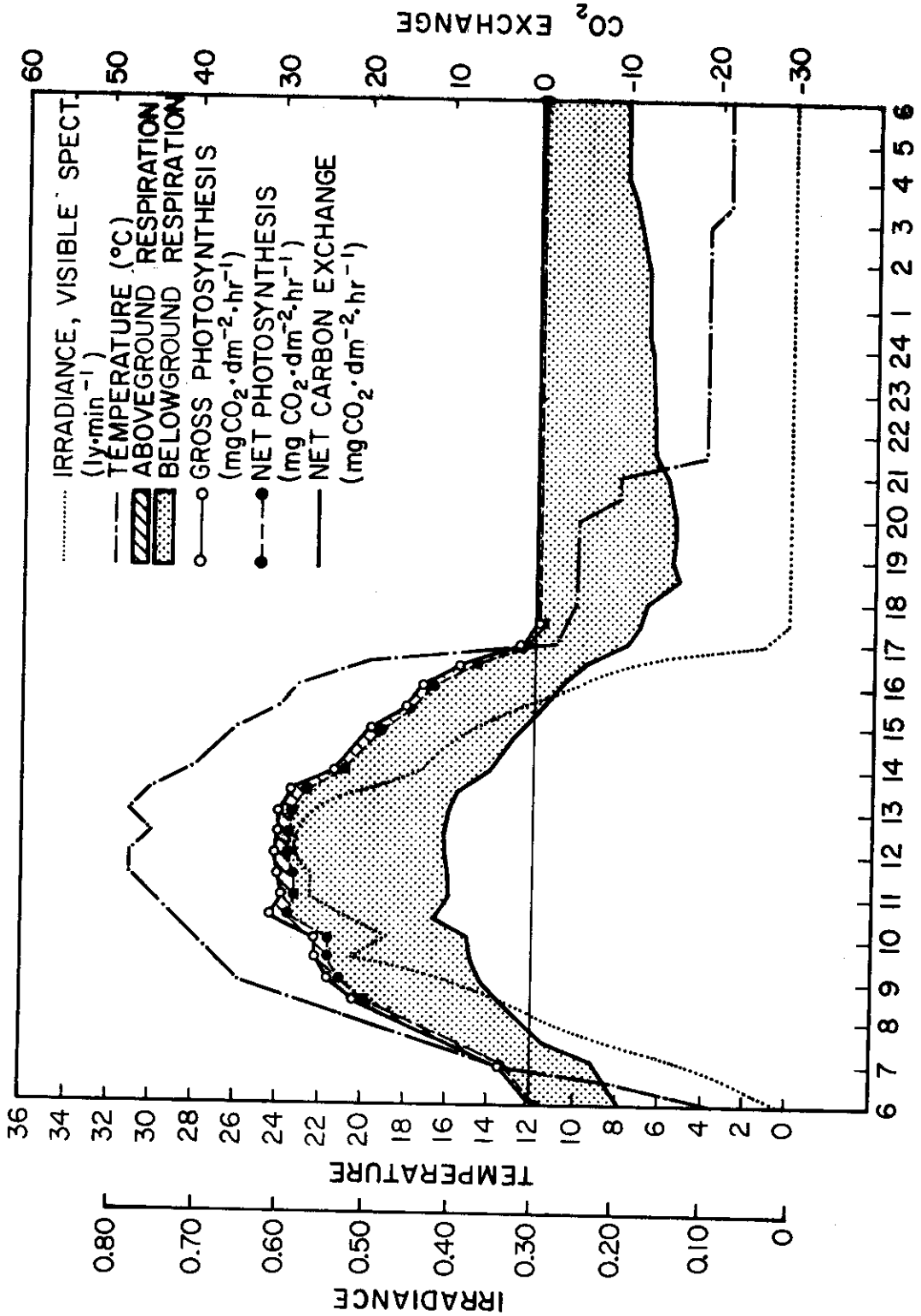

Figure 25. September 22-23, 1972, ambient track simulation for an in situ blue grama (*Bouteloua gracilis*) sod with LAI of 0.40, vegetative phenological stage, and soil water potential of zero bars at 10 cm depth.

respectively. All continuous 24-hour ambient simulation values are reported in Appendix A, Table 8, along with aboveground biomass determinations and productivity calculations from the computer model of seasonal blue grama productivity (to be discussed later).

Figure 23 illustrates the 24-hour ambient simulation during July 6-7, 1972. The effect of afternoon cloudiness is apparent. The irradiance dropped so low at about 13:30 MST that Pn was actually slightly negative for a short time during this potentially productive day. The integrated values of Pg, Pn and AGR were 11.6, 10.8, and 0.8 g $CH_2O \cdot m^{-2} GA \cdot day^{-1}$, respectively (Appendix A, Table 8).

The continuous 24-hour ambient simulation of August 11-12, 1972, is shown in Figure 24. This was a generally hazy day with typical afternoon cloudiness. The day was almost totally unproductive because of the high temperatures, high soil water stress and a reproductive stage of phenology. The integrated values of Pg, Pn and AGR were 3.9, 1.7, and 2.2 g $CH_2O \cdot m^{-2} GA \cdot day^{-1}$, respectively (Appendix A, Table 8). The BGR was greater throughout the day in relation to the other 24-hour simulations. The large BGR rates were believed to have been caused by near ideal conditions for microbial activity throughout the soil profile. The soil water potential at the 10-cm depth decreased from -12 to -32 bars during the 24-hour period. This indicated fast drying at that depth, although previous records for soil water showed ideal conditions throughout the profile two or three days earlier. This would indicate a probable soil water potential of zero at the 20-cm depth and lower, providing conditions which were neither too dry nor too wet for microbial activity.

Inspection of the calculated and measured BGR rates in Appendix A, Table 5, showed wide variation in BGR rates with respect to temperature, time of day, and soil water potential at the 10-cm depth.

The continuous 24-hour ambient simulation for September 22-23, 1972, is illustrated in Figure 25. The results of this late season simulation were quite different from the three previous simulations. It was a relatively cloud-free day, but the visible irradiance reached a high of only about 0.57 $ly \cdot min^{-1}$ and the daylight lasted only about ten and one-half hours. The soil water potential was zero, the phenological stage was vegetative (because of fall regrowth), and the temperatures were generally ideal. Productivity was, however, relatively low becasue of the low irradiances and shortened day length. The integrated values of Pg, Pn, and AGR were 6.1, 5.6, and 0.5 g $CH_2O \cdot m^{-2}GA \cdot day^{-1}$, respectively.

Efficiency of Energy Capture for the 24-Hour Ambient Simulations

There are many ways of calculating the efficiency of the capture of solar energy by green plants. It would be best to be able to calculate total efficiency of net primary production, but this is impossible to do for the 24-hour ambient simulations because of the lack of root respiration data. Therefore, the percent efficiency of Pg and Pn of visible irradiance was calculated using 4000 $cal \cdot g^{-1}$ as the calorie content of blue grama foliage taken from Sims and Singh (1971).

The total visible irradiance received during the June 28-29 ambient simulation was 3.33×10^6 $cal \cdot m^{-2}GA$. Utilizing this value, and the integrated values of Pg and Pn for June 28-29, the calculated

efficiency of Pg and Pn was 1.97 and 1.72 percent, respectively. (The percent efficiency based on total incoming radiation would be approximately 55 percent less than the above.)

Similar calculations for the percent efficiency for the other 24-hour periods during the 1972 growing season provided the following values: July 6-7, Pg = 1.70 and Pn = 1.58 percent; August 11-12, Pg = 0.56 and Pn = 0.24 percent; September 22-23, Pg = 0.99 and Pn = 0.91 percent. Thus, as would be expected, the lowest energy conversion efficiencies occurred during the relatively high water stress conditions of August 11-12.

These values compare favorably with a total net primary production efficiency of 0.57 percent for an entire season on an ungrazed pasture at the Pawnee Site reported by Sims and Singh (1971). They also compare favorably with 1-2 percent efficiency of total visible energy reported by Salisbury and Ross (1969) for many crops, forest trees and herbaceous species.

Comparison of Gross and Net Photosynthetic Rates of Blue Grama in the Field Study

The singular effects of the three variables of soil water potential, irradiance and temperature on the Pg and Pn rates of blue grama as determined in the field study are depicted in Figures 26 through 28. All values reported in the main effects graphs (Figures 26, 27, and 28) of photosynthetic rates for blue grama were averaged over all levels of the other three variables. The graphs illustrate the same overall effects of each of the variables on the photosynthetic rates of blue grama that were reported earlier. Values in Figure 9

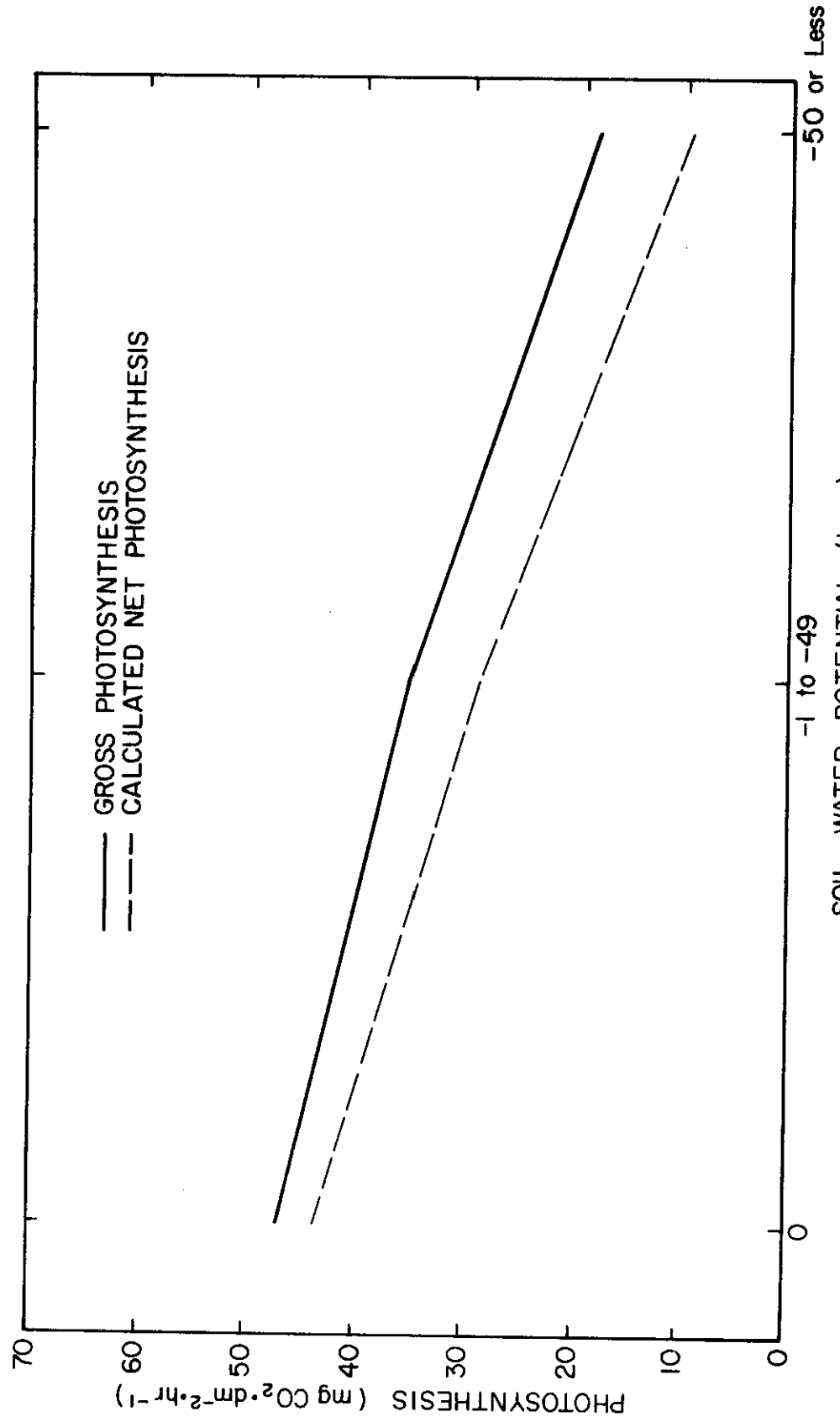

Figure 26. The effect of soil water potential at 10 cm depth on the gross and net photosynthetic rates for in situ blue grama (*Bouteloua gracilis*) as determined in the field study.

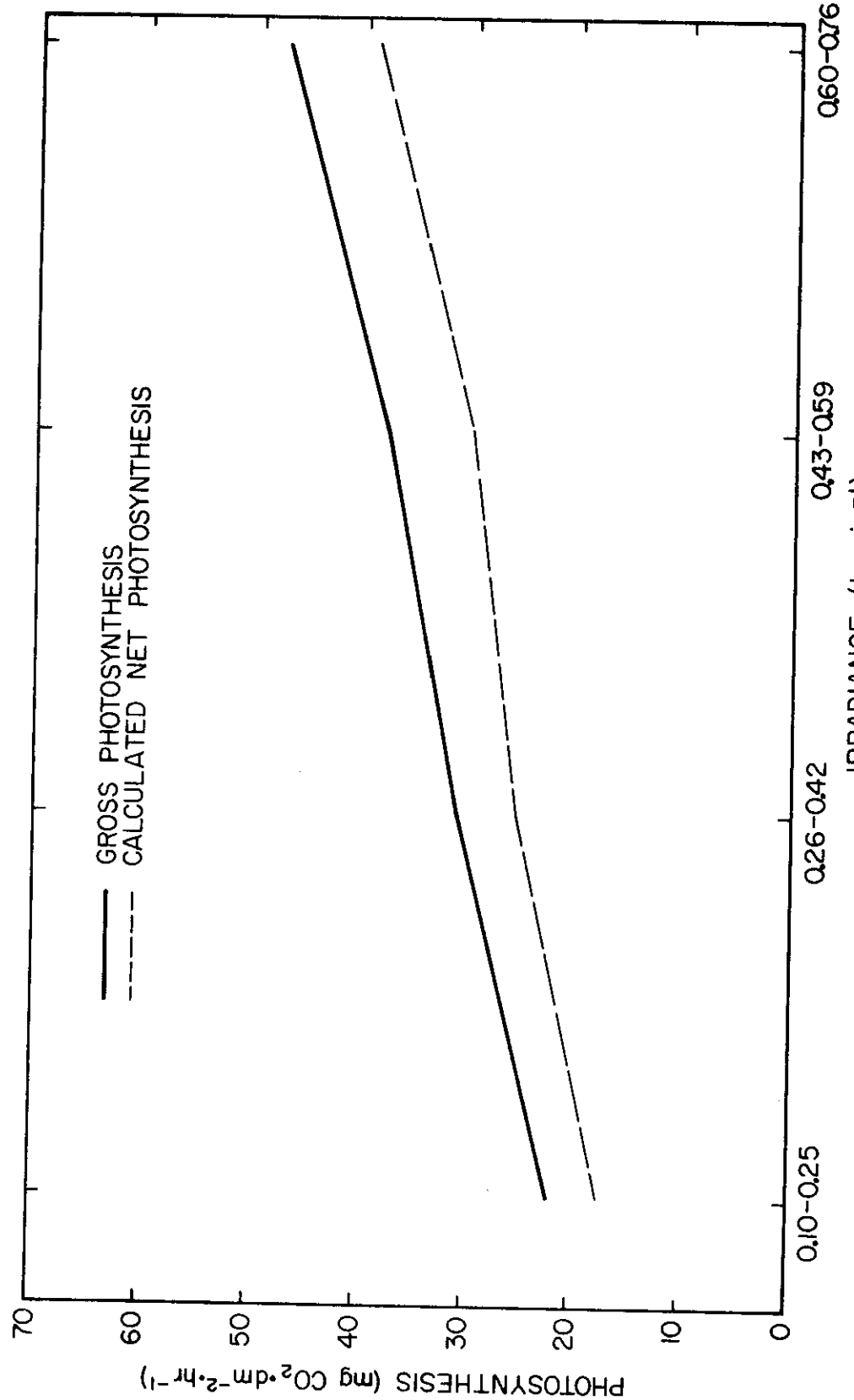

Figure 27. The effect of visible irradiance on the gross and net photosynthetic rates for in situ blue grama (*Bouteloua gracilis*) as determined in the field study.

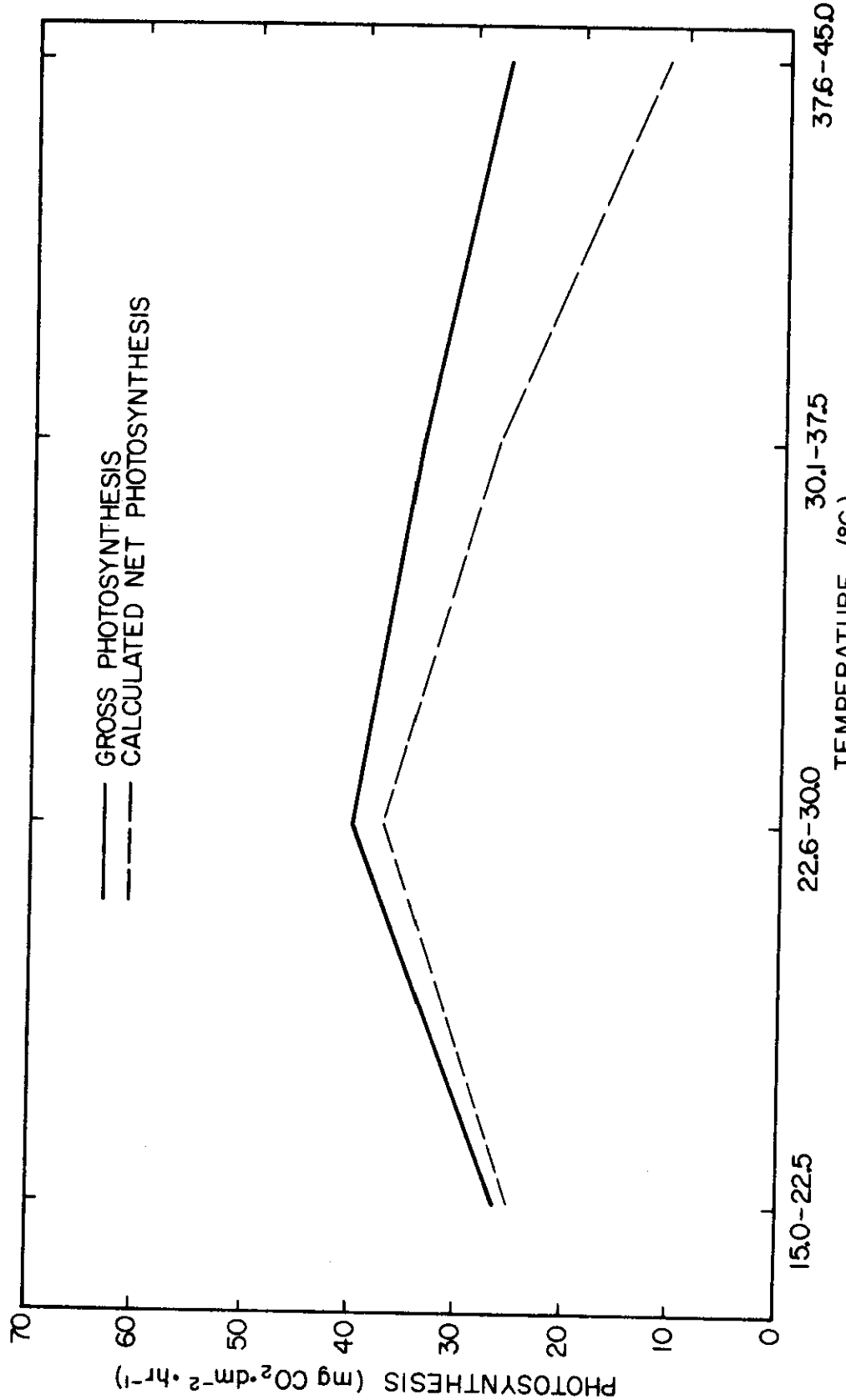

Figure 28. The effect of temperature on the gross and net photosynthetic rates for in situ blue grama (*Bouteloua gracilis*) as determined in the field study.

were used to determine the relationship between Pg and Pn. Because Figure 9 was derived from measurements made in both the greenhouse and field studies, Pn rates for the field study are termed calculated net photosynthesis.

The effects of soil water potential and irradiance on the photosynthetic rates of blue grama showed an essentially constant relationship between Pg and Pn in absolute values (Figures 26 and 27). Concurrently, the percentage of Pg accounted for by Pn decreased with increasing soil water stress but remained fairly constant with increasing irradiance. Figure 28 shows the significant divergence of the Pn rates in relation to the Pg rates with increasing temperatures as would be expected from Figure 9.

The effects of phenological stage on the photosynthetic rates of blue grama are not illustrated because the variable was reduced to only two levels. This produced two parallel straight lines, Pg and Pn, with a constant absolute difference of about 6.0 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$. Mean Pg and Pn rates were 46.0 and 40.0 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, respectively, at a vegetative stage of phenology and 22.5 and 16.5 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, respectively, at a reproductive stage of phenology. Thus, the percentage of Pg accounted for by Pn was much less for the reproductive phenological stage. Although it was not possible to test the statistical significance of the interactions of soil water potential, temperature, and irradiance with phenology, Figures 29 and 30 illustrate the probable significant interactions of temperature and irradiance with phenology on the Pn rates of blue grama.

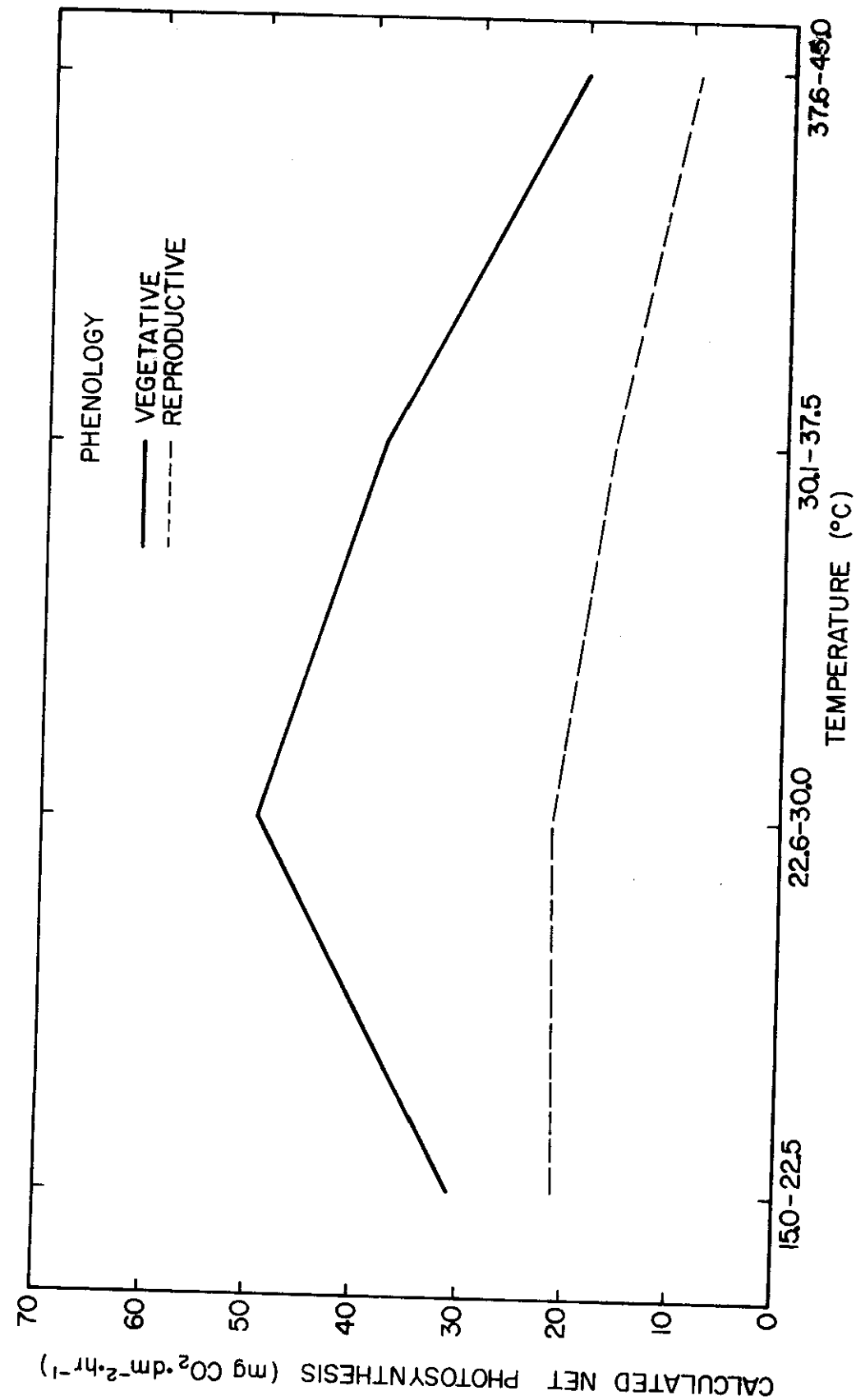

Figure 29. Two-way interaction effects of temperature and phenology on the net photosynthetic rate for in situ blue grama (*Bouteloua gracilis*) as determined in the field study.

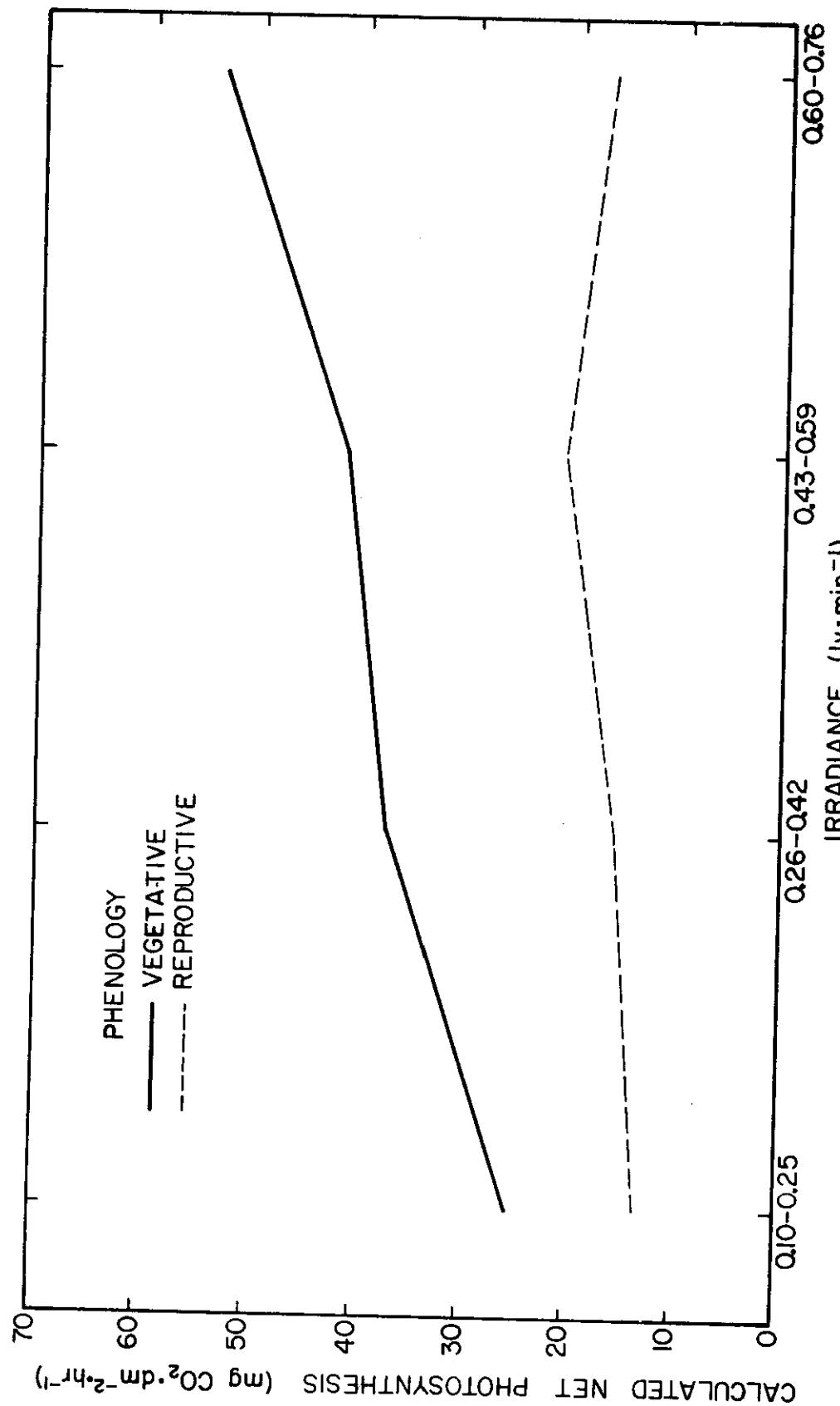

Figure 30. Two-way interaction effects of visible irradiance and phenology on the net photosynthetic rates for in situ blue grama (*Bouteloua gracilis*) as determined in the field study.

Comparison of Photosynthetic Rates for Blue Grama from Both the Greenhouse and the Field Studies

Photosynthetic rates for in situ blue grama sods at Pawnee Site were greater than the comparable rates determined for the potted sods of blue grama grown in the greenhouse. Photosynthetic rate determinations for 26 species of *Gossypium* made by El-Sharkawy, Hesketh and Muramoto (1965) also showed that plants grown in the growth chamber or greenhouse did not photosynthesize as rapidly as those in the field. An overall comparison of the Pn and Pg rates determined in the present studies could not be made because of the different ranges for each of the variables considered in the greenhouse and field studies. Therefore, a strict comparison between rates at comparable levels of each variable of soil water potential, irradiance, temperature and phenology was necessary (Appendix A, Tables 1 and 6). This type of comparison indicated that the Pn and Pg rates of blue grama determined in the greenhouse study were approximately 65 percent of the comparable rates determined in the field study.

The maximum mean Pn rates determined for blue grama in the greenhouse and field studies were 24.3 and 65.3 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, respectively (Appendix A, Tables 1 and 6). These two values are not directly comparable because they reflect Pn rates of blue grama at a reproductive phenological stage in the greenhouse and a vegetative stage in the field. Dye (1972) reported a maximum Pn rate for blue grama of 48 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$. Heichel and Musgrave (1969) reported Pn rates of 15 inbreds and hybreds of *Zea maize*, a C_4 species, ranged from 28 to 85 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$. Murata and Iyama (1963) reported

Pn rates of Bermuda grass (*Cynodon dactylon*), also a C_4 species, ranged from 35 to 43 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$.

Regression Analyses for Both the Field and Greenhouse Study Steady State Experiments

Several stepwise linear multiple regression analyses were performed on all steady state experiments for both the field and the greenhouse studies. The regression equations for the field steady state blue grama Pg and Pn rates in terms of LA and GA are presented in Appendix A, Table 9. The regression equations developed from the greenhouse study of Pn, Pg and AGR rates in terms of LA for both blue grama and western wheatgrass are presented in Appendix A, Table 10.

The multiple regression equations developed are essentially biologically uninterpretable, but are reported because of their value in the determination of the more important variables affecting the CO_2 exchange rates of the species studied. Regression equations were also helpful in determining the amount of variation in the dependent variable (Pn, Pg, or AGR) which could be accounted for by the independent variables (multiple r^2). The equations also allowed further comparison within and between species.

Soil water potential was the most important independent variable affecting the Pn rates of blue grama in the field study, while phenology was most important for the Pg rates (Appendix A, Table 9). The independent variables generally accounted for more of the variability in Pn rates of blue grama in the field than the Pg rates (Appendix A, Table 9). Also, more of the variability in both Pn and

Pg rates was accounted for by the independent variables when based on LA than when based on GA (Appendix A, Table 9).

Soil water potential was the most important independent variable affecting both Pn and Pg rates of both blue grama and western wheatgrass in the greenhouse study. The independent variable of temperature most affected the AGR rates of blue grama while soil water potential was most important in affecting the AGR rates of western wheatgrass.

Primary Productivity Model for Blue Grama

A primary productivity model utilizing difference equations was written in FORTRAN for the purpose of describing the dynamics of blue grama growth throughout a growing season. The model can be described as a mechanistic model to the extent that some of the flows are represented by mathematical functions of experimental results. However, the major attribute of the model is that the main flows of biomass are determined directly from CO_2 exchange data collected in the field photosynthesis study. The objective was to produce a biologically-oriented computer model.

Models described by Innis et al. (1972), Parton and Marshall (1973), Connor, Brown and Trlica (1973), and Connor (1973) have utilized the CO_2 exchange data collected in the field or greenhouse studies to some extent. However, each of these models has used the trends in photosynthetic rates to develop mathematical functions which describe the appropriate flows. This approach was necessary because these models described communities or ecosystems which were composed

of several different species, and CO_2 exchange data were not complete for each species. In fact, a complete set of CO_2 exchange data was not available for any of the species, including blue grama, until completion of the data analyses included in this report.

In contrast to the models previously referred to, the approach taken here was species specific for blue grama. A more simplified approach was possible because a relatively complete set of CO_2 exchange data was provided by the present study of the dominant species of the shortgrass prairie. All of the steady state Pg determinations from the field study were grouped into several ranges for each of the four variables: soil water potential, irradiance, temperature and phenology. The range of groupings for the variables were the same as those used for the analysis of covariance (Appendix A, Table 7) and for the discussion of the field study interaction and main effects on the photosynthetic rates of blue grama (Figures 20, 21, 26, 27, 28, 29, and 30). Twenty-four graphs depicting four-way interaction effects of the variables on Pg were plotted with temperature on the abscissa and Pg on the ordinate. These graphs provided Pg rates for blue grama at all daytime temperatures normally encountered during the growing season on the shortgrass prairie for any one of 24 different combinations of the three remaining variables of soil water potential, irradiance and phenology.

There were some missing CO_2 exchange data, and some data with no replicates. Therefore, no data were used in the interaction graphs unless replicated. In addition, some visual estimates of the Pg rate were necessary to complete the data set. The temperature

range for which Pg rates were determined in the field study was from 15°C to 45°C. However, temperatures above and below this range are sometimes encountered during the growing season on the shortgrass prairie. Therefore, estimates of Pg were made to complete a range of temperatures from 3.8°C to 48.8°C for each of the 24 sets of the three remaining variables.

In addition, three two-way interaction graphs were prepared in the same manner for data from the field study that described the effects of soil water potential and temperature on the AGR rates of blue grama within the temperature range of 3.8°C to 48.8°C. Root respiration estimates were provided by D. Coleman (personal communication) and considered in the model by utilizing three more two-way interaction graphs depicting the effects of soil water potential and soil temperature on root respiration.

Thus, a total of 30 interaction graphs were utilized in the computer program, in the form of data statements, to provide the dynamics of the major flows of biomass in the model.

The flow diagram of the primary productivity model is shown in Figure 31. The state variables are depicted by rectangular boxes, the driving variables by circles and the irregular figures represent the source and sinks of CO_2 in the system. The solid lines in Figure 31 represent the flows of biomass among state variables, while the dashed lines represent informational flows from driving variables regulating the flow of biomass among state variables. Valve symbols regulating flows are labeled (F2 through F7) to define each particular biomass flow in the system. Biomass (g $CH_2O \cdot m^{-2} GA \cdot hr^{-1}$) is common to all flows in the system.

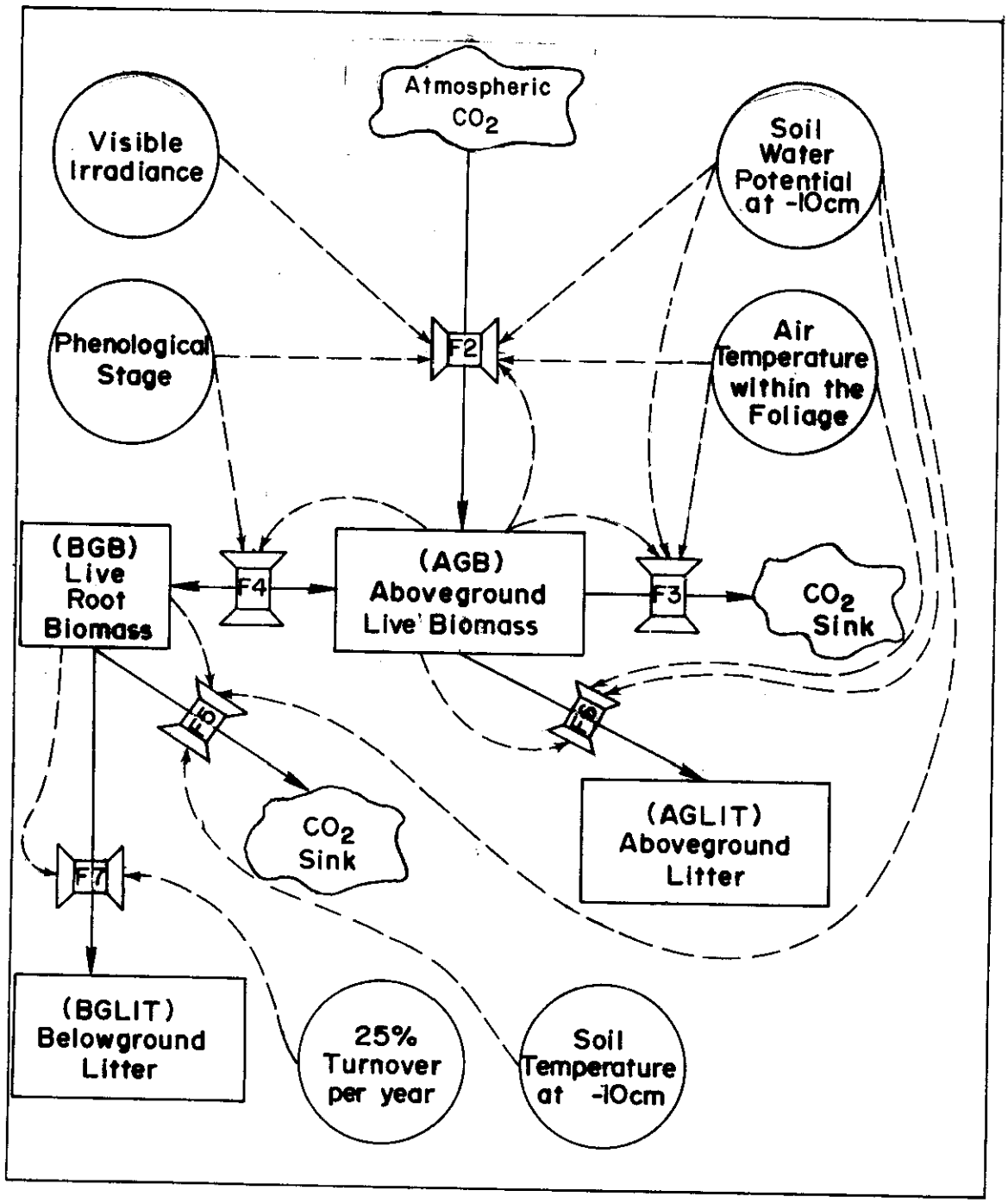

Figure 31. Flow diagram for the primary productivity model for blue grama (*Bouteloua gracilis*). The flows are: F2 = gross photosynthesis, F3 = aboveground dark respiration, F4 = translocation, F5 = root respiration, F6 = shoot death, and F7 = root death.

Driving Variable Data

Data for irradiance, air temperature within the canopy and soil temperature at 10-cm depth for the 1972 growing season at Pawnee Site was obtained from the IBP Grassland Biome Data Bank. Most of the soil water potential and all phenology values were personally recorded throughout the 1972 growing season at the Pawnee Site. Some of the early and late season soil water potential data utilized to drive the model were predicted from a sub-model. This sub-model utilized daily pan evaporation rates to arrive at a daily evapotranspiration rate which, with daily precipitation, resulted in a flux of soil water that was then transformed to soil water potential.

The primary productivity model operated on a three-hour time increment throughout the 1972 growing season. The growing season was arbitrarily determined to be 154 days in length, beginning on May 16 and ending on October 16. Each of the values for the five major driving variables previously referred to were hourly averages. Therefore, hourly averages of each variable were read into the program, for each three-hour iteration of the model.

The model was initialized utilizing state variable values of aboveground live (photosynyhetically-active) biomass (AGB) of 15.0 g $CH_2O \cdot m^{-2}GA$ and a live (functional) root biomass (BGB) of 517.0 g $CH_2O \cdot m^{-2}GA$ determined for that date (May 16, 1972) by Lauenroth (1973).

The Computer Program

The computer program (Appendix B) initially required performing some necessary transformations of the abiotic driving variables.

The addition of 5°C to the air and soil temperatures was deemed necessary to make the abiotic data more comparable with similar measurements made during the field study. Abiotic data were collected at a different site location and at a slightly different height above the canopy than in the field study. A basic transformation of blue grama biomass (AGB) to LA was necessary because all CO_2 exchange data in the interaction graphs were in terms of LA (mg $CO_2 \cdot dm^{-2} LA \cdot hr^{-1}$). The value, 0.53 $dm^2 \cdot g^{-1}$, was determined for blue grama by regression analysis. The program was then required to perform an extensive IF STATEMENT search utilizing the given driving variable data to determine the appropriate interaction graphs from which to extract Pg, AGR and root respiration rates. At this point a linear interpolation subroutine (FUNCTION TABLE) was called which linearly interpolated along the abscissa (temperature) to obtain the CO_2 exchange rates dictated by all four driving variables. The Pg and AGR rates, which are flows F2 and F3, respectively, were then transformed from mg $CO_2 \cdot m^{-2} GA \cdot hr^{-1}$ to g $CH_2O \cdot m^{-2} GA \cdot 3hr^{-1}$. The estimates of root respiration rates, flow F5, in the interaction graphs were in terms of mg $CO_2 \cdot g^{-1} \cdot day^{-1}$, from D. Coleman (personal communication). Therefore, the root respiration values required a slightly different transformation to arrive at g $CH_2O \cdot m^{-2} GA \cdot 3hr^{-1}$. All three of the preceeding transformations are simple arithmetic manipulations utilizing molecular weights of C, CO_2, and CH_2O of 12.01, 44.01 and 30.0 $g \cdot mole^{-1}$, respectively.

Flows F2, F3 and F5 (Figure 31) are not only regulated by the various driving variables, but are regulated by the amount of biomass

in each respective state variable. An obvious example is that the Pg rate per unit of LA would be constant, given certain abiotic and biotic conditions, but the rate of Pg per unit of GA must be proportional to the $LA \cdot GA^{-1}$. Therefore, a greater $AGB \cdot m^{-2}GA$ would result in a greater $Pg \cdot GA^{-1}$ until an optimum LAI was reached. Of course, this relationship would not be linear at high LAI's and the effects of LAI could be accounted for by utilizing a light extinction coefficient such as that used by Saeki (1963). Because of low LAI encountered on shortgrass prairie, a linear relationship between Pg and AGB was assumed and the model did not make use of a light extinction coefficient. Total light penetration into the canopy was considered to be a valid approach toward modeling productivity of the shortgrass prairie because the LAI seldom exceeded 0.5 or 0.6, and normally was in the range of 0.2 to 0.4 (Knight, 1973).

Translocation from AGB to BGB is flow F4 in Figure 31. This flow rate was based directly on ^{14}C translocation experiments conducted by Singh and Coleman (1973) on blue grama-dominated (90 percent by cover) sods during the 1972 growing season at the Pawnee Site. The informational input for F4 is from the phenological stage driving variable because the experiments were conducted only during May, July and September of 1972. Each of these dates provided a translocation value which represented the proportion of photosynthate translocated to the roots and crowns during that period of the growing season. The values were: May = 0.70, July = 0.80, and September = 0.88. Linear interpolation between the May and July values was used to obtain a June value of 0.75. The August value of 0.55 is more uncertain

and open to criticism because linear interpolation was not used. The translocation value for August was simply based on an estimate that a lesser proportion of the photosynthate would be translocated to BGB during a reproductive phenological stage.

Flows F6 and F7 (Figure 31) for shoot and root death rates, respectively, are the least important flows of the model because they had only a small effect on the net primary productivity of blue grama. The shoot death rate, F6, and the aboveground litter state variable (AGLIT) are, however, definitely necessary to the system. From a biological standpoint, AGLIT is necessary for obvious reasons. From a modeling standpoint, AGLIT is necessary because the accumulation of aboveground litter must be accounted for and the relationship between AGB and productivity previously referred to must be considered. In other words, if no AGB died throughout the growing season, a large amount of potentially productive foliage would be present in the winter. This is obviously not the case for the shortgrass prairie in the northern hemisphere.

The functions controlling the shoot death rate, F6, in the program (Appendix B) are based on soil water potential, air temperature, and AGB. Simply stated, if the soil water potential is less than -35 bars and the air temperature is greater than 39.0°C, shoot death will occur at a rate proportional to the difference between the actual temperature and 39.0°C. Also, if the temperature is below 4.0°C, shoot death will occur at the rate of five percent of the AGB for each °C below 4.0°C.

The function controlling root death rate, F7, and the state variable of belowground litter (BGLIT) are necessary to the model for accounting purposes only (Figure 31). The flow rate from BGB to BGLIT is based simply on general estimates (Innis et al., 1972) that the root biomass replacement rate of blue grama is about 25 percent per year.

After computation of each of the flows, F2 through F7, simple difference equations are used to calculate ongoing values of AGB, BGB and total live biomass (TOTBIO). After completion of these calculations, the program is returned to the next three-hour iteration.

Output of the Computer Model

At the end of each three-hour iteration, the values of all driving and state variables are printed out along with the date and time (Appendix B). Each flow is summed and printed after eight iterations (one day). Six examples of the printed output of the model, one example from each of the six months of 1972 under consideration, are also given in Appendix B.

Graphic representations of the model output was accomplished by using another subroutine (PLOTIT) and are shown in Figures 32 through 38. Figure 32 illustrates Pg and net primary productivity of blue grama throughout the 1972 growing season at the Pawnee Site. Net primary productivity (NPP) was determined by: NPP = Pg - AGR - root respiration. Totals for each of the flows in the model for the season are shown in Appendix B and in Appendix A, Table 11. The total NPP of blue grama, 714 g $CH_2O \cdot m^{-2} GA \cdot yr^{-1}$, is comparable

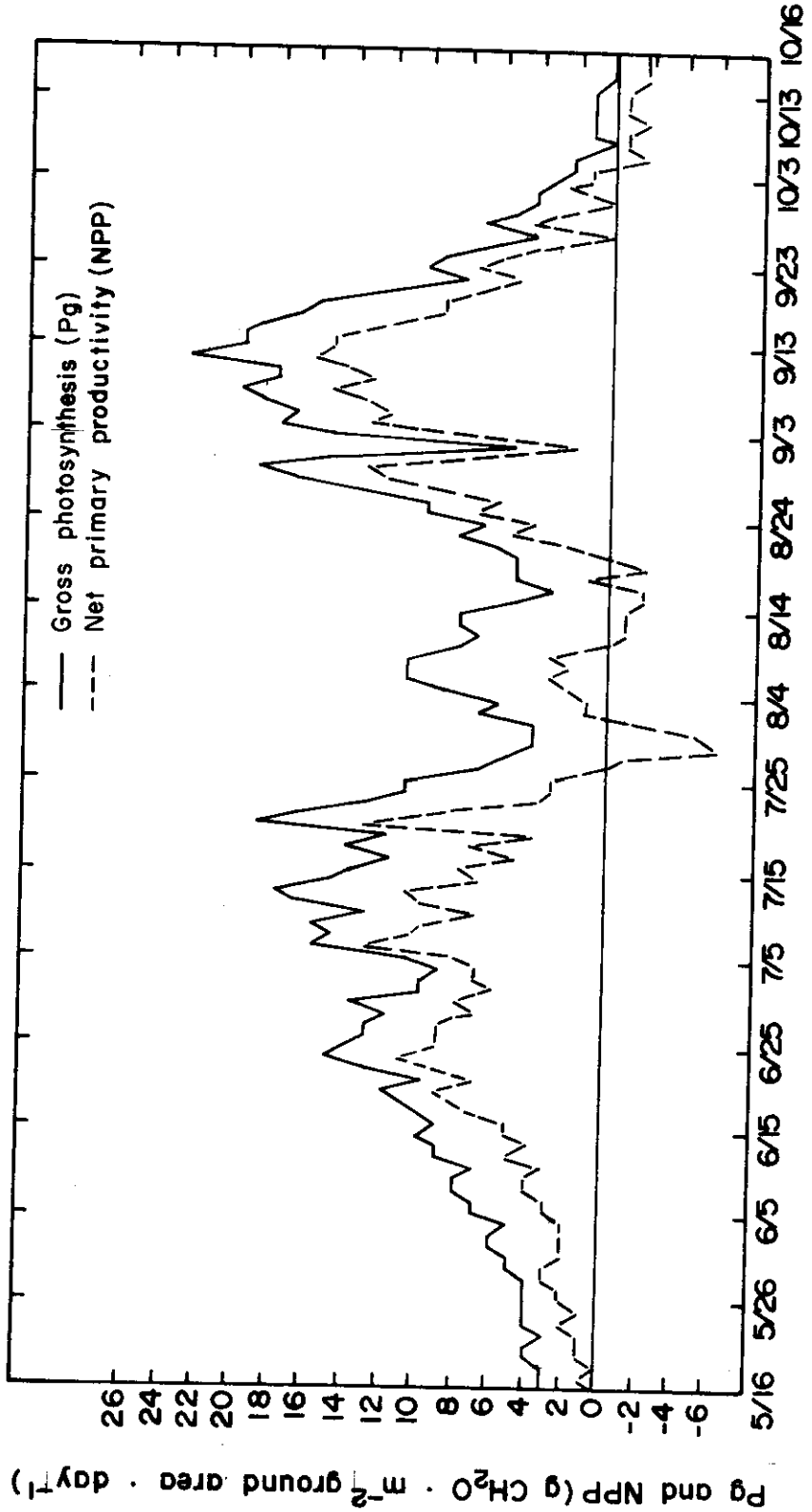

Figure 32. The dynamics of gross photosynthesis and net primary productivity of blue grama (*Bouteloua gracilis*) throughout the 1972 growing season at the Pawnee Site as derived from the computer model.

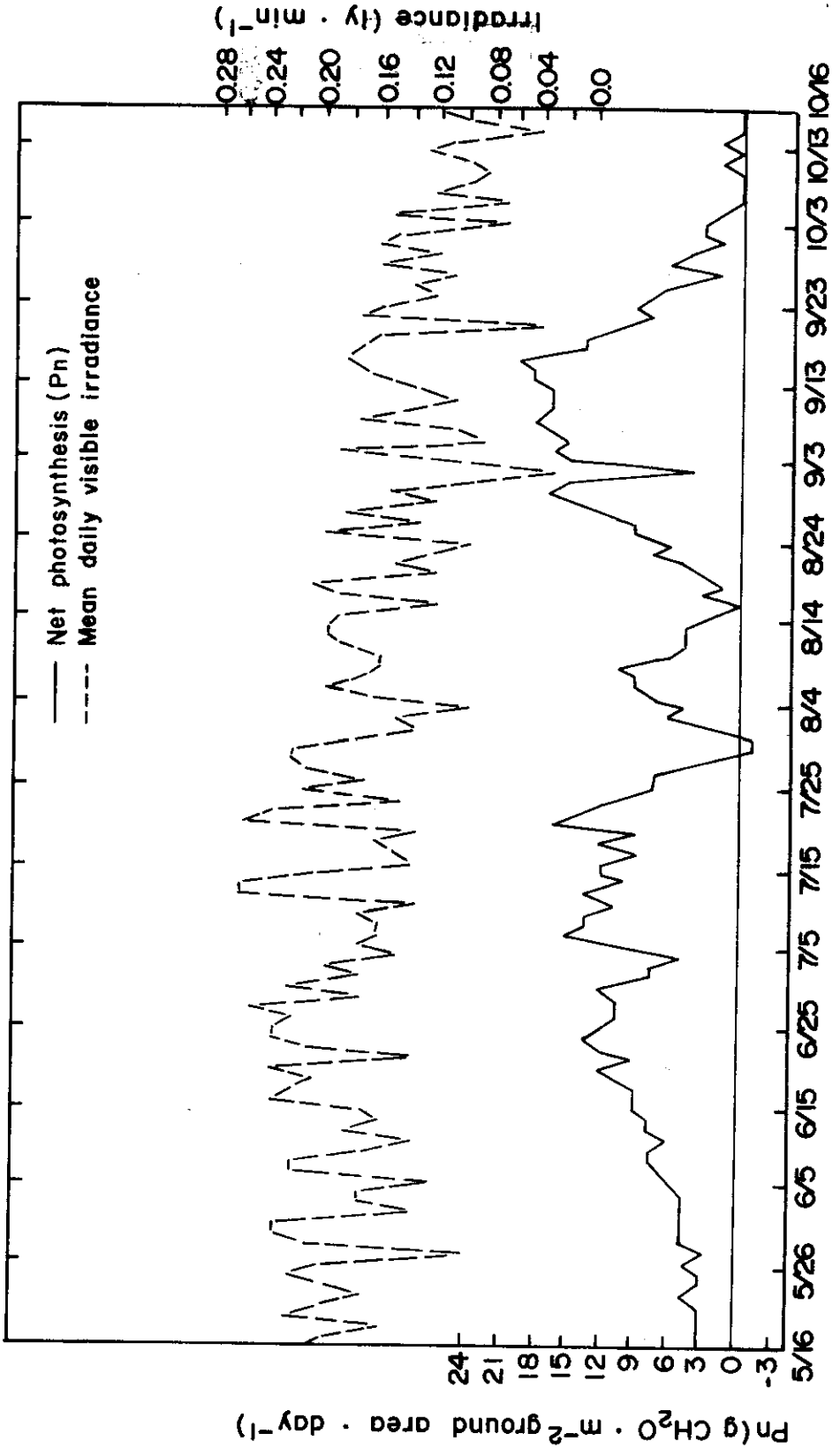

Figure 33. The dynamics of net photosynthesis of blue grama (*Bouteloua gracilis*) as affected by the mean daily visible irradiance throughout the 1972 growing season at the Pawnee Site as derived from the computer model.

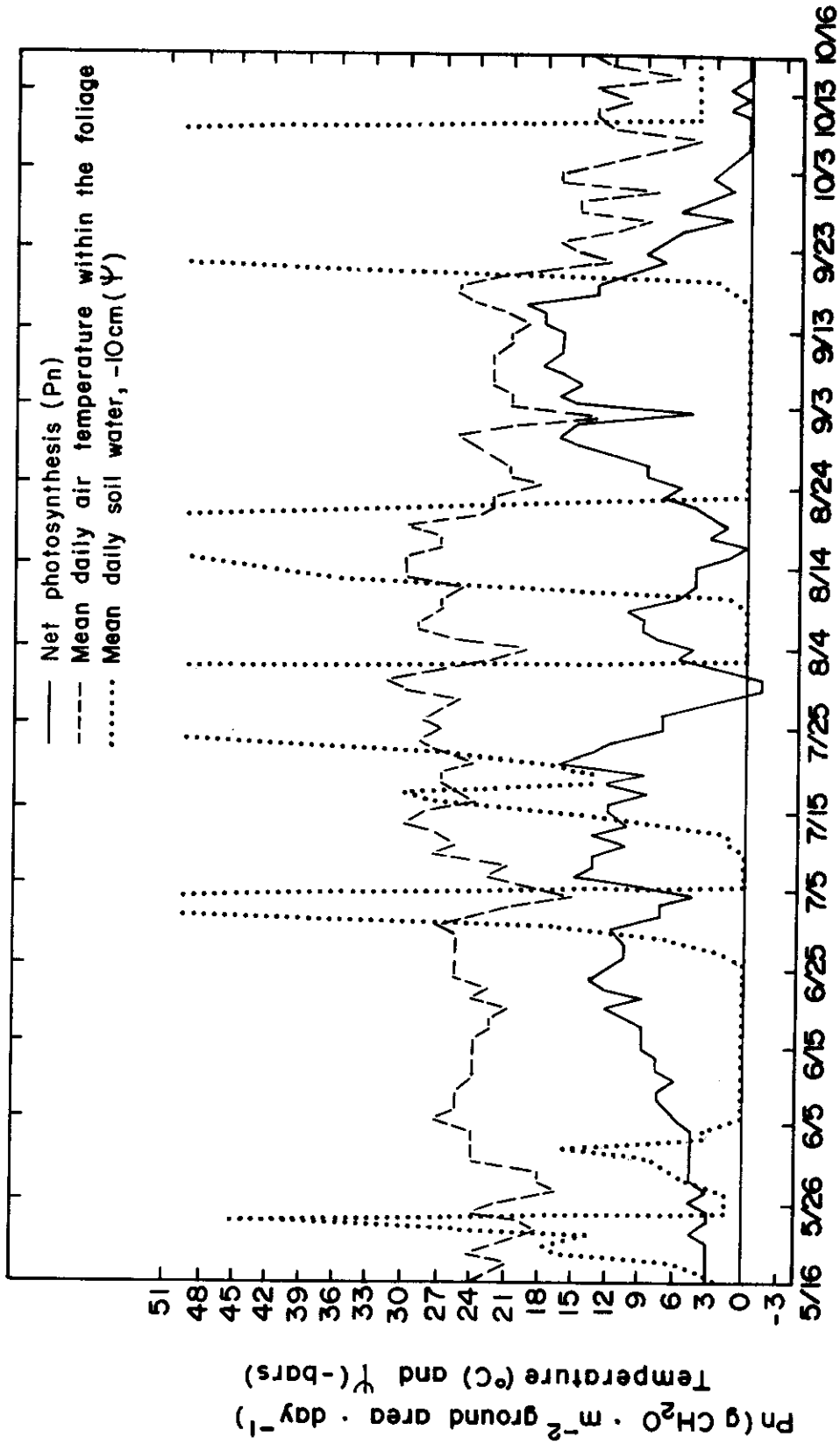

Figure 34. The dynamics of net photosynthesis of blue grama (*Bouteloua gracilis*) as affected by mean daily air temperature and soil water potential throughout the 1972 growing season at the Pawnee Site as derived from the computer model.

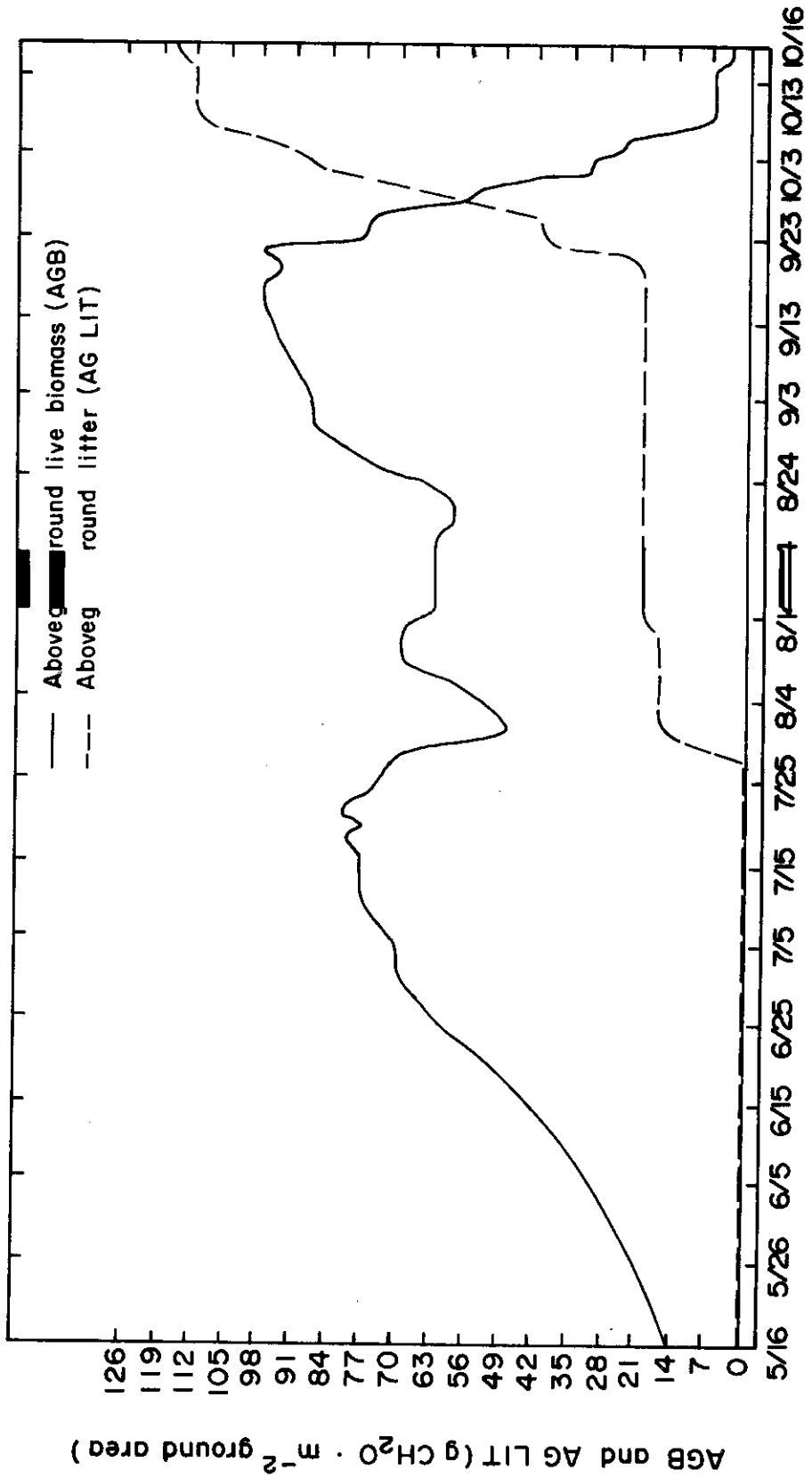

Figure 35. The dynamics of the aboveground biomass of blue grama (*Bouteloua gracilis*) throughout the 1972 growing season at the Pawnee Site as derived from the computer model.

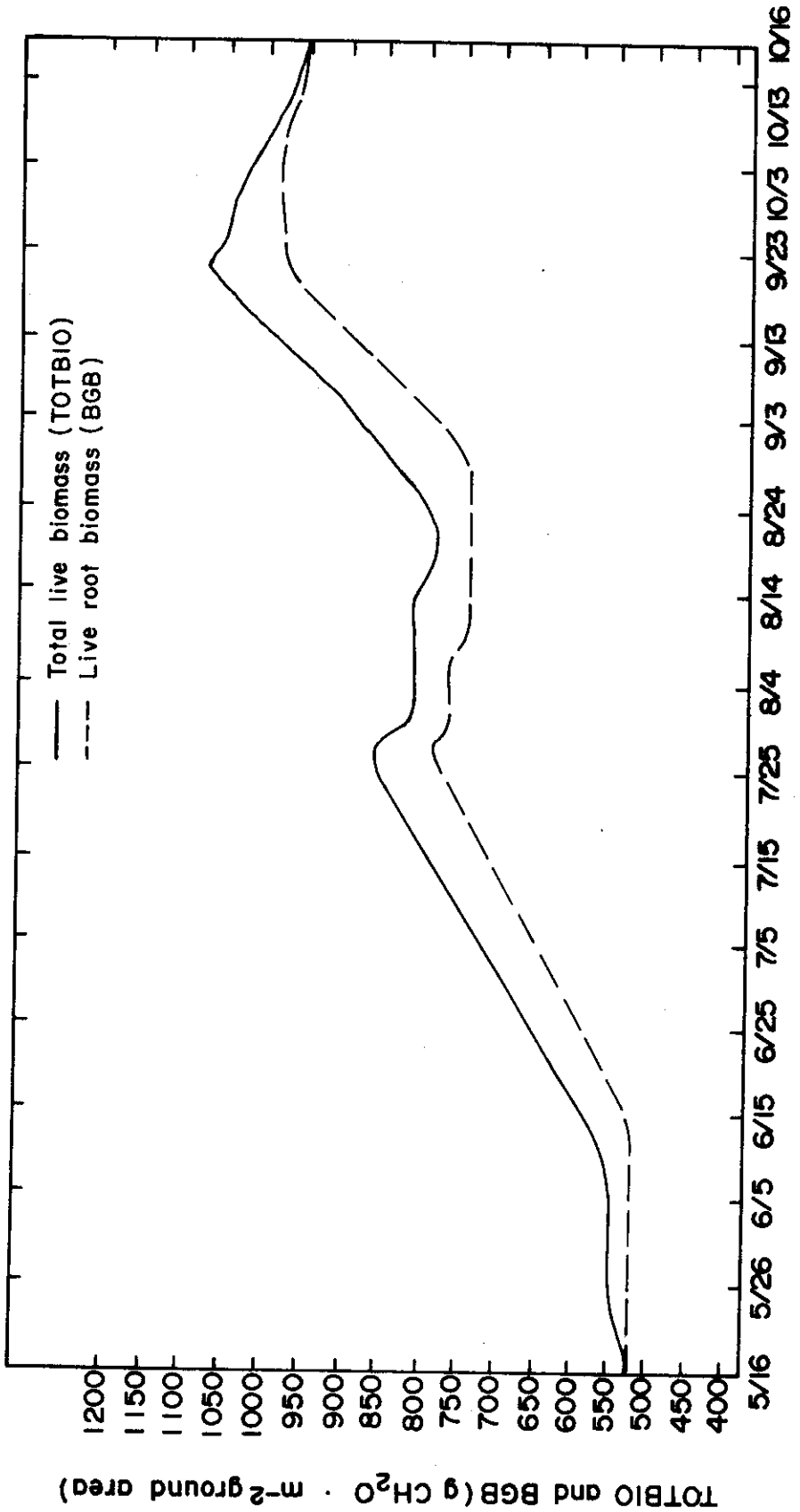

Figure 36. The dynamics of the total live biomass and live root biomass of blue grama (*Bouteloua gracilis*) throughout the 1972 growing season at the Pawnee Site as derived from the computer model.

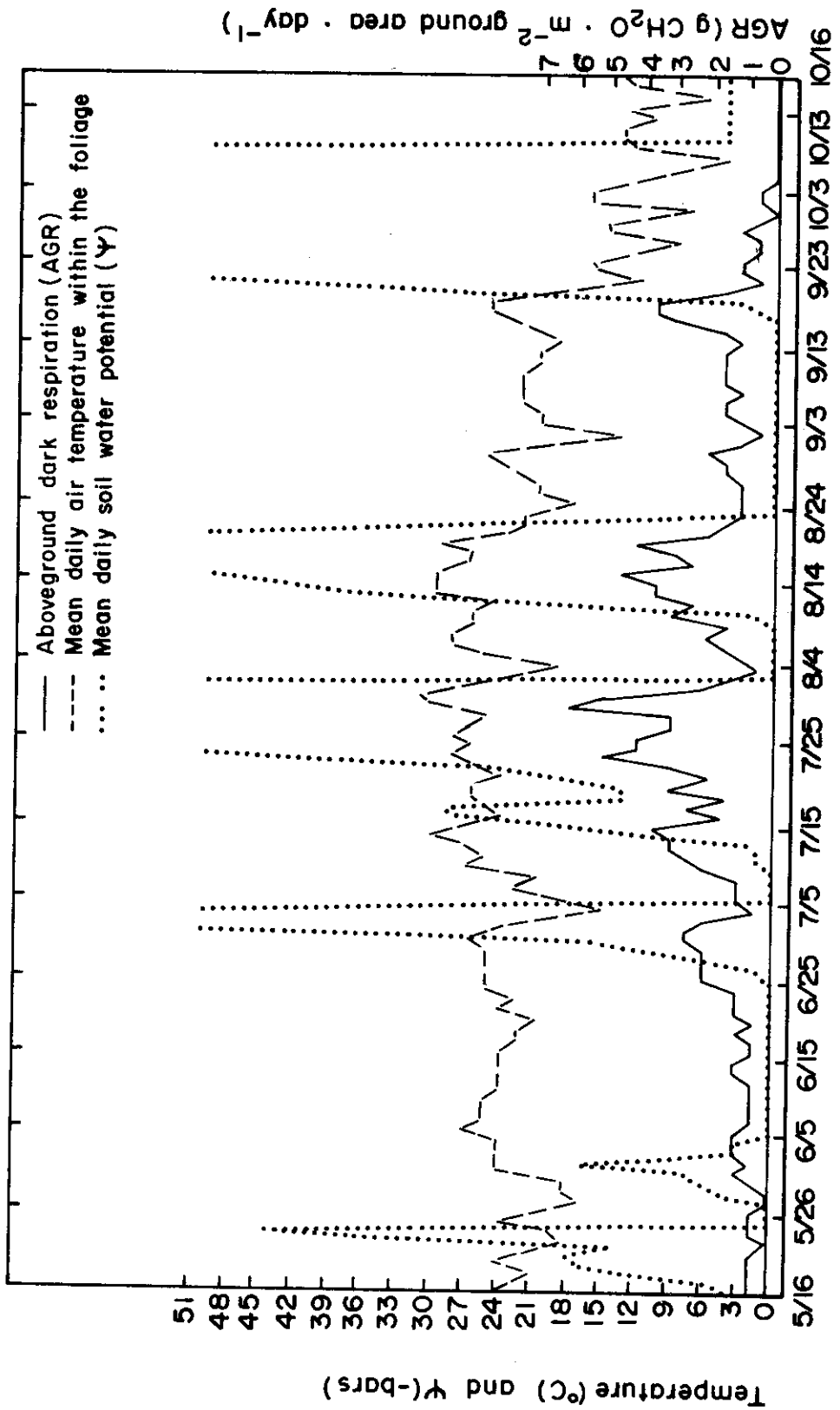

Figure 37. The dynamics of aboveground dark respiration of blue grama (*Bouteloua gracilis*) as affected by the mean daily air temperature and soil water potential throughout the 1972 growing season at the Pawnee Site as derived from the computer model.

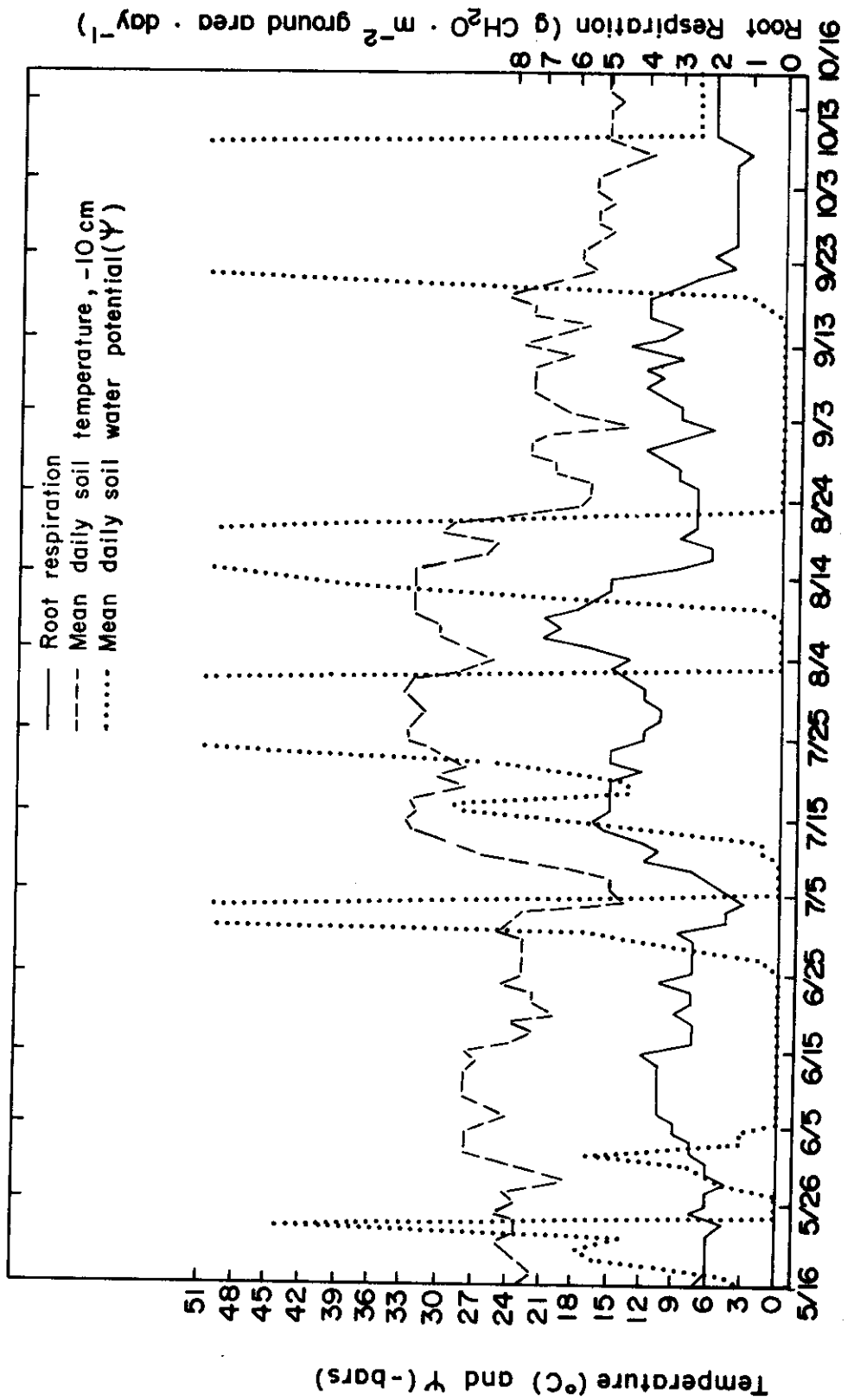

Figure 38. The dynamics of root respiration of blue grama (*Bouteloua gracilis*) as affected by the mean daily soil temperature and soil water potential throughout the 1972 growing season at the Pawnee Site as derived from the computer model.

to the 809 $g \cdot m^{-2} \cdot yr^{-1}$ total NPP determined by Lauenroth (1973) for all species of the Pawnee Site for the same season. The total Pg for the season was 1412 g $CH_2O \cdot m^{-2} \cdot yr^{-1}$. Therefore, the difference between NPP and Pg, 698 g $CH_2O \cdot m^{-2} \cdot yr^{-1}$, represents the yearly expenditure of biomass for respiration purposes. This represented approximately 49 percent of the total energy transformed by blue grama.

Figures 33 and 34 show the modelled Pn rates for blue grama throughout the growing season as affected by mean daily visible irradiance (Figure 33) and by mean daily soil water potential and air temperature within the plant canopy (Figure 34). A detailed comparison of Figures 33 and 34 provides the effects of those three variables on Pn rates of blue grama throughout the season. Optimum levels of all three variables such as observed during most of the month of June resulted in high Pn rates. Low irradiance with the concomitant low temperatures on about September 2 resulted in a sharp decrease in Pn, whereas high soil water stress was the limiting factor for Pn from about August 15 to August 20. The total Pn of blue grama for the season (Appendix A, Table 11 and Appendix B) was 1188 g $CH_2O \cdot m^{-2} \cdot yr^{-1}$.

Figure 35 shows the modelled dynamics of AGB and AGLIT for blue grama throughout the 1972 growing season. The peak standing green biomass as depicted by the model was 99 g $CH_2O \cdot m^{-2}$ and occurred during the middle of September following fall regrowth caused by precipitation received during the last part of August and the first part of September (Figure 10). The depressions in

AGB during the middle of the season were primarily caused by high soil water stress and a reproductive stage of phenology.

Figure 36 shows the modelled dynamics of total aboveground biomass (TOTBIO) and BGB for blue grama throughout the 1972 growing season. The peak TOTBIO occurs at the same time as the peak AGB, with the peak BGB occurring slightly later. BGB built up rapidly after the first of September, while AGB remained fairly constant because 88 percent of the photosynthate was being translocated belowground from that time on.

Figures 37 and 38 depict the modelled AGR and root respiration rates for blue grama throughout the 1972 growing season, respectively. Both rates are shown as affected by mean daily soil water potentials and the respective temperatures (air and soil). The effect of the respective variables on AGR and root respiration can easily be seen in Figures 37 and 38. The total AGR and root respiration for blue grama for the season (Appendix A, Table 11 and Appendix B) were 224 and 474 g $CH_2O \cdot m^{-2} \cdot yr^{-1}$, respectively.

A comprehensive comparison of model output, continuous 24-hour ambient simulations and clipping data is shown in Appendix A, Table 8. Discrepancies between Lauenroth's (1973) data and the model predictions could be caused by the abundance and growth of *Carex eleocharis* and *Artemisia frigida* during the early and late parts of the season, respectively, which were not accounted for in the primary productivity model.

Sensitivity Analysis of the Primary Productivity Model

An assessment of the sensitivity of the model was performed by changing various abiotic variables or mathematical constants in the model. The results are shown in Appendix A, Table 11. The analysis clearly indicated the impact of rather drastic abiotic perturbations on the modelled description of a biological system. The addition of 5°C to all temperatures through the season reduced NPP from 714 to 31 g $CH_2O \cdot m^{-2} \cdot yr^{-1}$, whereas the reduction of all temperatures by 5°C increased the NPP to 1107 g $CH_2O \cdot m^{-2} \cdot yr^{-1}$. This trend was caused by the exponential effect of temperature on respiration rates. The ecophysiological implications of these results indicated that NPP of the shortgrass prairie could possibly be greater during a cooler season, even though it is dominated by a C_4 species with a high optimum photosynthetic temperature. However, a cooler season would probably not occur without a concomitant reduction of irradiance, which would tend to reduce NPP.

The addition of 10°C to all temperatures resulted in negative NPP (Appendix A, Table 11). The exponential effect of temperature on respiration rates coupled with low Pg rates were the causes for the negative NPP. Negative NPP caused by the subtraction of 10°C from all temperatures resulted from very low Pg rates at the low temperatures.

Optimum soil water potentials throughout the season (Appendix A, Table 11) resulted in extremely high NPP, demonstrating the ecophysiological significance of this abiotic driving variable for primary productivity of the shortgrass prairie. Extremely limiting

soil water potentials resulted in an anticipated negative NPP. A ten percent reduction in visible irradiance also resulted in an anticipated reduction of NPP (Appendix A, Table 11).

The constant determined for converting weight of AGB to LA was changed from the original 0.53 to 0.56 to assess its sensitivity on the biological system (Appendix A, Table 11). This resulted in an increase in NPP of 156 g $CH_2O \cdot m^{-2} \cdot yr^{-1}$, indicating the importance of this constant.

The percentage of photosynthate translocated to BGB during reproductive phenology was changed from 0.55 to either 0.45 or 0.65 (Appendix A, Table 11). These ten percent changes resulted in an approximately equal decrease and increase of 22 percent, respectively, in NPP for the season. These results indicated the importance of translocation and the need for more research in this area.

Critique of the Model

The model, as presently constructed, is relatively simple. It could be made more comprehensive with the inclusion of more variables such as the effect of nutrients on photosynthetic rates, or with the inclusion of more flows such as decomposition. I have chosen to leave it in its present form because of the lack of comprehensive validated data. Each addition of unknowns to the model adds more uncertainty to the results. Indeed, there are already a sufficient number of estimates included in the model. The temperature data obtained from the Grassland Biome Data Bank required extensive editing and repletion and the sensitivity analysis (Appendix A, Table 11) clearly demonstrated the importance of temperature to

the biological system. An accurate and comprehensive abiotic data set would, therefore, be a prerequisite to any further refinements of the model.

The need for more comprehensive translocation data is evident from the sensitivity analysis (Appendix A, Table 11). More accurate and comprehensive root respiration data are also needed, but are simply not available because of the complexity involved in the determination of this flow of biomass in the ecosystem. The shoot and root death rates in the model could also be better represented. The photosynthesis and aboveground respiration data set could even be more complete to provide a greater degree of accuracy to the model.

Withstanding these criticisms, the model is still a fair approximation of the primary productivity of blue grama for the 1972 growing season. The comparable values determined by Lauenroth (1973) (Appendix A, Table 8) provide some test of the validity of the model. Similar abiotic data sets with slight modifications to the program would allow predictive output to be determined for other seasons. Considering the dominance of blue grama in the shortgrass prairie, the predictions of net primary productivity of blue grama might even be extrapolated to NPP for the shortgrass prairie.

SUMMARY AND CONCLUSIONS

Two studies were conducted during 1971 and 1972 on the carbon dioxide (CO_2) exchange rates of a dominant and a sub-dominant grass of the shortgrass prairie. The greenhouse study involved the determination of photosynthetic rates and the aboveground dark respiration rates for blue grama (*Bouteloua gracilis*), a C_4 species, and western wheatgrass (*Agropyron smithii*), a C_3 species, as each was affected by similar levels of soil water potential, temperature and visible irradiance. Undisturbed sods of each species were taken from the field and grown in the greenhouse under conditions somewhat similar to those which the plants experience in the field. Carbon dioxide exchange rates were measured using a closed system and an infrared gas analyzer. Contribution of CO_2 to the system from the soil was excluded by sealing the sods at the soil-atmosphere interface with heavy mineral oil.

The field study involved the determination of gross photosynthetic rates for in situ blue grama sods as affected by soil water potential, temperature, visible irradiance and phenological stage. The field study was conducted on an undistubed portion of the shortgrass prairie at the Pawnee Site of the U.S.-IBP Grassland Biome in northeastern Colorado. A portable open system of CO_2 exchange was used along with an infrared gas analyzer and an automatic data acquisition system. One field experiment was conducted to determine gross photosynthetic rates of blue grama at different levels of each of the above four variables. Another type of experiment was

conducted to monitor the CO_2 exchange of in situ blue grama sods during four 24-hour periods throughout the 1972 growing season.

It was found that all four of the main treatments (soil water potential, temperature, visible irradiance and phenological stage) significantly affected the photosynthetic rates of blue grama. All three main treatments (soil water potential, temperature, and visible irradiance) significantly affected the photosynthetic rates of western wheatgrass. Varying soil water potential and temperature also significantly affected the aboveground dark respiration rates of both species. Interactions among most of the above variables also significantly affected the CO_2 exchange rates of both species.

Blue grama was not light saturated under any but severe stress conditions for photosynthesis. High temperatures and high soil water stress resulted in light saturation of blue grama at very high irradiances. Western wheatgrass demonstrated light saturation at relatively low irradiances. The optimum temperature for photosynthesis of blue grama varied between 26°C and 33°C, depending on soil water stress and irradiance. High soil water stress and low irradiances resulted in lower optimum photosynthetic temperatures of blue grama. The optimum photosynthetic temperature of western wheatgrass was not determined because it was lower than the lowest (20°C) used in the greenhouse study. Increasing soil water stress resulted in decreasing rates of photosynthesis and aboveground dark respiration for both species. Aboveground dark respiration of both species increased with increasing temperatures. A reproductive stage of phenology caused significant decreases in

the photosynthetic rates of blue grama. The effect of phenology on photosynthetic rates of western wheatgrass was not determined.

A comparison of the photosynthetic rates of blue grama and western wheatgrass on a dry weight basis showed western wheatgrass to be slightly superior to blue grama. However, when compared on the more traditional basis of leaf area, the C_4 species, blue grama, demonstrated far superior photosynthetic rates to the C_3 species, western wheatgrass.

A comparison among gross photosynthetic rates for blue grama in the field and greenhouse studies showed the rates determined in the greenhouse to be about 65 percent of the rates of the in situ blue grama sods in the field study.

Integration of daily net photosynthesis throughout each of four 24-hour continuous ambient simulations studied during the 1972 growing season at the Pawnee Site provided values ranging from 1.7 to 14.3 g $CH_2O \cdot m^{-2}$ ground area$\cdot day^{-1}$. The greater photosynthetic rates were noted during near optimum conditions of soil water potential, visible irradiance and temperature.

Multiple linear regression analyses were performed on gross and net photosynthesis and aboveground respiration rates for both blue grama and western wheatgrass. With transgenerations, 81 to 91 percent of the variability in the CO_2 exchange rates were accounted for by the three variables of soil water potential, temperature and visible irradiance. Similar regression analyses on gross and net photosynthetic rates of blue grama in the field study showed 64 to 81 percent of the variability in the photosynthetic rates to be

accounted for by the variables of soil water potential, temperature, visible irradiance and phenological stage.

A primary productivity simulation model of the seasonal dynamics of blue grama was constructed making use of the fairly complete set of CO_2 exchange data collected in the field study. The model operated on a three-hour time increment for a 154-day growing season during 1972. Total net primary production of 714 g $CH_2O \cdot m^{-2}$ ground area$\cdot yr^{-1}$ for blue grama was predicted using the model, which is comparable to clipping data of 809 $g \cdot m^{-2} \cdot yr^{-1}$ determined by Lauenroth (1973) for the same growing season, which included all species.

LITERATURE CITED

Balegh, S. E. and O. Biddulph. 1970. The photosynthetic action spectrum of the bean plant. Plant Physiol. 46:1-5.

Benson, A. A. and M. Calvin. 1947. The dark reduction of photosynthesis. Science. 105:648-651.

Bielorai, H. and K. Mendel. 1969. The simultaneous measurement of apparent photosynthesis and transpiration of citrus seedlings at different soil moisture levels. J. Am. Soc. Hort. Sci. 94:201-204.

Bierhuizen, J. F., M. A. Nunes, and C. Ploegman. 1969. Studies on productivity of coffee. II. Effect of soil moisture on photosynthesis and transpiration of *Coffea arabica*. Acta. Bot. Neerl. 18:367-374.

Bjorkman, O. 1966. The effect of oxygen concentration on photosynthesis in higher plants. Physiol. Plant. 19:618-633.

Bjorkman, O. 1968. Further studies on differentiation of photosynthetic properties in sun and shade ecotypes of *Solidago virgaurea*. Physiol. Plant. 21:84-99.

Bjorkman, O. 1971. Comparative photosynthetic CO_2 exchange in higher plants. Pages 18-32 *in* M. D. Hatch, C. B. Osmond and B. O. Slayter, eds. Photosynthesis and Photorespiration. John Wiley and Sons, New York.

Bjorkman, O. and J. Berry. 1973. High-efficiency photosynthesis. Sci. Am. 229:80-93.

Bjorkman, O. and P. Holmgren. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiol. Plant. 16:889-914.

Bjorkman, O., R. W. Pearcy, A. T. Harrison, and H. Mooney. 1972. Photosynthetic adaptation to high temperatures: A field study in Death Valley, California. Science 175:786-789.

Black, C. A. 1968. Soil Plant Relationships. John Wiley and Sons, New York. 792 p.

Botkin, D. B. and C. R. Malone. 1968. Efficiency of net primary production based on light intercepted during the growing season. Ecology 49:438-444.

Botkin, D. B., G. M. Woodwell and N. Tempel. 1970. Forest productivity estimated from carbon dioxide uptake. Ecology 51:1057-1060.

Boyer, J. S. 1970a. Leaf enlargement and metabolic rates in corn, soybean, and sunflower at various leaf water potentials. Plant Physiol. 46:233-235.

Boyer, J. S. 1970b. Differing sensitivity of photosynthesis to low leaf water potentials in corn and soybean. Plant Physiol. 46:236-239.

Boyer, J. S. 1971. Recovery of photosynthesis in sunflower after a period of low leaf water potential. Plant Physiol. 47:816-820.

Brown, K. W. 1968. Experimental considerations for the measurement of photosynthetic rates by means of carbon dioxide exchange in leaf chambers. Agr. Exp. Sta. Univ. of Neb. Prog. Rep. 66. 40 p.

Brown, K. W. 1969. A model of the photosynthesizing leaf. Physiol. Plant. 22:620-637.

Brown, K. W. and N. J. Rosenberg. 1970. Effect of windbreaks and soil water potential on stomatal diffusion resistance and photosynthetic rate of sugar beets (*Beta vulgaris*). Agron. J. 62:4-8.

Brown, R. H., R. E. Blaser, and H. L. Dunton. 1966. Leaf-area index and apparent photosynthesis under various microclimates for different pasture species. Proc. X International Grassland Congress. p. 108-113.

Brown, R. W. 1970. Measurement of water potential with thermocouple psychrometers: construction and application. USDA Forest Service Res. Pap. INT-80. 27 p.

Brown, W. V. 1958. Leaf anatomy in grass systematics. Bot. Gaz. 5:517-521.

Caldwell, N. M., R. T. Moore, R. S. White and E. J. DePuit. 1972. Gas exchange of great basin shrubs. Desert Biome-U.S. International Biological Program RM 72-20. Utah State Univ., Logan. 30 p.

Cannon, W. A. 1921. Plant habits and habitats in the arid portions of South Australia. The Carnegie Institution of Washington. Washington, D. C. 123 p.

Chen, H. L., H. T. Mederski, and R. B. Carry. 1971. Water stress effects on photosynthesis and stem diameter in soybean plants. Crop Sci. 11:428-431.

Connor, D. J. 1973. Gromax: A potential productivity routine for a total grassland ecosystem model. Grassland Biome-U.S. International Biological Program Tech. Rep. No. 208. Colo. State Univ., Fort Collins. 27 p.

Connor, D. J., L. F. Brown, and M. J. Trlica. 1974. Plant cover, light interception, and photosynthesis of shortgrass prairie - a functional model. Photosynthetica (at press).

Curry, R. B. 1971. Dynamic simulation of plant growth. 1. Development of a model. Trans. Am. Soc. Agr. Eng. 14:946-949 and 959.

Curry, R. B. and L. H. Chen. 1971. Dynamic simulation of plant growth. 2. Incorporation of actual daily weather data and partitioning of net photosynthate. Trans. Am. Soc. Agr. Eng. 14:1170-1174.

Decker, J. P. 1947. The effect of air supply on apparent photosynthesis. Plant Physiol. 22:561-571.

Decker, J. P. 1957. Further evidence of increased carbon dioxide production accompanying photosynthesis. J. Sol. Energy Sci. Eng. 1:30-33.

deWit, C. T. 1965. Photosynthesis of leaf canopies. Agr. Res. Rep., Wageningen. 663:1-57.

Downton, W. J. S. 1971. Adaptive and evolutionary aspects of C_4 photosynthesis. Pages 3-17 *in* M. D. Hatch, C. B. Osmond, and R. O. Slayter, eds. Photosynthesis and Photorespiration. John Wiley and Sons, New York.

Downton, W. J. S., J. Berry, and E. B. Tregunna. 1969. Photosynthesis: temperature and tropical characteristics within a single grass genus. Science 163:78-79.

Downton, W. J. S. and E. Tregunna. 1968. Carbon dioxide compensation - its relation to photosynthetic carboxylation reaction, systematics of *Gramineae*, and leaf anatomy. Can. J. Bot. 46:207-215.

Duncan, W. G. and B. J. Barfield. 1971. Description of photosynthesis within plant canopies. Trans. Am. Soc. Agr. Eng. 14:960-963.

Duncan, W. G., R. S. Loomis, W. A. Williams and R. Hanau. 1967. A model for simulating photosynthesis in plant communities. Hilgardia 38:181-204.

Dye, A. J. 1972. Carbon dioxide exchange of blue grama swards in the field. Ph.D. Diss., Colo. State Univ., Fort Collins. 64 p.

Dye, A. J., L. F. Brown, and M. J. Trlica. 1972. Carbon dioxide exchange of blue grama as influenced by several ecological parameters, 1971. Grassland Biome-U.S. International Biological Program Tech. Rep. No. 181. Colo. State Univ., Fort Collins. 44 p.

Dye, A. J. and W. H. Moir. 1971. CO_2 exchange over shortgrass sods. Grassland Biome-U.S. International Biological Program Tech. Rep. No. 81. Colo. State Univ., Fort Collins. 13 p.

El-Sharkawy, M. and J. Hesketh. 1965. Photosynthesis among species in relation to characteristics of leaf anatomy and CO_2 diffusive resistances. Crop Sci. 5:517-521.

El-Sharkawy, M., J. Hesketh, and H. Muramoto. 1965. Leaf photosynthetic rates and other growth characteristics among 26 species of *Gossypium*. Crop Sci. 5:173-175.

Evans, L. T. 1971. Evolutionary, adaptive, and environmental aspects of the photosynthetic pathway: assessment. Pages 130-136 *in* M. D. Hatch, C. B. Osmond and R. O. Slayter, eds. Photosynthesis and Photorespiration. John Wiley and Sons, New York.

Gauhl, E. and O. Bjorkman. 1969. Simultaneous measurements on the effect of oxygen concentration on water vapor and carbon dioxide exchange in leaves. Planta 88:187-191.

Geronimo, J. and H. Beevers. 1964. Effect of aging and temperature on respiratory metabolism of green leaves. Plant Physiol. 39:786-793.

Ghorashy, S. R., J. W. Pendleton, R. L. Bernard, and M. E. Bauer. 1971. Effect of leaf pubescence on transpiration, photosynthetic rate and seed yield of three near-isogenic lines of soybeans. Crop Sci. 11:426-427.

Hadley, E. B. and L. C. Bliss. 1964. Energy relationships of alpine plants on Mt. Washington, New Hampshire. Ecol. Monogr. 34:331-357.

Hatch, M. D. 1971. Mechanism and function of the C_4 pathway of photosynthesis. Pages 139-152 *in* M. D. Hatch, C. B. Osmond and R. O. Slayter, eds. Photosynthesis and Photorespiration. John Wiley and Sons, New York.

Hatch, M. D. and C. R. Slack. 1966. Photosynthesis in sugar cane leaves. A new carboxylation reaction and the pathway of sugar formation. Biochem. J. 101:103-111.

Hatch, M. D. and C. R. Slack. 1968. A new enzyme for the interconversion of pyruvate and phosphopyruvate and its role in the C-4 bicarboxylic acid pathway of photosynthesis. Biochem. J. 106:141-146.

Hatch, M. D. and C. R. Slack. 1970. Photosynthetic CO_2-fixation pathways. Ann. Rev. Plant Physiol. 21:141-162.

Heichel, G. H. 1971. Confirming measurements of respiration and photosynthesis with dry matter accumulation. Photosynthetica 5:93-98.

Heichel, G. H. and R. B. Musgrave. 1969. Relation of CO_2 compensation concentration to apparent photosynthesis in maize. Plant Physiol. 44:1724-1728.

Hellmuth, E. O. 1970. Eco-physiological studies on plants in arid and semi-arid regions in western Australia. III. Comparative studies on photosynthesis, respiration and water relations of ten arid zone and two semi-arid zone plants under winter and late summer climatic conditions. J. Ecol. 58:225-258.

Hesketh, J. D. 1963. Limitations to photosynthesis responsible for differences among species. Crop Sci. 3:493-496.

Hesketh, J. and D. Baker. 1967. Light and carbon assimilation by plant communities. Crop Sci. 7:285-293.

Hesketh, J. D. and D. N. Moss. 1963. Variation in the response of photosynthesis to light. Crop Sci. 3:107-110.

Hew, Choy-Sin, G. Krotkov, and D. T. Canvin. 1969. Determination of the rate of CO_2 evolution by green leaves in light. Plant Physiol. 44:662-670.

Hofstra, G. and J. D. Hesketh. 1969. Effect of temperature on the gas exchange of leaves in the light and dark. Planta 85:228-237.

Iljin, W. S. 1957. Drought resistance in plants and physiological processes. Ann. Rev. of Plant Phy. 8:257-274.

Innis, George S., Jerry C. Anway, Ed G. Brittain, H. William Hunt, William J. Parton, Charles F. Rodell, and Ronald H. Sauer. 1972. ELM: Version 1.0. Grassland Biome-U.S. International Biological Program Tech. Rep. No. 156. Colo. State Univ., Fort Collins. 67 p.

Jameson, D. A. 1969. General description of the Pawnee Site. Grassland Biome-U.S. International Biological Program Tech. Rep. No. 1. Colo. State Univ., Fort Collins. 32 p.

Jewiss, O. R. and J. Woledge. 1967. The effect of age on the rate of apparent photosynthesis in leaves of tall fescue (*Festuca arundinacea* Schreb.). Ann. Bot. 31:661-671.

Kaul, R. 1966. Effect of water stress on respiration of wheat. Can. J. Bot. 44:623-632.

Knight, D. H. 1971. Some measurements of vegetation structure on the Pawnee Grassland, 1970. Grassland Biome-U.S. International Biological Program Tech. Rep. No. 72. Colo. State Univ., Fort Collins. 43 p.

Knight, D. H. 1972. Leaf area dynamics on the Pawnee Grassland, 1970-1971. Grassland Biome-U.S. International Biological Program Tech. Rep. No. 164. Colo. State Univ., Fort Collins. 22 p.

Knight, D. H. 1973. Leaf area dynamics of a shortgrass prairie in Colorado. Ecology 54:891-896.

Kozlowski, T. T. 1964. Water Metabolism in Plants. Harper and Row, New York. 227 p.

Kramer, P. J. 1969. Plant and Soil Water Relationships: a modern synthesis. McGraw-Hill Book Co., New York. 482 p.

Krenger, Jr., E. G. and D. Moss. 1969. Carbon dioxide compensation in grasses. Crop Sci. 9:619-621.

Kuiper, P. J. C. 1961. The effects of environmental factors on the transpiration of leaves with special reference to stomata light response. Meded. Lundb. Hoogesch, Wageningen 61:1-49.

Lauenroth, W. K. 1973. Effects of water and nitrogen stresses on a shortgrass prairie ecosystem. Ph.D. Diss. Colo. State Univ., Fort Collins. 114 p.

Lawlor, D. W. 1970. Absorption of polyethylene glycols by plants and their effects on plant growth. New Phytol. 69:501-513.

Lemon, E., L. H. Allen, Jr. and L. Muller. 1970. Carbon dioxide exchange of a tropical rain forest. II. Bioscience 20:1054-1059.

Loomis, R. S. and W. A. Williams. 1963. Maximum crop productivity: An estimate. Crop Sci. 3:67-72.

Mayland, H. F. 1969. Air-flow planimeter for measuring detached leaf area. J. Range Manage. 22:357-359.

Moir, W. H., J. P. Boratgis, R. Sherman, and G. Paetsch. 1969. Photosynthesis of shortgrasses under field conditions. Grassland Biome-U.S. International Biological Program Tech. Rep. No. 31. Colo. State Univ., Fort Collins. 17 p.

Mooney, H. A. and W. D. Billings. 1969. Comparative physiologic ecology of arctic and alpine populations of *Oxyria digyma*. Ecol. Monogr. 31:1-28.

Moss, D. N. 1966. Respiration of leaves in light and in darkness. Crop Sci. 6:351-354.

Moss, R. A. and W. E. Loomis. 1952. Absorption spectra of leaves. I. The visible spectrum. Plant Physiol. 27:370-391.

Mulchi, C. L., R. J. Volk and W. A. Jackson. 1971. Oxygen exchange of illuminated leaves at carbon dioxide compensation. Pages 35-50 *in* M. D. Hatch, C. B. Osmond and R. O. Slayter, eds. Photosynthesis and Photorespiration. John Wiley and Sons, New York.

Murata, Y. and J. Iyama. 1963. Studies on the photosynthesis of forage crops. II. Influence of air-temperature upon the photosynthesis of some forage and grain crops. Proc. Crop Sci. Soc. Jap. 31:315-322.

Osmond, C. B., J. H. Troughton and D. J. Goodchild. 1969. Physiological, biochemical and structural studies of photosynthesis and photorespiration in two species of *Atriplex*. Z. Pflanzephysiol. 61:218-237.

Parton, W. J. and J. K. Marshall. 1973. Modenv: A grassland ecosystem model. Summer Computer Simulation Conference, July 17-19, 1973. Montreal, Canada. 8 p.

Pearce, R. B., R. H. Brown, and R. E. Blaser. 1967a. Photosynthesis in plant communities as influenced by leaf angle. Crop Sci. 7:321-324.

Pearce, R. B., R. H. Brown, and R. E. Blaser. 1967b. Net photosynthesis of barley seedlings as influenced by leaf area index. Crop Sci. 7:545-546.

Prat, H. 1936. Lasystematiques des graminees. Ann. Sci. Nat. (Botan.) Ser. 10. 18:165-258.

Redmann, R. E. 1973. Photosynthesis, plant respiration and soil respiration measured with controlled environment chambers in the field. I. Methods and Results. The Canadian Committee for the IBP, Tech. Rep. 18. Univ. of Saskatchewan, Saskatoon, Sask. 77 p.

Ronco, F. 1967. The influence of high light intensity on the survival of planted engelmann spruce. Ph.D. Diss., Duke Univ., Durham, North Carolina. 108 p.

Ronco, F. 1969. Assimilation chamber for measuring carbon dioxide exchange of tree seedlings in the laboratory. USDA Forest Service Res. Note RM-143. 7 p.

Ronco, F. 1970. Influence of high light intensity on survival of planted engelmann spruce. USDA Forest Service. 16:331-339.

Saeki, T. 1963. Light relations in plant communities. Pages 79-94 *in* L. T. Evans, ed. Environmental Control of Plant Growth. Academic Press, New York.

Salisbury, F. B. and Cleon Ross. 1969. Plant Physiology. Wadsworth Pub. Co., Inc., Belmont, California. 747 p.

Samish, Y. and D. Koller. 1968. Estimation of photorespiration of green plants and of their mesophyll resistance to CO_2 uptake. Ann. Bot. (London) 32:687-694.

Shearman, L. L., J. D. Eastin, C. Y. Sullivan, and E. J. Kinbacher. 1972. Carbon dioxide exchange in water-stressed sorghum. Crop Sci. 12:406-409.

Shields, Lora M. 1950. Leaf xeromorphology as related to physiological and structural influences. Bot. Rev. 16:399-447.

Sims, P. L. and J. S. Singh. 1971. Herbage dynamics and net primary production in certain ungrazed and grazed grasslands in North America. Pages 59-113 *in* N. R. French, ed. Preliminary Analysis of Structure and Function in Grasslands. Range Sci. Dept. Sci. Ser. No. 10. Colo. State Univ., Fort Collins.

Singh, J. S. and D. C. Coleman. 1973. Distribution of photoassimilated carbon-14 on the root system of a shortgrass prairie (unpublished data).

Slayter, R. O. 1957. The significance of the permanent wilting percentage in studies of plant and soil water relations. Bot. Rev. 23:585-636.

Stalfelt, M. G. 1959. Die stomatare transpiration und die physiologie de spaltoffnungen. Pages 351-426 *in* W. Ruhland, ed. Hanbuch der Pflanzenphysiologie, Springer-Verlag, Berlin.

Staple, W. J., and J. J. Lehane. 1941. The use of the wilting coefficient in soil moisture studies in southwestern Saskatchewan. Soil Ag. 21:440-447.

Stapleton, H. N. and R. P. Meyers. 1971. Modeling subsystems for cotton - the cotton plant simulation. Trans. Am. Soc. Agr. Eng. 14:950-953.

Stephens, G. R. and P. E. Waggoner. 1970. Carbon dioxide exchange of a tropical rain forest. I. Bioscience 20:1050-1053.

Taylor, A. O. and J. A. Rowley. 1971. Plants under climatic stress. I. Low temperature, high light effects on photosynthesis. Plant Physiol. 47:713-718.

Taylor, C. A., H. F. Blaney, and W. W. McLaughlin. 1934. The wilting-range in certain soils and the ultimate wilting-point. Am. Geophys. Union Trans. 15:436-444.

Tregunna, E., G. Krotkov, and C. Nelson. 1964. Further evidence on the effects of light on respiration during photosynthesis. Can. J. Bot. 42:989-997.

Treharne, J. J., J. P. Cooper, and T. H. Taylor. 1968. Growth response of orchard grass to different light and temperature environments. II. Leaf age and photosynthetic activity. Crop Sci. 8:441-445.

Tripathy, P. C., J. A. Eastin, and L. E. Schrader. 1972. A comparison of ^{14}C-labelled photosynthate export from two leaf positions in a corn (*Zea mays* L.) canopy. Crop Sci. 12:495-497.

Trlica, M. J., A. J. Dye, W. H. Moir, L. F. Brown, D. A. Jameson, and W. A. Rice. 1973. A field laboratory for gas exchange measurements of grassland swards. Photosynthetica 7:257-261.

Troughton, J. H. 1971. Aspects of the evolution of the photosynthetic carboxylation reaction in plants. Pages 124-129 *in* M. D. Hatch, C. B. Osmond, and R. O. Slayter, eds. Photosynthesis and Photorespiration. John Wiley and Sons, New York.

Uresk, D. W. 1971. Dynamics of blue grama within a shortgrass ecosystem. Ph.D. Diss., Colo. State Univ., Fort Collins. 52 p.

Voskresenskaya, N. P., G. S. Grishina, S. N. Chmora, and N. M. Poyarkova. 1970. The influence of red and blue light on the rate of photosynthesis and the CO_2 compensation point at various oxygen concentrations. Can. J. Bot. 48:1251-1257.

Waggoner, P. E. 1969a. Predicting the effect upon net photosynthesis of changes in leaf metabolism and physics. Crop Sci. 9:315-321.

Waggoner, P. E. 1969b. Environmental manipulation for higher yields. Pages 343-373 *in* J. D. Eastin, et al., eds. Physiological Aspects of Crop Yield. A.S.A. and C.S.S.A., Madison, Wisconsin.

Wallace, A., R. Q. Hale, G. E. Kleinkopf, and R. C. Huffaker. 1971. Carboxydismutase and phosphoenolpyruvate carboxylase activities from leaves of some plant species from northern Mojave and southern Great Basin Deserts. Ecology 52:1093-1095.

Wardlaw, I. F. 1969. The effect of water stress on translocation in relation to photosynthesis and growth. II. Effect during leaf development in *Lolium temulentum* L. Aust. J. Biol. Sci. 22:1-16.

Warren-Wilson, J. 1963. Estimation of foliage denseness and foliage angle by inclined point quadrats. Aust. J. Biol. 11:95-105.

Warren-Wilson, J. 1967. Stand structure and light penetration. III. Sunlit foliage area. J. Appl. Ecol. 4:159-165.

Weaver, J. E. and F. W. Albertson. 1956. Grasslands of the Great Plains. Johnson Publ. Co., Lincoln, Nebraska. 395 p.

Wiebe, H. H., G. S. Cambpell, W. H. Gardner, S. L. Rawlins, J. W. Cary, and R. W. Brown. 1971. Measurement of plant and soil water status. Utah Agr. Exp. Sta. Bull. 484. 71 p.

Williams, G. J., III and J. L. Markley. 1973. The photosynthetic pathway type of North American shortgrass prairie species and some ecological implications. Photosynthetica 7:262-270.

Williams, W. A., R. S. Loomis, W. G. Duncan, A. Dovat and F. Nunez. 1968. Canopy architecture at various population densities and the growth and grain yield of corn. Crop Sci. 8:303-308.

Wittwer, S. H. and W. Robb. 1964. Carbon dioxide enrichment of greenhouse atmospheres for food crop production. Econ. Bot. 18:34-56.

Woledge, Jane and O. R. Jewiss. 1969. The effect of temperature during growth on the subsequent rate of photosynthesis in leaves of tall fescue (*Festuca arundinacea* Schreb.). Ann. Bot. 33:897-913.

Wolf, F. T. 1969. Photosynthetic and respiratory rates as influenced by temperature and light intensity. J. Tenn. Acad. Sci. 44:15-17.

Wright, J. L. and E. R. Lemon. 1966. Photosynthesis under field conditions IX. Vertical distribution of photosynthesis within a corn crop. Agron. J. 58:265-268.

Wuenscher, J. E. and T. T. Kozlowski. 1971. Relationship of gas-exchange resistance to tree-seedling ecology. Ecology 52:1016-1023.

Zelitch, I. 1968. Investigations on photorespiration with a sensitive ^{14}C-assay. Plant Physiol. 43:1829-1837.

Zelitch, I. 1971. Photosynthesis, Photorespiration, and Plant Productivity. Academic Press, New York. 347 p.

Zelitch, I. and P. E. Waggoner. 1962. Effect of chemical control of stomata on transpiration and photosynthesis. Proc. Nat. Acad. Sci. U.S. 48:1101-1108.

APPENDIX A

Table 1. Three-way interaction means (followed by their standard errors in parenthesis) of net and gross photosynthetic rates and aboveground dark respiration rates (mg $CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$) of blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*). Carbon dioxide exchange measurements were replicated three times in the greenhouse at various levels of soil water potential, irradiance and temperature. A reproductive stage of phenology was constant throughout all determinations for both species.

Soil water potential, spatial center of container (bars)	Irradiance, visible spectrum ($ly \cdot min^{-1}$)	Air temperature within canopy (^oC)	Blue grama			Western wheatgrass		
			Gross photosynthetic rate (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Net photosynthetic rate (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Aboveground dark respiration rate (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Gross photosynthetic rate (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Net photosynthetic rate (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Aboveground dark respiration rate (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)
0	0.30	20	14.1(2.8)	10.7(2.6)	3.4(0.2)	10.5(0.3)	9.4(0.3)	1.1(0.5)
0	0.30	30	19.7(2.3)	10.9(1.5)	8.7(0.8)	11.2(0.9)	8.4(0.8)	2.8(0.9)
0	0.30	40	11.3(0.9)	1.4(1.3)	9.8(0.5)	7.6(1.4)	2.8(0.8)	4.9(0.6)
0	1.12	20	18.6(1.4)	15.3(1.2)	3.4(0.2)	14.8(2.3)	13.7(2.1)	1.1(0.5)
0	1.12	30	32.6(5.8)	23.9(5.0)	8.7(0.8)	16.2(2.2)	13.4(2.1)	2.8(0.9)
0	1.12	40	22.8(2.6)	13.0(2.9)	9.8(0.5)	12.0(2.7)	7.1(2.1)	4.9(0.6)
0	1.54	20	16.9(2.7)	13.5(2.5)	3.4(0.2)	15.5(3.4)	14.4(3.1)	1.1(0.5)
0	1.54	30	33.0(3.0)	24.3(2.3)	8.7(0.8)	17.0(3.5)	14.2(2.8)	2.8(0.9)
0	1.54	40	31.9(1.4)	22.0(1.8)	9.8(0.5)	11.0(2.1)	6.1(1.6)	4.9(0.6)
-15	0.30	20	9.4(0.4)	9.3(0.4)	0.1(0.1)	6.8(1.3)	6.1(1.1)	0.7(0.5)
-15	0.30	30	13.5(5.0)	10.2(3.2)	3.4(1.8)	3.3(1.1)	1.7(0.9)	1.6(0.2)
-15	0.30	40	8.8(2.4)	2.1(2.1)	6.7(1.4)	3.5(1.0)	0.5(0.5)	2.9(0.5)

Table 1. Continued

Soil water potential, spatial center of container (bars)	Irradiance, visible spectrum ($ly \cdot min^{-1}$)	Air temperature within canopy (°C)	Blue grama			Western Wheatgrass		
			Gross photosynthetic rate ($mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Net photosynthetic rate ($mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Gross photosynthetic rate ($mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Net photosynthetic rate ($mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$)
-15	1.12	20	13.2(3.7)	13.1(3.8)	0.1(0.1)	7.8(2.0)	7.1(1.8)	0.7(0.5)
-15	1.12	30	17.2(3.6)	13.9(2.1)	3.4(1.8)	4.3(0.7)	2.7(0.7)	1.6(0.2)
-15	1.12	40	11.5(4.8)	4.8(4.3)	6.7(1.4)	3.4(1.4)	0.5(0.9)	2.9(0.5)
-15	1.54	20	14.3(3.8)	14.2(3.8)	0.1(0.1)	7.7(1.9)	7.1(1.5)	0.7(0.5)
-15	1.54	30	20.8(7.5)	17.4(5.7)	3.4(1.8)	5.6(1.7)	3.9(1.6)	1.6(0.2)
-15	1.54	40	11.4(5.0)	4.7(5.1)	6.7(1.4)	3.4(1.3)	0.5(0.8)	2.9(0.5)
-30	0.30	20	5.4(4.4)	5.0(5.0)	0.4(0.7)	1.1(0.9)	0.7(0.7)	0.4(0.2)
-30	0.30	30	7.5(3.0)	4.5(1.9)	3.0(1.0)	1.6(1.2)	0.2(0.7)	1.4(0.5)
-30	0.30	40	4.4(1.5)	-0.3(0.9)	4.8(0.6)	1.3(0.5)	-0.9(0.5)	2.2(0.6)
-30	1.12	20	8.4(2.1)	8.0(2.7)	0.4(0.7)	2.2(0.8)	1.8(0.8)	0.4(0.2)
-30	1.12	30	8.5(3.6)	5.5(2.5)	3.0(1.0)	2.0(1.2)	0.6(0.8)	1.4(0.5)
-30	1.12	40	4.4(1.9)	-0.3(1.3)	4.8(0.6)	1.5(0.9)	-0.7(0.4)	2.2(0.6)
-30	1.54	20	8.8(1.1)	8.4(1.8)	0.4(0.7)	2.2(0.5)	1.8(0.6)	0.4(0.2)
-30	1.54	30	8.1(3.2)	5.1(2.4)	3.0(1.0)	2.1(1.2)	0.7(0.7)	1.4(0.5)
-30	1.54	40	4.6(1.8)	-0.1(1.2)	4.8(0.6)	1.2(0.8)	-1.0(0.6)	2.2(0.6)

Table 2. Analyses of variance of net photosynthetic rates (mg $CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$) for blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) in the greenhouse study at three levels each of soil water potential, irradiance, and temperature. Both species were at a reproductive phenological stage of growth.

		Blue grama	Western wheatgrass
Source of variation	df	Mean square	Mean square
Reps	2	0.001	0.003
Soil water (W)	2	0.064***	0.181***
Error (a)	4	0.003	0.003
Irradiance (I)	2	0.022***	0.010***
Temperature (T)	2	0.032***	0.053***
W x I	4	0.006***	0.004***
W x T	4	0.005***	0.008***
I x T	4	0.001*	0.001**
W x I x T	8	0.002***	0.0001
Error (b)	48	0.0005	0.0002
Total	80		

*** indicates significant difference at the 0.01 level of probability
** indicates significant difference at the 0.05 level of probability
* indicates significant difference at the 0.10 level of probability

Table 3. Analyses of variance of aboveground dark respiration rates (mg $CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$) for blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) in the greenhouse at three levels each of soil water potential and temperature. Both species were at a reproductive phenological stage of growth.

Source of variation	df	Blue grama	Western wheatgrass
		Mean square	Mean square
Reps	2	0.003	0.0002
Soil water (W)	2	0.425***	0.002**
Error (a)	4	0.015	0.0001
Temperature (T)	2	0.607***	0.004***
W x T	4	0.019**	0.0002**
Error (b)	12	0.005	0.00005
Total	26		

*** indicates significant difference at the 0.01 level of probability
** indicates significant difference at the o.05 level of probability

Table 4. Analyses of variance of gross photosynthetic rates (mg $CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$) for blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) in the greenhouse at three levels each of soil water potential, irradiance, and temperature. Both species were at a reproductive phenological stage of growth.

Source of variation	df	Blue grama	Western wheatgrass
		Mean square	Mean square
Reps	2	0.001	0.005
Soil water (W)	2	0.128***	0.246***
Error (a)	4	0.006	0.005
Irradiance (I)	2	0.022***	0.010***
Temperature (T)	2	0.022***	0.014***
W x I	4	0.006***	0.004***
W x T	4	0.007***	0.005***
I x T	4	0.001	0.0005*
W x I x T	8	0.002***	0.0001
Error (b)	48	0.0005	0.0002
Total	80		

*** indicates significant difference at the 0.01 level of probability
* indicates significant difference at the 0.10 level of probability

Table 5. Field steady state carbon dioxide exchange rates for the various conditions of phenology, soil water potential, irradiance and temperature for in situ blue grama (*Bouteloua gracilis*) sods throughout the 1972 growing season at the Pawnee Site.

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum ($ly \cdot min^{-1}$)	Air temperature within the canopy (°C)	Net carbon dioxide exchange rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[1]	Total dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[2]	Gross photosynthetic rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[3]	% of gross photosynthetic rate accounted for by net photosynthetic rate[4]	Calculated net photosynthetic rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[5]	Calculated aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[6]	Measured aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[7]	Calculated belowground respiration rate ($mg\ CO_2 \cdot m^{-2}$ ground $area \cdot hr^{-1}$)[8]	Measured belowground respiration rate ($mg\ CO_2 \cdot m^{-2}$ ground $area \cdot hr^{-1}$)[9]
6/8	7:45	.260	veg	0	.39	24.0	16.0	55.2	39.2	96	37.6	1.6	---	1393.4	---
6/8	8:15	.260	veg	0	.45	21.0	16.0	49.6	33.6	96	32.2	1.3	---	1253.8	---
6/8	10:05	.260	veg	0	.64	30.0	14.5	68.6	54.1	95	51.4	2.7	---	1713.6	---
6/8	10:30	.260	veg	0	.61	30.0	-23.4	37.9	61.3	95	58.3	3.1	---	906.0	---
6/8	14:15	.260	veg	0	.53	29.5	-17.0	34.7	51.7	95	49.1	2.6	---	835.3	---
6/8	15:30	.260	veg	0	.48	29.5	-19.8	29.3	49.1	95	46.6	2.5	---	697.8	---
6/12	8:30	.320	veg	0	.50	24.5	22.1	68.2	46.1	96	44.3	1.8	---	2122.8	---
6/14	11:00	.350	veg	0	.00	30.0	0.0	70.2	0.0	5	-3.5	-3.5	---	2332.8	---
6/15	8:30	.335	veg	0	.49	20.0	-35.6	14.7	50.4	96	48.4	2.0	---	426.5	---
6/19	10:40	.355	veg	0	.70	30.0	46.0	45.4	91.5	95	86.9	4.6	---	1450.4	---

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum ($ly \cdot min^{-1}$)	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[1]	Total dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[2]	Gross photosynthetic rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[3]	% of gross photosynthetic rate accounted for by net photosynthetic rate[4]	Calculated net photosynthetic rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[5]	Calculated aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[6]	Measured aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)[7]	Calculated belowground respiration rate ($mg\ CO_2 \cdot m^{-2}$ ground $area \cdot hr^{-1}$)[8]	Measured belowground respiration rate ($mg\ CO_2 \cdot m^{-2}$ ground $area \cdot hr^{-1}$)[9]
6/19	12:45	.355	veg	0	.76	30.0	-40.5	44.2	84.7	95	80.5	4.2	---	1418.8	--
6/21	9:30	.315	veg	0	.59	25.0	-37.3	32.6	70.0	96	67.2	2.8	---	940.2	--
6/21	11:30	.315	veg	0	.69	30.0	-47.3	32.6	80.0	95	76.0	4.0	---	902.4	--
6/22	10:30	.000	veg	0	.00	20.0	-----	----	----	--	----	---	---	------	587.6
6/26	10:30	.385	veg	-1	.66	30.0	-62.0	17.7	79.7	95	75.7	4.0	---	528.6	--
6/26	11:00	.385	veg	-1	.23	30.0	-26.6	17.7	44.3	95	42.1	2.2	---	596.8	--
6/26	12:00	.385	veg	-1	.48	30.0	-57.0	17.4	74.5	95	70.7	3.7	---	528.2	--
6/26	12:25	.385	veg	-2	.35	30.0	-43.6	17.7	61.3	95	58.3	3.1	---	564.0	--
6/26	13:00	.385	veg	-2	.74	30.0	-65.6	17.6	83.2	95	79.0	4.2	---	516.7	--
6/27	11:20	.415	veg	-4	.67	25.0	-14.8	26.7	41.5	96	39.8	1.7	---	1038.7	--
6/28	8:45	.390	veg	-8	.51	30.0	-26.9	25.3	52.2	92	48.0	4.2	---	823.5	--

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum ($ly \cdot min^{-1}$)	Air temperature within the canopy (°C)	Net carbon dioxide exchange rate ($mg\ CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$)[1]	Total dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$)[2]	Gross photosynthetic rate ($mg\ CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$)[3]	% of gross photosynthetic rate accounted for by net photosynthetic rate[4]	Calculated net photosynthetic rate ($mg\ CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$)[5]	Calculated aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$)[6]	Measured aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$)[7]	Calculated belowground respiration rate ($mg\ CO_2 \cdot m^{-2}$ ground area$\cdot hr^{-1}$)[8]	Measured belowground respiration rate ($mg\ CO_2 \cdot m^{-2}$ ground area$\cdot hr^{-1}$)[9]
7/5	7:20	.400	veg	0	.34	15.0	-11.7	13.0	24.7	98	24.2	0.5	---	501.7	--
7/5	7:40	.400	veg	0	.17	15.0	- 7.7	13.2	20.9	98	20.5	0.4	---	512.4	--
7/5	9:50	.400	veg	0	.64	25.0	-36.4	23.3	59.7	96	57.3	2.4	---	837.6	--
7/5	10:15	.400	veg	0	.21	25.0	-14.9	23.0	37.9	96	36.3	1.5	---	858.8	--
7/5	12:00	.400	veg	0	.70	25.0	-30.4	22.6	53.0	96	50.8	2.1	---	819.3	--
7/5	14:00	.400	veg	0	.66	35.0	-30.0	34.0	63.9	92	58.8	5.1	---	1153.9	--
7/5	14:12	.400	veg	0	.43	35.0	-26.2	33.4	59.7	92	54.9	4.8	---	1146.9	--
7/5	14:30	.400	veg	0	.30	35.0	-10.6	33.7	44.3	92	40.7	3.5	---	1206.5	--
7/6	10:30	.430	veg	0	.69	30.0	-38.6	29.1	67.8	95	64.4	3.4	---	1107.4	--
7/7	13:50	.000	---	0	.00	32.0	-----	----	----	--	----	---	---	------	1252.0
7/7	15:30	.000	---	0	.00	25.0	-----	----	----	--	----	---	---	------	1379.0
7/10	8:15	.410	veg	-1	.31	25.0	-20.3	18.3	38.6	96	37.1	1.5	---	688.2	--
7/10	8:25	.410	veg	-1	.22	25.0	-13.5	18.1	31.6	96	30.3	1.3	---	688.4	--

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum (ly.min^{-1})	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate (mg CO_2.dm^{-2} leaf area.hr^{-1})1	Total dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})2	Gross photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})3	% of gross photosynthetic rate accounted for by net photosynthetic rate4	Calculated net photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})5	Calculated aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})6	Measured aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})7	Calculated belowground respiration rate8(mg CO_2.m^{-2} ground area.hr^{-1})	Measured belowground respiration rate (mg CO_2.m^{-2} ground area.hr^{-1})9
7/10	10:15	.410	veg	-1	.66	25.0	-40.0	22.5	62.5	96	60.0	2.5	---	820.1	---
7/10	10:55	.410	veg	-1	.47	25.0	-37.8	22.0	59.8	96	57.4	2.4	---	802.7	---
7/10	11:25	.410	veg	-1	.35	25.0	-33.8	22.1	56.0	96	53.7	2.2	---	816.3	---
7/11	7:48	.360	veg	-2	.37	22.0	-26.3	10.5	36.8	96	35.3	1.5	---	325.6	---
7/11	8:08	.360	veg	-2	.29	22.0	-22.5	10.5	33.1	96	31.7	1.3	---	331.0	---
7/11	8:22	.360	veg	-2	.23	22.0	-17.9	10.4	28.3	96	27.2	1.1	---	335.0	---
7/11	8:36	.360	veg	-2	.17	22.0	-14.2	10.4	24.6	96	23.6	1.0	---	340.3	---
7/11	9:35	.360	veg	-2	.60	30.0	-31.6	13.6	45.2	94	42.5	2.7	---	393.1	---
7/11	9:53	.360	veg	-2	.41	30.0	-29.4	14.0	43.3	94	40.7	2.6	---	408.7	---
7/11	10:04	.360	veg	-2	.32	30.0	-22.8	14.0	36.7	94	34.5	2.2	---	423.0	---
7/11	10:18	.360	veg	-2	.23	30.0	-14.6	13.8	28.4	94	26.7	1.7	---	437.1	---
7/11	11:06	.360	veg	-2	.72	35.0	-25.3	15.2	40.5	90	36.4	4.0	---	400.9	---
7/11	11:24	.360	veg	-2	.75	40.0	-17.4	15.2	32.5	77	25.1	7.5	---	277.2	---
7/12	8:58	.415	veg	-5	.44	24.5	-32.2	22.3	54.5	96	52.3	2.2	---	835.8	---

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum (ly·min^{-1})	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate (mg CO_2·dm^{-2} leaf area·hr^{-1})1	Total dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})2	Gross photosynthetic rate (mg CO_2·dm^{-2} leaf area·hr^{-1})3	% of gross photosynthetic rate accounted for by net photosynthetic rate4	Calculated net photosynthetic rate (mg CO_2·dm^{-2} leaf area·hr^{-1})5	Calculated aboveground dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})6	Measured aboveground dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})7	Calculated belowground respiration rate (mg CO_2·m^{-2} ground area·hr^{-1})8	Measured belowground respiration rate (mg CO_2·m^{-2} ground area·hr^{-1})9
7/12	9:11	.415	veg	-5	.37	24.5	-26.3	22.3	48.6	96	46.6	1.9	---	845.6	---
7/12	9:35	.415	veg	-5	.29	24.5	-20.4	22.3	42.7	96	41.0	1.7	---	855.4	---
7/12	9:55	.415	veg	-5	.21	24.5	-13.0	22.2	35.2	96	33.8	1.4	---	861.0	---
7/12	12:00	.415	veg	-5	.73	31.5	-43.3	25.1	68.4	92	62.9	5.5	---	814.3	---
7/12	12:14	.415	veg	-5	.49	31.5	-37.6	25.1	62.7	92	57.7	5.0	---	833.0	---
7/12	12:28	.415	veg	-5	.36	31.5	-26.5	25.3	51.8	92	47.7	4.1	---	877.3	---
7/12	12:48	.415	veg	-5	.24	31.5	-14.9	24.9	39.8	92	36.6	3.2	---	901.0	---
7/12	13:40	.415	veg	-5	.68	33.8	-34.9	28.6	63.5	89	56.5	7.0	---	898.4	---
7/12	13:53	.415	veg	-5	.67	35.0	-34.6	25.9	60.5	87	52.7	7.9	---	749.9	---
7/12	14:10	.415	veg	-5	.65	40.0	-26.3	25.1	51.5	73	37.6	13.9	---	465.8	---
7/14	9:30	.420	veg	-11	.38	45.0	- 5.3	36.3	41.6	39	16.2	25.4	---	460.1	---
7/14	9:50	.420	veg	-11	.21	45.0	12.3	36.3	24.0	39	9.4	14.7	---	910.7	---
7/14	12:30	.420	veg	-11	.71	40.0	-12.7	33.4	46.1	64	29.5	16.6	---	707.1	---
7/14	13:05	.420	veg	-11	.46	40.0	-12.3	34.0	46.3	64	29.6	16.7	---	727.8	---
7/14	13:40	.420	veg	-11	.33	40.0	- 4.7	34.0	38.7	64	24.8	13.9	---	843.0	---

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum ($ly \cdot min^{-1}$)	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)1	Total dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)2	Gross photosynthetic rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)3	% of gross photosynthetic rate accounted for by net photosynthetic rate4	Calculated net photosynthetic rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)5	Calculated aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)6	Measured aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)7	Calculated belowground respiration rate ($mg\ CO_2 \cdot m^{-2}$ ground $area \cdot hr^{-1}$)8	Measured belowground respiration rate ($mg\ CO_2 \cdot m^{-2}$ ground $area \cdot hr^{-1}$)9
7/18	12:40	.430	veg	-14	.70	35.0	-21.2	32.1	53.3	78	41.6	11.7	---	875.7	---
7/18	12:50	.430	veg	-14	.46	35.0	-13.9	32.1	46.0	78	35.9	10.1	---	944.4	---
7/18	13:05	.430	veg	-14	.22	35.0	2.4	31.6	29.2	78	22.8	6.4	---	1082.0	---
7/18	14:00	.430	veg	-14	.21	30.0	3.0	29.8	26.8	89	23.9	3.0	---	1154.6	---
7/18	14:15	.430	veg	-14	.41	30.0	-10.7	29.8	40.5	89	36.1	4.5	---	1089.7	---
7/18	14:30	.430	veg	-14	.61	30.0	-14.9	29.8	44.7	89	39.8	4.9	---	1070.0	---
7/18	15:35	.430	veg	-14	.10	25.0	10.1	28.2	18.0	90	16.2	1.8	---	1133.3	---
7/19	8:20	.430	veg	-12	.46	35.0	- 4.4	41.9	46.3	80	37.0	9.3	---	1404.5	---
7/19	8:40	.430	veg	-12	.33	35.0	3.8	42.3	38.4	80	30.7	7.7	---	1487.5	---
7/19	8:56	.430	veg	-12	.26	35.0	10.5	42.6	32.1	80	25.7	6.4	---	1557.3	---
7/19	9:12	.430	veg	-12	.20	35.0	17.7	42.6	24.9	80	19.9	5.0	---	1619.2	---
7/19	10:20	.430	veg	-12	.22	35.0	14.0	41.6	27.5	80	22.0	5.5	---	1550.2	---
7/19	10:35	.430	veg	-12	.33	35.0	6.0	41.9	35.9	80	28.7	7.2	---	1493.5	---
7/19	11:00	.430	veg	-12	.47	35.0	- 3.3	41.9	45.2	80	36.1	9.0	---	1413.9	---
7/19	12:46	.430	veg	-12	.74	40.0	- 5.9	43.7	49.7	61	30.3	19.4	---	1047.1	---

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum (ly.min^{-1})	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^1	Total dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^2	Gross photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^3	% of gross photosynthetic rate accounted for by net photosynthetic rate^4	Calculated net photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^5	Calculated aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^6	Measured aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^7	Calculated belowground respiration rate (mg CO_2.m^{-2} ground area.hr^{-1})^8	Measured belowground respiration rate (mg CO_2.m^{-2} ground area.hr^{-1})^9
7/21	11:00	.430	veg	-25	.71	35.0	-10.4	37.3	47.8	59	28.2	19.6	---	763.3	---
7/21	12:05	.430	veg	-25	.47	35.0	- 3.8	37.0	40.8	59	24.1	16.7	---	872.0	---
7/21	12:15	.430	veg	-25	.24	35.0	8.2	37.3	29.1	59	17.2	11.9	---	1092.5	---
7/21	13:00	.430	veg	-25	.23	30.0	8.9	33.8	24.9	76	18.9	6.0	---	1195.4	---
7/21	13:25	.430	veg	-25	.45	30.0	- 0.6	33.8	34.3	76	26.1	8.2	---	1098.2	---
7/21	13:45	.430	veg	-25	.66	31.5	- 4.4	34.3	38.8	71	27.5	11.2	---	993.0	---
7/21	14:30	.430	veg	-25	.20	40.0	17.2	38.2	21.0	29	6.1	14.9	---	1000.6	---
7/21	15:00	.430	veg	-25	.37	40.0	6.6	37.9	31.3	29	9.1	22.2	---	673.6	---
7/21	15:15	.430	veg	-25	.55	40.0	0.0	37.9	37.9	29	11.0	26.9	---	472.4	---
7/21	15:35	.430	veg	-25	.49	45.0	14.8	45.6	30.7	-8	-2.5	33.2	---	531.7	---
7/26	8:00	.370	rep	-50	.39	30.0	4.7	17.4	12.7	70	8.9	3.8	3.6	503.9	512.8
7/26	8:25	.370	rep	-50	.29	30.0	5.4	18.1	12.7	70	8.9	3.8	4.2	528.7	512.8
7/26	8:40	.370	rep	-50	.16	30.0	8.7	18.1	9.4	70	6.6	2.8	4.2	565.9	512.8
7/26	9:20	.370	rep	-50	.19	35.0	12.4	19.6	7.2	52	3.7	3.5	3.5	598.6	598.1
7/26	9:35	.370	rep	-50	.39	35.0	11.0	19.5	8.4	52	4.4	4.0	3.3	570.6	598.1

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum (ly.min^{-1})	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[1]	Total dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[2]	Gross photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[3]	% of gross photosynthetic rate accounted for by net photosynthetic rate[4]	Calculated net photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[5]	Calculated aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[6]	Measured aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[7]	Calculated belowground respiration rate (mg CO_2.m^{-2} ground area.hr^{-1})[8]	Measured belowground respiration rate (mg CO_2.m^{-2} ground area.hr^{-1})[9]
7/26	9:50	.370	rep	-50	.61	35.0	8.5	19.6	11.1	52	5.8	5.3	3.5	528.9	598.1
7/26	11:10	.370	rep	-50	.46	35.0	8.4	18.8	10.4	52	5.4	5.0	2.7	512.0	598.1
7/26	11:25	.370	rep	-50	.23	35.0	9.2	19.1	9.9	52	5.1	4.8	3.0	532.3	598.1
7/26	11:55	.370	rep	-50	.26	35.0	8.4	18.7	10.3	52	5.4	4.9	2.5	507.7	598.1
7/26	14:20	.000	rep	-50	.00	40.0	----	----	----	--	---	---	---	------	632.0
7/27	8:00	.415	rep	-50	.39	21.0	-14.4	8.4	22.7	91	20.7	2.0	---	262.6	--
7/27	8:15	.415	rep	-50	.27	20.0	-12.0	8.4	20.3	93	18.9	1.4	---	288.4	--
7/27	8:30	.415	rep	-50	.31	20.0	-12.5	8.3	20.8	93	19.3	1.5	---	284.4	--
7/27	9:30	.415	rep	-50	.58	27.5	-18.2	10.0	28.2	78	22.0	6.2	---	157.2	--
7/27	9:45	.415	rep	-50	.39	25.0	-15.3	9.4	24.7	84	20.8	4.0	---	226.6	--
7/27	9:55	.415	rep	-50	.20	25.0	- 8.8	9.3	18.1	84	15.2	2.9	---	267.3	--
7/27	11:50	.415	rep	-50	.26	30.0	-16.5	11.8	28.2	70	19.8	8.5	---	136.7	--
7/28	14:45	.340	rep	-50	.59	41.0	2.8	23.4	20.7	13	2.7	18.0	---	184.9	--
7/28	15:10	.340	rep	-50	.36	41.0	5.5	23.4	17.9	13	2.3	15.6	---	266.4	--

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum (ly.min^{-1})	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[1]	Total dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[2]	Gross photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[3]	% of gross photosynthetic rate accounted for by net photosynthetic rate[4]	Calculated net photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[5]	Calculated aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[6]	Measured aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[7]	Calculated belowground respiration rate (mg CO_2.m^{-2} ground area.hr^{-1})[8]	Measured belowground respiration rate (mg CO_2.m^{-2} ground area.hr^{-1})[9]
7/28	15:30	.340	rep	-50	.18	41.0	9.6	23.4	13.8	13	1.8	12.0	---	388.6	--
7/28	16:15	.340	rep	-50	.40	45.0	10.0	24.9	15.0	-31	-4.6	19.6	---	181.4	--
7/31	10:24	.410	rep	-50	.12	22.5	5.5	18.5	12.9	88	11.4	1.6	---	693.2	--
8/1	8:50	.345	rep	-50	.50	25.0	16.0	45.0	29.0	84	24.4	4.6	---	1391.3	--
8/1	8:58	.345	rep	-50	.35	25.0	18.7	44.6	25.9	84	21.8	4.1	---	1395.9	--
8/1	9:12	.345	rep	-50	.18	25.0	24.8	43.9	19.1	84	16.1	3.1	---	1408.4	--
8/1	9:58	.345	rep	-50	.62	35.0	13.3	46.3	33.0	52	17.2	15.8	---	1051.9	--
8/1	10:15	.345	rep	-50	.65	40.0	19.7	47.7	28.1	22	6.2	21.9	---	891.1	--
8/1	10:27	.345	rep	-50	.43	40.0	24.2	46.9	22.8	22	5.0	17.8	---	1006.3	--
8/1	10:38	.345	rep	-50	.23	40.0	31.3	47.3	16.0	22	3.5	12.5	---	1202.1	--
8/1	12:10	.345	rep	-50	.72	45.0	24.8	49.0	24.2	-31	-7.5	31.6	---	598.9	--
8/1	12:35	.345	rep	-50	.46	45.0	30.3	47.8	17.5	-31	-5.4	22.9	---	857.3	--
8/1	12:50	.345	rep	-50	.23	45.0	30.7	47.3	16.7	-31	-5.2	21.8	---	879.9	--

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum (Ly·min^{-1})	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate (mg CO_2·dm^{-2} leaf area·hr^{-1})1	Total dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})2	Gross photosynthetic rate (mg CO_2·dm^{-2} leaf area·hr^{-1})3	% of gross photosynthetic rate accounted for by net photosynthetic rate4	Calculated net photosynthetic rate (mg CO_2·dm^{-2} leaf area·hr^{-1})5	Calculated aboveground dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})6	Measured aboveground dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})7	Calculated belowground respiration rate (mg CO_2·m^{-2} ground area·hr^{-1})8	Measured belowground respiration rate (mg CO_2·m^{-2} ground area·hr^{-1})9
8/2	8:55	.405	rep	-2	.24	20.0	4.9	23.3	18.4	96	17.7	0.7	---	913.4	---
8/2	9:05	.405	rep	-2	.35	20.0	0.0	23.1	23.1	96	22.2	0.9	---	898.1	---
8/2	9:20	.405	rep	-2	.18	20.0	5.5	23.3	17.8	96	17.1	0.7	---	914.4	---
8/6	8:55	.390	rep	0	.51	30.0	-5.1	40.4	45.5	95	43.2	2.3	---	1487.0	---
8/6	9:20	.390	rep	0	.19	30.0	15.9	40.7	24.8	95	23.6	1.2	---	1540.2	---
8/6	10:05	.390	rep	0	.20	30.0	15.2	40.4	25.3	95	24.0	1.3	---	1526.4	---
8/6	10:45	.390	rep	0	.22	40.0	19.1	46.8	27.7	81	22.4	5.3	---	1619.8	---
8/6	11:00	.390	rep	0	.45	40.0	3.1	46.8	43.7	81	35.4	8.3	---	1501.1	---
8/6	11:15	.390	rep	0	.68	42.0	-5.5	46.4	51.9	74	38.4	13.5	---	1283.5	---
8/6	11:45	.390	rep	0	.46	45.0	9.9	49.3	39.4	65	25.6	13.8	---	1383.2	---
8/6	11:55	.390	rep	0	.24	45.0	22.2	49.3	27.1	65	17.6	9.5	---	1551.3	---
8/6	13:40	.390	rep	0	.00	36.0	0.0	43.7	0.0	10	-4.4	4.4	---	1532.1	---
8/8	10:46	.360	rep	0	.68	35.0	-23.5	31.6	55.2	92	50.7	4.4	---	979.3	---
8/8	11:00	.360	rep	0	.45	35.0	-15.5	31.6	47.1	92	43.3	3.8	---	1002.5	---

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum (ly.min^{-1})	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[1]	Total dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[2]	Gross photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[3]	% of gross photosynthetic rate accounted for by net photosynthetic rate[4]	Calculated net photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[5]	Calculated aboveground dark respiration$_2$rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[6]	Measured aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[7]	Calculated belowground respiration rate (mg CO_2 m^{-2} ground area.hr^{-1})[8]	Measured belowground respiration rate (mg CO_2 m^{-2} ground area.hr^{-1})[9]
8/8	11:17	.360	rep	0	.23	35.0	0.0	31.4	31.4	92	28.8	2.5	---	1038.4	--
8/9	8:10	.375	rep	-2	.41	25.0	-20.2	15.5	35.7	96	34.2	1.4	1.8	526.7	512.8
8/9	8:30	.375	rep	-2	.22	25.0	-11.3	15.3	26.7	96	25.6	1.1	1.7	535.5	512.8
8/9	9:20	.375	rep	-2	.53	27.0	-20.7	15.5	36.2	95	34.4	1.8	1.5	513.4	525.9
8/9	9:45	.375	rep	-2	.59	30.0	-19.7	15.9	35.6	94	33.4	2.1	1.6	515.3	537.2
8/9	10:00	.375	rep	-2	.39	30.0	-15.9	15.9	31.7	94	29.8	1.9	1.6	523.9	537.2
8/9	10:15	.375	rep	-2	.22	30.0	-10.8	15.9	26.7	94	25.1	1.6	1.6	535.3	537.2
8/9	10:45	.375	rep	-2	.00	35.0	0.0	17.9	0.0	10	-1.8	1.8	2.6	605.3	576.3
8/9	11:00	.375	rep	-2	.24	35.0	- 7.7	17.9	25.6	90	23.1	2.6	2.6	576.3	576.3
8/9	11:50	.375	rep	-2	.47	35.0	-12.7	17.8	30.5	90	27.4	3.0	2.4	552.4	576.3
8/9	13:00	.375	rep	-2	.00	40.0	0.0	21.2	0.0	22	-4.7	4.7	5.1	620.7	605.4
8/9	13:25	.375	rep	-2	.23	40.0	3.1	21.4	18.3	78	14.2	4.0	5.3	652.1	605.4
8/9	14:05	.375	rep	-2	.41	40.0	- 2.5	21.2	23.7	78	18.4	5.2	5.1	600.2	605.4
8/9	14:20	.375	rep	-2	.60	40.0	- 4.4	21.2	25.6	78	20.0	5.6	5.1	584.7	605.4
8/9	14:35	.375	rep	-2	.57	45.0	3.6	22.9	19.3	59	11.4	7.9	6.6	562.3	610.4

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum (ly·min^{-1})	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate (mg CO_2·dm^{-2} leaf area·hr^{-1})[1]	Total dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})[2]	Gross photosynthetic rate (mg CO_2·dm^{-2} leaf area·hr^{-1})[3]	% of gross photosynthetic rate accounted for by net photosynthetic rate[4]	Calculated net photosynthetic rate (mg CO_2·dm^{-2} leaf area·hr^{-1})[5]	Calculated aboveground dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})[6]	Measured aboveground dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})[7]	Calculated belowground respiration rate (mg CO_2·m^{-2} ground area·hr^{-1})[8]	Measured belowground respiration rate (mg CO_2·m^{-2} ground area·hr^{-1})[9]
8/9	14:45	.375	rep	-2	.36	45.0	5.5	23.3	17.8	59	10.5	7.3	7.0	600.7	610.4
8/9	15:00	.375	rep	-2	.18	45.0	8.1	23.7	15.6	59	9.2	6.4	7.4	649.6	610.4
8/9	15:35	.375	rep	-2	.00	40.0	0.0	20.0	0.0	22	-4.4	4.4	3.8	584.3	605.4
8/9	17:35	.000	rep	-2	.00	20.0	-----	----	----	--	----	---	---	------	492.4
8/10	9:00	.380	rep	-4	.49	30.0	- 6.4	23.6	30.0	93	27.9	2.1	---	816.3	--
8/10	9:10	.380	rep	-4	.34	30.0	- 3.2	23.6	26.8	93	24.9	1.9	---	824.8	--
8/10	9:20	.380	rep	-4	.18	30.0	4.5	23.6	19.1	93	17.8	1.3	---	845.1	--
8/10	10:30	.380	rep	-4	.64	32.0	- 6.8	24.2	31.1	91	28.3	2.8	---	814.6	--
8/10	10:50	.380	rep	-4	.68	37.0	- 4.4	27.2	31.6	84	26.5	5.1	---	840.5	--
8/10	11:00	.380	rep	-4	.45	37.0	0.0	26.9	26.9	84	22.6	4.3	---	860.1	--
8/10	12:20	.380	rep	-4	.72	40.5	1.3	29.1	27.8	72	20.0	7.8	---	808.8	--
8/10	12:30	.380	rep	-4	.48	40.5	3.8	29.1	25.3	72	18.2	7.1	---	835.7	--
8/10	12:45	.380	rep	-4	.24	40.5	9.4	28.8	19.4	72	14.0	5.4	---	888.7	--
8/10	13:30	.380	rep	-4	.76	45.0	9.3	31.1	21.7	56	12.2	9.6	---	816.9	--

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum ($ly \cdot min^{-1}$)	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)1	Total dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)2	Gross photosynthetic rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)3	% of gross photosynthetic rate accounted for by net photosynthetic rate4	Calculated net photosynthetic rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)5	Calculated aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)6	Measured aboveground dark respiration rate ($mg\ CO_2 \cdot dm^{-2}$ leaf $area \cdot hr^{-1}$)7	Calculated belowground respiration rate8 ($mg\ CO_2 \cdot m^{-2}$ ground $area \cdot hr^{-1}$)	Measured belowground respiration rate9 ($mg\ CO_2 \cdot m^{-2}$ ground $area \cdot hr^{-1}$)
8/11	8:55	.365	rep	-16	.50	25.0	13.0	30.2	17.1	95	16.3	0.9	---	1069.7	--
8/11	9:15	.365	rep	-16	.34	25.0	14.0	29.4	15.4	95	14.6	0.8	---	1046.3	--
8/11	9:30	.365	rep	-16	.18	25.0	19.6	29.7	10.1	95	9.6	0.5	---	1064.8	--
8/11	10:35	.365	rep	-16	.22	30.0	17.5	31.0	13.5	87	11.7	1.8	---	1068.5	--
8/11	11:00	.365	rep	-16	.45	30.0	13.4	30.8	17.4	87	15.1	2.3	---	1040.7	--
8/11	11:30	.365	rep	-17	.69	35.0	12.6	33.2	20.6	72	14.8	5.8	---	1000.6	--
8/11	11:45	.365	rep	-17	.70	36.0	13.3	33.2	19.9	65	12.9	7.0	---	956.5	--
8/11	12:10	.365	rep	-17	.70	37.0	13.7	32.6	18.9	62	11.7	7.2	---	928.2	--
8/11	12:40	.365	rep	-18	.46	37.0	16.3	32.6	16.3	61	9.9	6.4	---	958.4	--
8/11	13:00	.365	rep	-18	.23	37.0	19.7	32.9	13.2	61	8.0	5.1	---	1013.4	--
8/11	13:35	.365	rep	-18	.64	43.0	16.2	34.3	18.1	29	5.3	12.9	---	782.0	--
8/11	13:50	.365	rep	-18	.41	43.0	18.1	34.3	16.2	29	4.7	11.5	---	832.3	--
8/11	15:00	.365	rep	-18	.21	43.0	21.7	34.9	13.2	29	3.8	9.3	---	931.7	--
8/12	12:43	.000	rep	-37	.00	45.0	-----	----	----	--	----	----	---	------	584.8
8/12	13:00	.000	rep	-37	.00	40.0	-----	----	----	--	----	----	---	------	600.6

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum (ly.min^{-1})	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[1]	Total dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[2]	Gross photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[3]	% of gross photosynthetic rate accounted for by net photosynthetic rate[4]	Calculated net photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[5]	Calculated aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[6]	Measured aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})[7]	Calculated belowground respiration rate (mg CO_2.m^{-2} ground area.hr^{-1})[8]	Measured belowground respiration rate (mg CO_2.m^{-2} ground area.hr^{-1})[9]
8/12	13:12	.000	rep	-37	.00	35.0	-----	----	----	--	----	----	---	------	620.5
8/12	13:30	.000	rep	-37	.00	30.0	-----	----	----	--	----	----	---	------	615.5
8/15	9:15	.355	rep	-50	.57	34.0 - 7.6		19.4	27.0	56	15.1	11.9	---	266.9	--
8/16	9:50	.355	rep	-50	.23	16.0 - 2.9		13.1	16.0	97	15.5	0.5	---	447.9	--
8/16	10:15	.355	rep	-50	.12	17.0 - 3.6		13.0	16.6	96	15.9	0.7	---	437.7	--
8/16	11:45	.355	rep	-50	.28	22.0 - 5.6		14.1	19.7	89	17.6	2.2	---	423.4	--
8/16	12:25	.355	rep	-50	.11	22.0 - 4.2		14.1	18.3	89	16.3	2.0	---	428.9	--
8/16	12:35	.355	rep	-50	.12	30.0 - 4.4		13.8	18.2	70	12.7	5.5	---	297.0	--
8/16	13:08	.355	rep	-50	.22	30.0 - 7.3		13.9	21.3	70	14.9	6.4	---	268.1	--
8/18	8:45	.350	rep	-50	.45	30.0 - 0.7		15.7	16.5	70	11.5	4.9	---	377.8	--
8/18	9:00	.350	rep	-50	.31	30.0	0.7	15.7	15.0	70	10.5	4.5	---	392.9	--
8/18	9:15	.350	rep	-50	.17	30.0	4.3	15.7	11.4	70	8.0	3.4	---	430.4	--
8/18	10:25	.350	rep	-50	.63	35.0	1.4	17.6	16.2	52	8.4	7.8	---	343.7	--

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum (ly·min^{-1})	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate (mg CO_2·dm^{-2} leaf area·hr^{-1})1	Total dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})2	Gross photosynthetic rate (mg CO_2·dm^{-2} leaf area·hr^{-1})3	% of gross photosynthetic rate accounted for by net photosynthetic rate4	Calculated net photosynthetic rate (mg CO_2·dm^{-2} leaf area·hr^{-1})5	Calculated aboveground dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})6	Measured aboveground dark respiration rate (mg CO_2·dm^{-2} leaf area·hr^{-1})7	Calculated belowground respiration rate8 (mg CO_2·m^{-2} ground area·hr^{-1})	Measured belowground respiration rate9 (mg CO_2·m^{-2} ground area·hr^{-1})
8/18	10:45	.350	rep	-50	.43	35.0	2.1	17.9	15.7	52	8.2	7.5	---	361.3	--
8/18	11:00	.350	rep	-50	.22	35.0	5.7	17.9	12.2	52	6.3	5.8	---	421.4	--
8/18	13:40	.350	rep	-50	.67	44.5	5.7	22.2	16.4	-26	-4.3	20.7	---	50.5	--
8/18	13:55	.350	rep	-50	.41	44.5	8.6	22.2	13.6	-26	-3.5	17.1	---	176.7	--
8/18	14:35	.350	rep	-50	.19	39.5	8.6	20.0	11.4	25	2.9	8.6	---	400.4	--
8/18	14:55	.350	rep	-50	.18	44.5	12.2	22.2	10.0	-26	-2.6	12.6	---	334.3	--
8/18	16:10	.350	rep	-50	.36	39.5	8.6	20.0	11.4	-11	-1.3	12.7	---	256.2	--
8/25	9:16	.165	rep	0	.53	19.0	48.9	97.8	48.9	97	47.5	1.5	---	1590.2	--
8/25	9:35	.165	rep	0	.27	19.0	70.9	98.6	27.7	97	26.9	0.8	---	1613.6	--
8/25	9:47	.165	rep	0	.19	19.0	71.9	97.8	26.0	97	25.2	0.8	---	1601.5	--
8/25	10:40	.165	rep	0	.63	25.0	56.1	100.1	44.0	96	42.2	1.8	---	1622.5	--
8/25	11:05	.165	rep	0	.32	25.0	59.1	100.1	40.0	96	39.3	1.6	---	1624.5	--
8/28	9:10	.320	rep	0	.49	25.0	20.0	56.2	36.2	96	34.7	1.4	---	1750.0	--
8/28	9:28	.320	rep	0	.34	25.0	26.4	56.6	30.3	96	29.0	1.2	---	1773.2	--

Table 5. Continued

Date	Standard time (hours)	Leaf area index	Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum (ly.min^{-1})	Air temperature within the canopy (^{o}C)	Net carbon dioxide exchange rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^{1}	Total dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^{2}	Gross photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^{3}	% of gross photosynthetic rate accounted for by net photosynthetic rate^{4}	Calculated net photosynthetic rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^{5}	Calculated aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^{6}	Measured aboveground dark respiration rate (mg CO_2.dm^{-2} leaf area.hr^{-1})^{7}	Calculated belowground respiration rate (mg CO_2.m^{-2} ground area.hr^{-1})^{8}	Measured belowground respiration rate (mg CO_2.m^{-2} ground area.hr^{-1})^{9}
8/28	9:43	.320	rep	0	.17	25.0	37.2	56.6	19.4	96	18.6	0.8	---	1787.1	--
8/30	9:00	.315	veg	0	.48	22.0	0.0	39.7	39.7	96	38.1	1.6	---	1201.1	--
8/30	9:15	.315	veg	0	.24	22.0	12.7	39.7	27.0	96	25.9	1.1	---	1217.1	--
8/30	10:25	.315	veg	0	.61	28.0	- 6.5	42.1	48.5	96	46.5	1.9	---	1265.2	--
8/30	10:40	.315	veg	0	.42	28.0	1.6	42.1	40.5	96	38.9	1.6	---	1275.2	--
9/12	9:46	.205	veg	0	.35	25.0	3.7	65.9	62.3	96	59.8	2.5	4.0	1300.2	1269.7
9/12	9:55	.205	veg	0	.19	25.0	24.2	65.4	41.2	96	39.5	1.6	3.4	1306.6	1269.7
9/12	10:45	.205	veg	0	.20	30.0	33.6	64.9	31.2	95	29.7	1.6	2.9	1297.4	1269.7
9/12	10:55	.205	veg	0	.39	30.0	8.4	64.9	56.4	95	53.6	2.8	2.9	1271.6	1269.7
9/12	11:08	.205	veg	0	.60	30.0	-10.8	64.9	75.7	95	71.9	3.8	2.9	1251.9	1269.7
9/12	11:45	.205	veg	0	.62	30.0	-13.2	64.9	78.1	95	74.2	3.9	2.9	1249.4	1269.7

Table 5. Continued - Footnotes

[1]The net carbon dioxide exchange rate (NCE) was defined as the rate at which the carbon dioxide (CO_2) in the ambient air being pumped into the CO_2 exchange system was utilized during photosynthesis. NCE could be positive, negative or zero, depending on the relationship between the photosynthetic rate and the respiration rate.

[2]The total dark respiration rate (RESP) was the rate at which carbon dioxide was liberated into the CO_2 exchange system in darkness from both the aboveground foliage respiration (AGR) and the belowground root and soil microbial respiration (BGR). Resp = AGR + BGR.

[3]The gross photosynthetic rate (Pg) was the actual rate at which carbon dioxide was fixed by the plant during photosynthesis. It was determined by: Pg = -(NCE) + RESP = -(NCE) + AGR + BGR.

[4]The percentage of the gross photosynthetic rate accounted for by the net photosynthetic rate was determined from figure 9. The figure was derived from both field and greenhouse measurements of CO_2 exchange of blue grama.

[5]The calculated net photosynthetic rate (Pn) was determined by multiplying the previously determined percentage at the existing conditions by the gross photosynthetic rate. Net photosynthesis was defined as gross photosynthesis minus aboveground respiration. Pn = Pg - AGR = -(NCE) + BGR. In darkness Pn was equal but opposite in sign to AGR.

[6]The calculated aboveground dark respiration rate was the remaining portion of the gross photosynthetic rate not accounted for by net photosynthesis. AGR = Pg - Pn = Pg + (NCE) - BGR.

[7]The measured aboveground dark respiration rate was determined by the subtraction of the measured belowground respiration rate of a clipped sod from the total dark respiration rate. AGR = Resp - BGR.

[8]The calculated belowground respiration rate was determined by subtracting the calculated aboveground dark respiration rate from the total dark respiration rate. BGR = RESP - AGR.

[9]The measured belowground respiration rate was determined by measuring the CO_2 exchange rate of a clipped sod.

Table 6. Four-way interaction means (followed by standard errors in parenthesis) of measured gross and calculated net photosynthetic rate (mg $CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$) for in situ blue grama (*Bouteloua gracilis*) sods as influenced by phenology, soil water potential, irradiance and temperature throughout the 1972 growing season at the Pawnee Site.

Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum ($ly \cdot min^{-1}$)	Air temperature within the canopy (^oC)	Gross photosynthesis (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Calculated net photosynthesis (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Number of observations making up the means (n)
veg	0	.10 to .25	15.0 to 22.5	23.9(4.4)	23.2(3.9)	2
veg	0	.10 to .25	22.6 to 30.0	36.7(5.0)	35.2(5.0)	3
veg	0	.26 to .42	15.0 to 22.5	24.7(---)[1]	24.2(---)	1
veg	0	.26 to .42	22.6 to 30.0	49.6(11.5)	47.5(10.9)	4
veg	0	.26 to .42	30.1 to 37.5	44.2(---)	40.7(---)	1
veg	0	.43 to .59	15.0 to 22.5	41.2(8.2)	39.6(8.5)	3
veg	0	.43 to .59	22.6 to 30.0	54.2(10.7)	51.8(10.4)	4
veg	0	.43 to .59	30.1 to 37.5	59.6(---)	54.9(---)	1
veg	0	.60 to .76	22.6 to 30.0	68.5(14.3)	65.3(13.4)	11
veg	0	.60 to .76	30.1 to 37.5	63.9(---)	58.8(---)	1
veg	-1 to -49	.10 to .25	15.0 to 22.5	26.5(2.6)	25.4(2.5)	2
veg	-1 to -49	.10 to .25	22.6 to 30.0	29.8(8.3)	27.4(8.9)	7
veg	-1 to -49	.10 to .25	30.1 to 37.5	30.1(5.7)	23.7(7.6)	5
veg	-1 to -49	.10 to .25	37.6 to 45.0	22.5(2.1)	7.7(2.3)	2

Table 6. Continued

Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum ($ly \cdot min^{-1}$)	Air temperature within the canopy (^{o}C)	Gross photosynthesis ($mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Calculated net photosynthesis ($mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Number of observations making up the means (n)
veg	-1 to -49	.26 to .42	15.0 to 22.5	34.9(2.7)	33.5(2.5)	2
veg	-1 to -49	.26 to .42	22.6 to 30.0	45.9(8.7)	43.5(8.7)	8
veg	-1 to -49	.26 to .42	30.1 to 37.5	39.6(8.6)	33.2(9.9)	4
veg	-1 to -49	.26 to .42	37.6 to 45.0	37.2(5.3)	16.7(7.9)	3
veg	-1 to -49	.43 to .59	22.6 to 30.0	55.0(14.5)	50.9(16.3)	5
veg	-1 to -49	.43 to .59	30.1 to 37.5	48.2(8.4)	38.2(12.2)	5
veg	-1 to -49	.43 to .59	37.6 to 45.0	38.3(7.8)	12.7(16.1)	3
veg	-1 to -49	.60 to .76	22.6 to 30.0	59.4(18.6)	56.1(18.1)	6
veg	-1 to -49	.60 to .76	30.1 to 37.5	53.2(11.5	43.7(14.0)	7
veg	-1 to -49	.60 to .76	37.6 to 45.0	44.9(8.6)	30.6(5.2)	4
rep	0	.10 to .25	15.0 to 22.5	25.9(---)	25.2(---)	1
rep	0	.10 to .25	22.6 to 30.0	23.1(3.3)	22.1(3.0)	3
rep	0	.10 to .25	30.1 to 37.5	31.3(---)	28.8(---)	1
rep	0	.10 to .25	37.6 to 45.0	27.4(0.5)	20.0(3.4)	2
rep	0	.26 to .42	15.0 to 22.5	27.7(---)	26.9(---)	1
rep	0	.26 to .42	22.6 to 30.0	35.6(7.6)	34.2(7.3)	2

Table 6. Continued

Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum ($ly \cdot min^{-1}$)	Air temperature within the canopy (^{o}C)	Gross photosynthesis (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Calculated net photosynthesis (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Number of observations making up the means (n)
rep	0	.43 to .59	15.0 to 22.5	48.9(---)	47.5(---)	1
rep	0	.43 to .59	22.6 to 30.0	40.8(6.7)	38.9(6.0)	2
rep	0	.43 to .59	30.1 to 37.5	47.0(---)	43.3(---)	1
rep	0	.43 to .59	37.5 to 45.0	41.6(3.0)	30.5(6.9)	2
rep	0	.60 to .76	22.6 to 30.0	43.9(---)	42.2(---)	1
rep	0	.60 to .76	30.1 to 37.5	55.1(---)	50.8(---)	1
rep	0	.60 to .76	37.6 to 45.0	51.9(---)	38.4(---)	1
rep	-1 to -49	.10 to .25	15.0 to 22.5	18.0(0.4)	17.4(0.4)	2
rep	-1 to -49	.10 to .25	22.6 to 30.0	19.2(7.5)	18.0(7.4)	5
rep	-1 to -49	.10 to .25	30.1 to 37.5	19.4(8.8)	15.5(10.6)	2
rep	-1 to -49	.10 to .25	37.6 to 45.0	16.6(2.8)	10.3(4.9)	4
rep	-1 to -49	.26 to .42	15.0 to 22.5	23.1(---)	22.2(---)	1
rep	-1 to -49	.26 to .42	22.6 to 30.0	27.3(8.8)	25.9(8.4)	4
rep	-1 to -49	.26 to .42	37.6 to 45.0	19.2(4.0)	11.2(6.9)	3
rep	-1 to -49	.43 to .59	22.6 to 30.0	27.2(9.4)	25.4(9.2)	5
rep	-1 to -49	.43 to .59	30.1 to 37.5	24.5(7.3)	20.0(9.0)	3
rep	-1 to -49	.43 to .59	37.6 to 45.0	22.2(4.2)	14.8(4.8)	2

Table 6. Continued

Phenology (vegetative or reproductive)	Soil water potential, 10.0 cm depth (bars)	Irradiance, visible spectrum ($ly \cdot min^{-1}$)	Air temperature within the canopy (^{o}C)	Gross photosynthesis ($mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Calculated net photosynthesis ($mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Number of observations making up the means (n)
rep	-1 to -49	.60 to .76	30.1 to 37.5	24.4(6.3)	18.9(7.9)	5
rep	-1 to -49	.60 to .76	37.6 to 35.0	23.3(4.3)	14.4(7.1)	4
rep	-50 or less	.10 to .25	15.0 to 22.5	16.0(2.3)	14.8(2.3)	4
rep	-50 or less	.10 to .25	22.6 to 30.0	16.2(4.7)	12.2(4.0)	6
rep	-50 or less	.10 to .25	30.1 to 37.5	9.7(2.5)	5.1(1.3)	3
rep	-50 or less	.10 to .25	37.6 to 45.0	13.5(2.9)	0.1(3.8)	5
rep	-50 or less	.26 to .42	15.0 to 22.5	20.9(1.3)	19.1(1.3)	4
rep	-50 or less	.26 to .42	22.6 to 30.0	19.9(7.2)	15.1(6.3)	6
rep	-50 or less	.26 to .42	30.1 to 37.5	9.4(1.3)	4.9(0.7)	2
rep	-50 or less	.26 to .42	37.6 to 45.0	14.4(2.7)	-1.8(3.1)	4
rep	-50 or less	.43 to .59	22.6 to 30.0	24.5(7.1)	19.3(6.8)	3
rep	-50 or less	.43 to .59	30.1 to 37.5	20.9(9.4)	10.6(4.6)	4
rep	-50 or less	.43 to .59	37.6 to 45.0	20.2(2.7)	0.8(5.5)	3
rep	-50 or less	.60 to .76	30.1 to 37.5	20.0(11.4)	10.5(5.9)	3
rep	-50 or less	.60 to .76	37.6 to 45.0	24.3(5.7)	0.8(7.9)	4

[1]When no standard error is shown, the mean was derived from one observation.

Table 7. Analyses of covariance of net and gross photosynthetic rates (mg $CO_2 \cdot dm^{-2}$ leaf area$\cdot hr^{-1}$) of blue grama (*Bouteloua gracilis*) in the field study at four levels each of irradiance and temperature, three levels of soil water potential and adjusted to two levels of phenology as the covariate.

Source of variation	df	Calculated net photosynthesis	Gross photosynthesis
		Mean square	Mean square
Soil water (W)	2	2845.94***	1465.74***
Irradiance (I)	3	943.64***	1677.36***
Temperature (T)	3	1548.16***	284.58**
W x I	6	95.87	58.86
W x T	6	249.19***	238.55***
I x T	9	137.51*	80.47
Phenology (covariate)	1	4953.05***	8013.41***
Error	175	84.09	77.15
Total	205		

*** indicates significant difference at the 0.01 level of probability
** indicates significant difference at the 0.05 level of probability
* indicates significant difference at the 0.10 level of probability

Table 8. A comparison of integrated daily values of CO_2 exchange during 24-hour ambient simulations with clipped aboveground biomass and primary productivity model predictions for blue grama (*Bouteloua gracilis*) on various dates throughout the 1972 growing season at the Pawnee Site. Pg = gross photosynthesis (gross productivity), Pn = net photosynthesis, AGR = aboveground respiration (AGR = Pg - Pn), DWG = dry weight green photosynthetically-active foliage, NPP = net primary productivity (NPP = Pg - AGR - root respiration), AGB = dry weight of aboveground live biomass.

Date (1972)	CO_2 exchange during 24-hour ambient simulations ($gCH_2O \cdot m^{-2}$ ground area $\cdot$ day^{-1})			Clipped aboveground biomass ($g \cdot m^{-2}$ ground area)	Primary productivity model predictions ($gCH_2O \cdot m^{-2}$ ground area $\cdot$ day^{-1})				($gCH_2O \cdot m^{-2}$ ground area)
	Pg	Pn	AGR	DWG	Pg	Pn	AGR	NPP	AGB
May 19				37.8[1]	3.3	3.0	0.3	1.1	17.1
June 9				55.6[1]	8.1	7.4	0.7	3.7	35.0
June 21				50.0[2]	10.3	9.2	1.1	6.6	55.0
June 28-29	16.4	14.3	2.1		11.9	9.7	2.2	7.2	66.5
July 5				72.6[1]	10.6	9.6	1.0	7.7	71.3
July 6-7	11.6	10.8	0.8	84.3[2]	14.9	13.9	1.0	11.5	75.1
July 21				77.4[1]	16.7	13.5	3.2	8.7	80.3
July 26				55.8[2]	10.6	7.0	3.6	3.2	71.9
Aug. 9				72.3[2]	8.7	6.3	2.4	0.2	70.1
Aug. 11-12	3.9	1.7	2.2	62.7[2]	8.1	4.4	3.7	-0.7	69.0
Aug. 14				82.1[1]	6.7	2.4	4.3	-1.6	64.5
Sept. 4				128.2[1]	18.0	16.7	1.3	13.4	89.3
Sept. 12				51.7[2]	22.5	20.8	1.7	16.2	96.2
Sept. 20				89.1[2]	14.8	14.1	0.7	11.7	96.6
Sept. 22-23	6.1	5.6	0.5	71.3[2]	9.9	8.7	1.2	7.0	76.1

[1]Means for dry weight of green photosynthetically-active foliage from numerous plots, including varying species composition from the Pawnee Site (Lauenroth, 1973). [2]Dry weight of green photosynthetically-active foliage of single 0.29 m^2 plots of pure blue grama stands.

Table 9. Prediction equations developed for blue grama (*Bouteloua gracilis*) field steady state net and gross photosynthetic rates as determined from regression analyses using soil water potential, visible irradiance, air temperature within the canopy and phenological stage as independent variables.

Symbol	Definition	Measurement or units	Range of data
	Dependent variables		
Pn (LA)	Net photosynthesis	mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$	
Pn (GA)	Net photosynthesis	mg $CO_2 \cdot m^{-2} \cdot hr^{-1}$	
Pg (LA)	Gross photosynthesis	mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$	
Pg (GA)	Gross photosynthesis	mg $CO_2 \cdot m^{-2} \cdot hr^{-1}$	
	Independent variables[1]		
W	Soil water potential at -10.0 cm	- bars	0 to -50 (or less)
I	Visible irradiance	ly $\cdot$ min^{-1}	0.10 to 0.76
T	Air temperature within the canopy	°C	15.0 to 45.0
P	Phenological stage	vegetative = 1 reproductive = 2	vegetative to reproductive
	Number of observations = 204		

1. Linear regressions
   a. Pn (LA) = 37.9 + 0.62 (W) (r^2 = .43)
   b. Pn (GA) = 1347.5 + 21.1 (W) (r^2 = .37)
   c. Pg (LA) = 69.8 - 23.5 (P) (r^2 = .45)
   c. Pg (GA) = 3022.7 - 269.0 (P) (r^2 = .37)

2. Multiple linear regressions (no interactions)
   a. Pn (LA) = 65.2 + 0.36 (W) - 12.3 (P) + 37.7 (I) - 0.89 (T) (r^2 = .72)
   b. Pn (GA) = 2642.5 + 14.2 (W) - 167.9 (P) + 1166.2 (I) - 24.4 (T) (r^2 = .66)
   c. Pg (LA) = 53.8 - 15.5 (P) + 42.8 (I) + 0.23 (W) - 0.32 (T) (r^2 = .70)
   d. Pg (GA) = 2163.6 - 195.6 (P) + 1324.3 (I) + 10.7 (W) (r^2 = .62)

3. Multiple linear regressions (with interactions)
   a. Pn (LA) = 18.7 + 0.005 (TxW) - 0.93 (P) + 82.0 (I) - 0.06 $(T)^2$ + 0.02 (TxIxW) + 3.04 (T) - 24.9 (PxI) (r^2 = .81)
   b. Pn (GA) = -1753.6 + 0.17 (TxW) + 76.8 (P) + 1424.1 (I) - 2.39 $(T)^2$ + 195.3 (T) + 0.68 (TxIxW) - 8.30 (PxT) (r^2 = .77)
   c. Pg (LA) = -9.6 - 4.5 (P) + 117.7 $(I)^{1/2}$ + 0.02 (TxIxW) - 27.2 (PxI) - 0.003 $(T)^2$ (r^2 = .75)
   d. Pg (GA) = 292.0 - 98.5 (P) + 3658.8 $(I)^{1/2}$ + 0.38 (TxIxW) (r^2 = .64)

[1]Variables in all equations are listed in the order of their importance as determined by stepwise multiple regression.

Table 10. Prediction equations developed from regression analyses of data from the greenhouse study of blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) net and gross photosynthetic rates and aboveground dark respiration rates. Soil water potential, visible irradiance, and air temperature within the canopy were considered as independent variables in the analyses. All rate values are in terms of mg CO_2 · dm^{-2} leaf area · hr^{-1}.

Symbol	Definition	Measurement or units	Range of data
	Dependent variables		
Pn	Net photosynthesis	mg CO_2 · dm^{-2} · hr^{-1}	
Pg	Gross photosynthesis	mg CO_2 · dm^{-2} · hr^{-1}	
AGR	Aboveground dark respiration	mg CO_2 · dm^{-2} · hr^{-1}	
	Independent variables[1]		
W	Soil water potential	- bars	0 to -30
I	Visible irradiance	ly · min^{-1}	0.30 to 1.54
T	Air temperature within the canopy	°C	20.0 to 40.0

Number of observations, 81 for gross and net photosynthesis and 27 for respiration

Blue grama	
1. Linear regressions	
a. $Pn = 15.2 + 0.37\ (W)$	($r^2 = .38$)
b. $Pg = 21.9 + 0.52\ (W)$	
c. $AGR = -4.27 + 0.29\ (T)$	($r^2 = .52$)
2. Multiple linear regressions (no interactions)	
a. $Pn = 18.5 + 0.37\ (W) + 5.11\ (I) - 0.28\ (T)$	($r^2 = .60$)
b. $Pg = 16.9 + 0.52\ (W) + 5.11\ (I)$	($r^2 = .64$)
c. $AGR = -1.98 + 0.29\ (T) + 0.15\ (W)$	($r^2 = .84$)
3. Multiple linear regressions (with interactions)	
a. $Pn = 47.9 + 0.001\ (TxW) + 2.14\ (I)^{1/2} + 0.01\ (TxIxW) - 0.02\ (T)^2 - 664.0\ (1/T) + 0.30\ (TxI)$	($r^2 = .81$)
b. $Pg = 114.1 + 0.17\ (W) + 2.14\ (I)^{1/2} + 0.01\ (TxIxW) - 1356.3\ (1/T) - 1.18\ (T) + 0.31\ (TxI)$	($r^2 = .83$)
c. $AGR = 15.7 - 232.2\ (1/T) - 1.37\ (\ln W)$	($r^2 = .91$)
Western wheatgrass	
1. Linear regressions	
a. $Pn = 9.34 + 0.32\ (W)$	($r^2 = .61$)
b. $Pg = 12.1 + 0.37\ (W)$	($r^2 = .75$)
c. $AGR = -1.87 + 0.13\ (W)$	($r^2 = .59$)
2. Multiple linear regressions (no interactions)	
a. $Pn = 15.4 + 0.32\ (W) - 0.26\ (T) + 1.77(I)$	($r^2 = .82$)

Table 10. Continued

b.	$Pg = 14.37 + 0.38\ (W) - 0.13\ (T) + 1.77\ (I)$	$(r^2 = .82)$
c.	$AGR = -1.08 + 0.13\ (T) + 0.05\ (W)$	$(r^2 = .81)$
3.	Multiple linear regressions (with interactions)	
a.	$Pn = 10.14 - 0.01\ (TxW) - 0.01\ (T)^2 + 0.41\ (W) + 6.35\ (I)^{1/2} + 36.3\ (1/W) + 0.12\ (WxI)$	$(r^2 = .91)$
b.	$Pg = 9.00 - 2.21\ (\ln W) - 0.002\ (T)^2 + 6.39\ (I)^{1/2} + 0.12\ (WxI)$	$(r^2 = .88)$
c.	$AGR = -2.48 + 0.18\ (T) + 0.003\ (TxW) + 20.6\ (1/W) + 0.64\ (\ln W)$	$(r^2 = .89)$

[1]Variables in all equations are listed in the order of their importance as determined by stepwise multiple regression.

Table 11. An assessment of the sensitivity of the primary productivity model predictions for blue grama (*Bouteloua gracilis*) to variations in driving variables, coefficients and constants. The actual values of the model are compared to output produced when rather drastic perturbations are introduced by altering the indicated variables or constants.

	Season totals (g $CH_2O \cdot m^{-2}$ ground area)								
	F2[1]	Pn[2]	F3[3]	F4[4]	F5[5]	F6[6]	F7[7]	NPP[8]	AGB max[9]
Original predictions	1412	1188	224	1083	474	115	182	714	99
Changes made to the model									
Temperatures increased by 5°C	385	294	90	291	260	17	129	34	35
Temperatures reduced by 5°C	1660	1472	187	1279	365	200	197	1107	193
Temperatures increased by 10°C	105	65	40	77	395	3	69	-329	15[10]
Temperatures reduced by 10°C	13	12	1	99	145	18	97	-133	15[10]
Soil water potentials set at 0 bars	6466	5813	652	5028	1157	766	408	4656	759
Soil water potentials set at -50 bars or less	229	167	62	171	203	10	114	-36	20
Visible irradiance reduced by 10%	1162	970	192	889	436	93	166	534	79
Dry matter coefficient changed from 0.53 x AGB to 0.56 x AGB	1640	1380	260	1261	509	130	198	870	109
Reproductive translocation changed from 0.55 to 0.45	1680	1422	259	1271	488	160	192	934	145
Reproductive translocation changed from 0.55 to 0.65	1224	1023	199	953	464	84	176	561	80

[1] F2 = gross photosynthesis = gross productivity. [2] Pn = net photosynthesis = F2 - F3. [3] F3 = aboveground dark respiration. [4] F4 = translocation. [5] F5 = root respiration. [6] F6 = shoot death. [7] F7 = root death. [8] NPP = net primary production = F2 - F3 - F5. [9] AGB max = peak standing crop of aboveground biomass. [10] 15 g $CH_2O \cdot m^{-2}$ ground area was the value used to initialize the model.

APPENDIX B

```
      PROGRAM PMODEL(INPUT,OUTPUT,TAPE5=INPUT,TAPE6=OUTPUT)
C
C     ACTUAL PHOTOSYNTHESIS AND ABIOTIC DATA FOR THE 1972 GROWING SEASON AT
C     THE PAWNEE SITE IS USED TO PREDICT PRODUCTIVITY FOR WARM SEASON
C     GRASSES ON THE SHORTGRASS PRAIRIE ECOSYSTEM.  THE INPUTS REGULATING
C     THE PHOTOSYNTHETIC AND RESPIRATORY RATES ARE   1) AIR TEMP IN THE
C     FOLIAGE  2) SOIL TEMP AT -10 CM  3) TOTAL INCOMING RADIATION (ALL FROM
C     JOHN NUMN)  4) SOIL WATER POTENTIALS RECORDED AND PREDICTED, AND
C     5) PHENOLOGICAL OBSERVATIONS (FROM L. BROWN).
C
      DIMENSION P111(7),P112(7),P113(7),P114(7),P121(7),P122(7),P123(7),
     1P124(7),P131(7),P132(7),P133(7),P134(7),P211(7),P212(7),
     1P213(7),P214(7),P221(7),P222(7),P223(7),P224(7),P231(7),
     1P232(7),P233(7),P234(7),R1(7),R2(7),R3(7),YA(154),YB(154),X(154),
     1RR1(7),RR2(7),RR3(7),YL(154),YR(154),YP(154),YI(154),YG(154),
     1YN(154),Y=(154),YD(154),YE(154),YT(154),YS(154)
      REAL LIGHT
      DATA(P111(I),I=1,7)/0.,2.,23.9,36.7,33.0,20.,2./
      DATA(P112(I),I=1,7)/0.,3.,24.7,49.6,44.2,22.,3./
      DATA(P113(I),I=1,7)/0.,4.,41.2,54.2,59.6,38.,4./
      DATA(P114(I),I=1,7)/0.,5.,45.,68.5,63.9,40.,5./
      DATA(P121(I),I=1,7)/0.,1.,26.5,29.8,30.1,22.5,1./
      DATA(P122(I),I=1,7)/0.,2.,34.9,45.9,39.6,37.2,2./
      DATA(P123(I),I=1,7)/0.,3.,42.,55.,48.2,38.3,3./
      DATA(P124(I),I=1,7)/0.,4.,43.,59.4,53.2,44.9,4./
      DATA(P131(I),I=1,7)/0.,0.,21.,23.,23.,16.,0./
      DATA(P132(I),I=1,7)/0.,1.,28.,33.,27.,20.,1./
      DATA(P133(I),I=1,7)/0.,2.,31.,40.,35.,29.,2./
      DATA(P134(I),I=1,7)/0.,3.,32.,42.,36.,22.,3./
      DATA(P211(I),I=1,7)/0.,1.,16.,23.1,31.3,27.4,1./
      DATA(P212(I),I=1,7)/0.,2.,27.7,35.6,33.,15.,2./
      DATA(P213(I),I=1,7)/0.,3.,35.,40.8,47.,41.6,3./
      DATA(P214(I),I=1,7)/0.,4.,38.,43.9,50.,35.,4./
      DATA(P221(I),I=1,7)/0.,0.,18.,19.2,19.4,16.6,0./
      DATA(P222(I),I=1,7)/0.,1.,23.1,27.3,23.0,19.2,1./
      DATA(P223(I),I=1,7)/0.,2.,23.,27.2,24.5,22.2,2./
      DATA(P224(I),I=1,7)/0.,3.,25.,30.,24.4,23.3,3./
      DATA(P231(I),I=1,7)/0.,0.,16.,16.2,9.7,13.5,0./
      DATA(P232(I),I=1,7)/0.,0.,20.9,19.9,9.4,14.4,0./
      DATA(P233(I),I=1,7)/0.,1.,20.,24.5,20.9,20.2,1./
      DATA(P234(I),I=1,7)/0.,2.,20.,26.,20.,24.3,2./
      DATA(R1(I),I=1,7)/.3,.5,1.1,2.3,4.,10.,22.5/
      DATA(R2(I),I=1,7)/.3,.5,1.,2.4,7.2,13.,27.5/
      DATA(R3(I),I=1,7)/.3,.5,1.4,4.5,7.8,17.8,36./
      DATA(RR1(I),I=1,7)/2.,3.4,5.2,8.7,15.4,25.2,42.3/
      DATA(RR2(I),I=1,7)/1.5,2.5,4.1,6.6,11.6,19.,31./
      DATA(RR3(I),I=1,7)/1.1,1.7,2.7,4.2,7.8,12.9,21./
C
C     EACH P TABLE ABOVE IS THE 4 WAY INTERACTION GRAPH OF
C     GROSS PHOTO WITH PHENOLOGY, LIGHT, SOIL WATER POTENTIAL AND
C     TEMP.,TEMP. ON THE X AXIS.
C     EACH R TABLE IS THE 2 WAY INTERACTION GRAPH OF
C     ABOVE GROUND RESP. OF BOGR WITH TEMP. AND SOIL WATER POTENTIAL.
C     EACH RR TABLE IS THE 2 WAY INTERACTION GRAPH OF BELOWGROUND RESP WITH
C     SOIL TEMP AND SOIL WATER POTENTIAL FROM COLEMAN
```

```
      C     AGB AND BGB ARE INITIAL ABOVEGROUND AND BELOWGROUND BIOMASS VALUES
      C     FROM LAUENROTH.
      C
            AGB=15.
 60         BGB=517.
            SSUMF2=0.
            SSUMF3=0.
            SSUMF4=0.
            SSUMF5=0.
 65         SSUMF6=0.
            SSUMF7=0.
            DO 105 I=1,154
            WRITE(6,71)
           71  FORMAT(*0*,1X,*DATE*,2X,*TIME*,2X,*AIR TEMP*,2X,*SOIL TEMP*,2X
 70        1,*LIGHT*,2X,*WATER*,2X,*PHENO*,2X,*PHOTO*,4X,*AGB*,4X,*AG RESP*,
           13X,*TRANS*,4X,*BGB*,5X,*ROOT RESP*,3X,*TOTBIO*,2X,*AG LIT*,2X,
           1*BG LIT*)
            SUMF2=0.
            SUMF3=0.
 75         SUMF4=0.
            SUMF5=0.
            SUMF6=0.
            SUMF7=0.
            ATEMP=0.
 80         ARTEMP=0.
            AIATER=0.
            ALIGHT=0.
            DO 99 J=1,8
            READ(5,70)IDATE,ITIME,TEMP,RTEMP,LIGHT,IATER,IPHEN
 85         70  FORMAT(I4,1X,I2,2X,F4.1,2X,F4.1,2X,F4.2,1X,I2,1X,I1)
      C
      C     LIGHT IS TOTAL INCOMING RADIATION, 45 PERCENT OF WHICH IS IN THE
      C     VISIBLE SPECTRUM.
      C
 90         LIGHT=LIGHT*.45
            ITIME=ITIME+1
            IF(IDATE.GE.920)GOTO50
            TEMP=TEMP+5.
            RTEMP=RTEMP+5.
 95   C
      C     ALL PHOTO RATES ARE ON A LEAF AREA BASIS.
      C     DM PROVIDES A CONVERSION FROM CO2 EXCHANGE ON A DRY WT. BASIS TO
      C     A LEAF AREA BASIS.
      C
100        50  DM=.53*AGB
            ATEMP=ATEMP+TEMP
            ARTEMP=ARTEMP+RTEMP
            AIATER=AIATER+IATER
            ALIGHT=ALIGHT+LIGHT
105         IF(IPHEN.EQ.1.)GOTO1
            IF(IATER.EQ.0.)GOTO2
            IF(IATER.LT.50.)GOTO3
            IF(LIGHT.EQ.0.)GOTO4
            IF(LIGHT.LT..26)GOTO5
110         IF(LIGHT.LT..42)GOTO6
```

```
      IF(LIGHT.LT..60)GOTO7
      PHOTO=TABLE(P234,TEMP)
      GOTO100
    7 PHOTO=TABLE(P233,TEMP)
      GOTO100
    6 PHOTO=TABLE(P232,TEMP)
      GOTO100
    5 PHOTO=TABLE(P231,TEMP)
      GOTO100
    3 IF(LIGHT.EQ.0.)GOTO8
      IF(LIGHT.LT..26)GOTO9
      IF(LIGHT.LT..43)GOTO10
      IF(LIGHT.LT..60)GOTO11
      PHOTO=TABLE(P224,TEMP)
      GOTO100
   11 PHOTO=TABLE(P223,TEMP)
      GOTO100
   10 PHOTO=TABLE(P222,TEMP)
      GOTO100
    9 PHOTO=TABLE(P221,TEMP)
      GOTO100
    2 IF(LIGHT.EQ.0.)GOTO12
      IF(LIGHT.LT..26)GOTO13
      IF(LIGHT.LT..43)GOTO14
      IF(LIGHT.LT..60)GOTO15
      PHOTO=TABLE(P214,TEMP)
      GOTO100
   15 PHOTO=TABLE(P213,TEMP)
      GOTO100
   14 PHOTO=TABLE(P212,TEMP)
      GOTO100
   13 PHOTO=TABLE(P211,TEMP)
      GOTO100
    1 IF(IATER.EQ.0.)GOTO16
      IF(IATER.LT.50.)GOTO17
      IF(LIGHT.EQ.0.)GOTO4
      IF(LIGHT.LT..26)GOTO19
      IF(LIGHT.LT..43)GOTO20
      IF(LIGHT.LT..60)GOTO21
      PHOTO=TABLE(P134,TEMP)
      GOTO100
   21 PHOTO=TABLE(P133,TEMP)
      GOTO100
   20 PHOTO=TABLE(P132,TEMP)
      GOTO100
   19 PHOTO=TABLE(P131,TEMP)
      GOTO100
   17 IF(LIGHT.EQ.0.)GOTO8
      IF(LIGHT.LT..26)GOTO23
      IF(LIGHT.LT..43)GOTO24
      IF(LIGHT.LT..60)GOTO25
      PHOTO=TABLE(P124,TEMP)
      GOTO100
   25 PHOTO=TABLE(P123,TEMP)
      GOTO100
```

```
              24  PHOTO=TABLE(P122,TEMP)
                  GOTO100
              23  PHOTO=TABLE(P121,TEMP)
                  GOTO100
170           16  IF(LIGHT.EQ.0.)GOTO12
                  IF(LIGHT.LT..26)GOTO27
                  IF(LIGHT.LT..43)GOTO28
                  IF(LIGHT.LT..60)GOTO29
                  PHOTO=TABLE(P114,TEMP)
175               GOTO100
              29  PHOTO=TABLE(P113,TEMP)
                  GOTO100
              28  PHOTO=TABLE(P112,TEMP)
                  GOTO100
180           27  PHOTO=TABLE(P111,TEMP)
            C
            C     PHOTO = MGCO2 / DM SQUARED LEAF AREA / HOUR (FROM TABLES)
            C
              100 PHOTO=PHOTO*3.*DM
185         C
            C      PHOTO = MGCO2 / M SQUARED GROUND AREA / 3 HOURS
            C
                  PHOTO=PHOTO*30./(44.01*1000.)
            C
190         C     PHOTO = GRAMS CH2O / M SQUARED GROUND AREA / 3 HOURS
            C
                  F2=PHOTO
            C
            C     F2 = PHOTO = FLOW FROM INITIAL BIOMASS TO ABOVEGROUND BIOMASS
195         C
                  SUMF2=SUMF2+F2
                  SSUMF2=SSUMF2+F2
            C
            C      ABOVEGROUND RESPIRATION IS DETERMINED FROM AIR TEMP WITHIN THE
200         C      FOLIAGE = FLOW FROM AGB TO SINK = F3
            C     THE SAME IF STATEMENTS ARE USED TO DETERMINE ROOT RESPIRATION
            C     FROM THE SOIL TEMP = F5
            C     THE SAME MANIPULATION USED FOR GROSS PHOTOSYNTHESIS PROVIDES
            C     ABOVEGROUND RESPIRATION IN TERMS OF GRAMS CH2O / M SQUARED
205         C     GROUND AREA / 3 HOURS.
            C
                  IF(IATER.EQ.0.)GOTO12
                  IF(IATER.LT.50.)GOTO8
                4 RESP=TABLE(R3,TEMP)
210               RRESP=TABLE(RR3,RTEMP)
                  GOTO101
                8 RESP=TABLE(R2,TEMP)
                  RRESP=TABLE(RR2,RTEMP)
                  GOTO101
215             12 RESP=TABLE(R1,TEMP)
                  RRESP=TABLE(RR1,RTEMP)
                101 IF(LIGHT.EQ.0.)F2=0.
                  ARESP=RESP*3.*DM
                  ARESP=ARESP*30./(44.01*1000.)
220               F3=ARESP
```

```
      SUMF3=SUMF3+F3
      SSUMF3=SSUMF3+F3
C
C     FLOW FROM ABOVEGROUND TO BELOWGROUND = F4 = TRANSLOCATION.
C     TRANSLOCATION IS PROPORTIONAL TO THE PHENOLOGICAL STAGE BY DATE
C     ACCORDING TO SINGHS DATA.
C
      IF(IDATE.LT.599)RPROP=.7
      IF((IDATE.GE.600).AND.(IDATE.LT.700))RPROP=.75
      IF((IDATE.GE.700).AND.(IDATE.LT.727))RPROP=.8
      IF((IDATE.GE.727).AND.(IDATE.LT.829))RPROP=.55
      IF(IDATE.GE.829)RPROP=.88
      F4=F2*RPROP
      SUMF4=SUMF4+F4
      SSUMF4=SSUMF4+F4
C
C     ROOT RESPIRATION IS THE FLOW FROM BGH TO A SINK = F5
C     ROOT RESP GRAPHS ARE IN TERMS OF MGCO2/G/DAY, THEREBY REQUIRING
C     DIVISION BY 8 AND MULTIPLICATION BY BIOMASS AND CONVERSION TO G CH2O/M2/3H
C
      RRESP=RRESP/8.*BGH
      RRESP=RRESP*30./(44.01*1000.)
      F5=RRESP
      SUMF5=SUMF5+F5
      SSUMF5=SSUMF5+F5
C
C     F6 IS THE FLOW FROM ABOVEGROUND LIVE TO ABOVEGROUND DEAD, AND
C     IS BASED ON BOTH HIGH AND LOW TEMP, AND SOIL WATER
C
      IF((IATER.LT.35).OR.(TEMP.LT.39.))GOTO102
      SHDETH=AGB-(AGB*((1.+(39./TEMP))/2.))
      GOTO103
  102 SHDETH=0.
      IF(TEMP.LE.4.)SHDETH=.05*(4.-TEMP)*AGB
  103 F6=SHDETH
      SUMF6=SUMF6+F6
      SSUMF6=SSUMF6+F6
C
C     F7 IS THE FLOW FROM BELOWGROUND LIVE TO BELOWGROUND DEAD, AND IS BASED
C     ON A 25 PERCENT TURNOVER IN A GROWING SEASON
C
      RTDETH=.25*BGB/1232.
      F7=RTDETH
      SUMF7=SUMF7+F7
      SSUMF7=SSUMF7+F7
C
C     BIOMASS CHANGES ARE CALCULATED USING DIFFERENCE EQUATIONS.
C
      AGB=AGB+(F2-F3-F4-F6)
      BGB=BGB+(F4-F5-F7)
      TOTBIO=AGB+BGB
      IATER=IATER*(-1.)
      IDAY=I
      WRITE(6,72)IDATE,ITIME,TEMP,RTEMP,LIGHT,IATER,IPHEN,F2,AGB,F3,F4,
     1BGB,F5,TOTBIO,F6,F7
```

```
      72  FORMAT(*0*,I5,3X,I2,5X,F4.1,6X,F4.1,5X,F4.2,4X,I3,5X,I1,3X,
     1F5.2,2X,F7.2,3X,F5.2,4X,F5.2,2X,F8.2,3X,F6.2,4X,F8.2,2X,F6.2,
     11X,F6.2)
      99 CONTINUE
280       ATEMP=ATEMP/8.
          ARTEMP=ARTEMP/8.
          AIATER=AIATER/8.
          ALIGHT=ALIGHT/8.
          X(I)=I
285       YA(I)=AGB
          YB(I)=BGB
          YG(I)=SUMF2
          YN(I)=SUMF2-SUMF3
          YP(I)=SUMF2-SUMF3-SUMF5
290       YI(I)=ALIGHT*100.+10.
          YW(I)=AIATER
          YE(I)=APTEMP
          YD(I)=ATEMP
          YL(I)=SSUMF6
295       YS(I)=SUMF3*2.
          YR(I)=SUMF5*2.
          YT(I)=TOTBIO
          WRITE(6,73)IDATE,SUMF2,AGB,SUMF3,SUMF4,BGB,SUMF5,TOTBIO,SUMF6,
     1SUMF7
300     73  FORMAT(*0*,I5,*----------DAILY SUMS----------*,
     12X,F5.2,2X,F7.2,3X,F5.2,4X,F5.2,2X,F8.2,3X,F6.2,4X,F8.2,F8.2,
     1F7.2)
      105 CONTINUE
C
305   C     INTERPRETATION OF SOME OF THE FINAL VALUES PRINTED OUT ARE   PHOTO = GROSS
C     C     PRODUCTION, NET PHOTO = PHOTO - AG RESP ,  NET PROD = PHOTO - AG RESP - BG
C     C     RESP,  GROSS BG PROD = TRANS,  NET BG PROD = TRANS - BG RESP
C
          XPHOTO=SSUMF2-SSUMF3
310       PROD=SSUMF2-(SSUMF3+SSUMF5)
          BGPROD=SSUMF4-SSUMF5
          WRITE(6,75)IDAY,SSUMF2,AGB,SSUMF3,SSUMF4,BGB,SSUMF5,TOTBIO,
     1SSUMF6,SSUMF7
       75 FORMAT(*0*,*----------TOTALS FOR*,I5,* DAYS ARE----------*
315   1,F7.2,F9.2,F9.2,F9.2,F10.2,F9.2,F12.2,F8.2,F7.2)
          WRITE(6,76)XPHOTO
      76  FORMAT(*0*,*TOTAL NET PHOTO FOR THE TIME PERIOD WAS *,F8.2)
          WRITE(6,77)PROD
       77 FORMAT(*0*,*NET PRODUCTION FOR THE TIME PERIOD WAS *,F8.2)
320       WRITE(6,78)BGPROD
       78 FORMAT(*0*,*NET BELOWGROUND PRODUCTION FOR THE TIME PERIOD WAS*,
     1F8.2)
          CALL PLOTIT(154.,001.,43.,-07.,154,1BG,1,2,X,YG)
          CALL PLOTIT(154.,001.,43.,-07.,154,1RP,2,2,X,YP)
325       WRITE(6,85)
       85 FORMAT(*0*,60X,*TIME IN DAYS*)
          WRITE(6,79)
       79 FORMAT(*0*,*     G = GROSS PHOTO     P = NET PRIMARY PRODUCTIVITY
     1*)
330       CALL PLOTIT(154.,001.,72.,-3.,154,1RN,1,3,X,YN)
```

```
      CALL PLOTIT(154.,001.,72.,-3.,154,1RW,2,3,X,YW)
      CALL PLOTIT(154.,001.,72.,-3.,154,1RD,3,3,X,YD)
      WRITE(6,85)
      WRITE(6,80)
80    FORMAT(*0*,*     N = NET PHOTO     W = AVE SOIL  WATER POT     D =
     1 AVE AIR TEMP*)
      CALL PLOTIT(154.,001.,60.,-3.,154,1RN,1,2,X,YN)
      CALL PLOTIT(154.,001.,60.,-3.,154,1RI,2,2,X,YI)
      WRITE(6,85)
      WRITE(6,81)
81    FORMAT(*0*,*     N = NET PHOTO     I = AVE VISIBLE IRRADIANCE TIME
     1S 100 + 10*)
      CALL PLOTIT(154.,001.,175.,0.,154,1RA,1,2,X,YA)
      CALL PLOTIT(154.,001.,175.,0.,154,1RL,2,2,X,YL)
      WRITE(6,85)
      WRITE(6,82)
82    FORMAT(*0*,*     A = ABOVEGROUND LIVE BIOMASS     L = ABOVEGROUND
     1LITTER*)
      CALL PLOTIT(154.,001.,1600.,400.,154,1RB,1,2,X,YB)
      CALL PLOTIT(154.,001.,1600.,400.,154,1RT,2,2,X,YT)
      WRITE(6,85)
      WRITE(6,83)
83    FORMAT(*0*,*     B = BELOWGROUND LIVE BIOMASS      T = TOTAL ABOVE
     1GROUND AND BELOWGROUND LIVE BIOMASS*)
      CALL PLOTIT(154.,001.,50.,0.,154,1RR,1,3,X,YR)
      CALL PLOTIT(154.,001.,50.,0.,154,1RW,2,3,X,YW)
      CALL PLOTIT(154.,001.,50.,0.,154,1RE,3,3,X,YE)
      WRITE(6,85)
      WRITE(6,84)
84    FORMAT(*0*,*     R = ROOT RESPIRATION     W=AVE SOIL WATER POTENTI
     1AL     E = AVE SOIL TEMP*)
      CALL PLOTIT(154.,001.,50.,0.,154,1RS,1,3,X,YS)
      CALL PLOTIT(154.,001.,50.,0.,154,1RW,2,3,X,YW)
      CALL PLOTIT(154.,001.,50.,0.,154,1RD,3,3,X,YD)
      WRITE(6,85)
      WRITE(6,86)
86    FORMAT(*0*,*     S = AG RESP     W = AVE SOIL WATER POTENTIAL
     1D = AVE AIR TEMP*)
      STOP
      END
```

```
      FUNCTION TABLE (TBLNM,X)
      DIMENSION TBLNM (7)
      XMIN=3.8
      XMAX=48.8
      DT=7.5
      IF(X.LE. XMIN) GO TO 1
      GO TO 2
    1 TABLE = TBLNM(1)
      RETURN
    2 IF( X.GE. XMAX) GO TO 3
      GO TO 4
    3 N = (IFIX((XMAX-XMIN)/DT))+1
      TABLE = TBLNM(N)
      RETURN
    4 XSTEP = X-XMIN
      XI = XSTEP / DT
      I = IFIX(XI) + 1
      I2 = I +1
      DY = (TBLNM(I)- TBLNM(I2))
      DY = -DY
      D=X-(DT*(I-1)+XMIN)
      DI = D/DT
      TABLE = DI * DY + TBLNM(I)
      RETURN
      END
```

```
      SUBROUTINE PLOTIT (XMAX,XMIN,YMAX,YMIN,LAST,ISYMBOL,NO,MOST,X,Y)
      DIMENSION X(1),Y(1)
C     LAST=FINAL INDEX OF X AND Y TO BE PLOTTED
C     MOST=NUMBER OF LINES TO BE PLOTTED ON THIS GRAPH
C     NO = NUMBER OF LINE CURRENTLY BEING PLOTTED
      DIMENSION ZX(13),GRAPH(121,51)
      TYPE INTEGER GRAPH,COLUMNS,BLANK,BORDER
      ISYM=1RR    $  ISYM1=ISYMBOL    $   ISYM2=1R*
      DATA      (LINES=51),(COLUMNS=121)
      KMAX=COLUMNS/10+1
      IF(NO.NE.1)GOTO30
   10 YLAR=YMAX   $  YSMA=YMIN
      XLAR=XMAX   $  XSMA=XMIN
      BORDER=1RH
      BLANK =1R
      MATRIX=COLUMNS*LINES
      DO 20 I=1,MATRIX
   20 GRAPH(I)= BLANK
      DO 24 I=1,LINES
   24 GRAPH(1,I)=GRAPH(COLUMNS,I)=BORDER
      DO25I=1,COLUMNS
   25 GRAPH(I,26)=1H.
   26 XSCALE=(XLAR-XSMA)/(COLUMNS-1.)
      YSCALE=(YLAR-YSMA)/(LINES-1.)
      DO 28 K=1,KMAX
   28 ZX(K)=10.*FLOAT (K-1)*XSCALE+XSMA
   30 DO 40 I=1,LAST
      IF(X(I).EQ..001) ISYMBOL=ISYM
      IF(Y(I).EQ..001) ISYMBOL=ISYM
      IF(X(I).GT.XLAR.OR.X(I).LT.XSMA) ISYMBOL=ISYM2
      IF(Y(I).GT.YLAR.OR.Y(I).LT.YSMA) ISYMBOL=ISYM2
      IF (X(I).GT.XLAR) X(I)=XLAR
      IF (X(I).LT.XSMA) X(I)=XSMA
      IF (Y(I).GT.YLAR) Y(I)=YLAR
      IF (Y(I).LT.YSMA) Y(I)=YSMA
      IX=(X(I)-XSMA)/XSCALE+1.5
      IY=(Y(I)-YSMA)/YSCALE+.5
      IY=LINES-IY
      GRAPH(IX,IY)= ISYMBOL
      ISYMBOL=ISYM1
   40 CONTINUE
      IF(NO.NE.MOST)RETURN
      WRITE(6,2)
      YES=YLAR+YSCALE
      DO 60 I=1,LINES
      YES=YES-YSCALE
   58 WRITE(6,4)YES,(GRAPH(J,I),J=1,COLUMNS)
   60 CONTINUE
      WRITE(6,6)
      WRITE(6,7) ZX
      RETURN
    2 FORMAT(1H1,9X,*,*,11( 9(*,*),*I*))
    4 FORMAT(1H ,F4.2,1X,121H1)
    6 FORMAT(1H ,9X,*,*,12( 9(*,*),*I*))
    7 FORMAT (*  *,13F10.1)
```

DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
516	3	13.6	13.0	0.00	-2	1	0.00	14.99	.01	0.00	516.77	.13	531.76	0.00	.10
516	6	14.7	11.8	.08	-2	1	.20	15.04	.01	.14	516.69	.11	531.73	0.00	.10
516	9	31.0	24.9	.45	-2	1	.83	15.20	.09	.58	516.90	.27	532.09	0.00	.10
516	12	36.1	31.0	.67	-2	1	.83	15.30	.15	.58	516.95	.43	532.25	0.00	.10
516	15	33.6	33.4	.40	-2	1	.66	15.38	.12	.46	516.80	.50	532.19	0.00	.10
516	18	29.6	31.0	.12	-2	1	.50	15.46	.08	.35	516.62	.43	532.08	0.00	.10
516	21	17.9	23.9	0.00	-2	1	0.00	15.44	.02	0.00	516.26	.26	531.70	0.00	.10
516	24	11.7	15.7	0.00	-2	1	0.00	15.43	.01	0.00	516.00	.15	531.44	0.00	.10
516----------DAILY SUMS----------							3.02	15.43	.48	2.12	516.00	2.27	531.44	0.00	.84
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
517	3	9.6	12.1	0.00	-2	1	0.00	15.42	.01	0.00	515.78	.12	531.21	0.00	.10
517	6	15.8	11.7	.09	-2	1	.27	15.49	.01	.19	515.75	.11	531.25	0.00	.10
517	9	30.1	24.3	.42	-3	1	.72	15.63	.08	.50	515.89	.26	531.52	0.00	.10
517	12	34.3	27.5	.62	-3	1	.89	15.77	.13	.62	516.09	.33	531.85	0.00	.10
517	15	33.1	25.0	.28	-3	1	.69	15.86	.12	.48	516.19	.27	532.05	0.00	.10
517	18	29.0	25.4	.12	-3	1	.51	15.94	.07	.36	516.17	.28	532.11	0.00	.10
517	21	19.5	24.6	0.00	-4	1	0.00	15.92	.02	0.00	515.80	.27	531.72	0.00	.10
517	24	12.7	23.0	0.00	-4	1	0.00	15.91	.01	0.00	515.45	.24	531.36	0.00	.10
517----------DAILY SUMS----------							3.08	15.91	.45	2.16	515.45	1.87	531.36	0.00	.84
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
518	3	10.5	21.4	0.00	-5	1	0.00	15.90	.01	0.00	515.13	.22	531.03	0.00	.10
518	6	14.0	19.9	.09	-5	1	.18	15.94	.01	.12	514.95	.20	530.89	0.00	.10
518	9	29.1	20.4	.42	-6	1	.75	16.10	.07	.53	515.17	.20	531.27	0.00	.10
518	12	33.8	23.5	.59	-6	1	.84	16.22	.13	.59	515.41	.25	531.63	0.00	.10
518	15	29.2	26.1	.15	-7	1	.53	16.31	.07	.37	515.38	.29	531.69	0.00	.10
518	18	25.9	26.2	.04	-7	1	.52	16.42	.04	.37	515.36	.29	531.78	0.00	.10
518	21	21.4	25.1	0.00	-8	1	0.00	16.39	.03	0.00	514.98	.27	531.37	0.00	.10
518	24	17.1	23.6	0.00	-9	1	0.00	16.38	.02	0.00	514.62	.25	531.00	0.00	.10
518----------DAILY SUMS----------							2.82	16.38	.38	1.97	514.62	1.96	531.00	0.00	.84

DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
614	3	15.9	26.2	0.00	0	1	0.00	40.28	.04	0.00	529.92	.39	570.20	0.00	.11
614	6	16.5	25.3	.03	0	1	.75	40.43	.04	.56	530.00	.37	570.43	0.00	.11
614	9	29.1	25.8	.40	0	1	2.08	40.82	.13	1.56	531.08	.38	571.90	0.00	.11
614	12	34.4	28.6	.49	0	1	2.56	41.26	.20	1.92	532.40	.49	573.66	0.00	.11
614	15	31.8	31.2	.45	0	1	2.60	41.75	.16	1.95	533.65	.59	575.40	0.00	.11
614	18	26.9	31.3	.03	0	1	1.65	42.05	.11	1.24	534.18	.60	576.23	0.00	.11
614	21	21.0	29.7	0.00	0	1	0.00	41.99	.07	0.00	533.54	.53	575.53	0.00	.11
614	24	19.9	28.3	0.00	0	1	0.00	41.93	.06	0.00	532.95	.48	574.88	0.00	.11
614----------DAILY SUMS----------							9.64	41.93	.80	7.23	532.95	3.83	574.88	0.00	.86
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
615	3	11.5	20.0	0.00	0	1	0.00	41.91	.02	0.00	532.58	.26	574.49	0.00	.11
615	6	11.9	15.4	.13	0	1	.17	41.92	.02	.13	532.40	.20	574.33	0.00	.11
615	9	28.3	16.0	.39	0	1	2.19	42.35	.13	1.64	533.73	.21	576.08	0.00	.11
615	12	35.3	25.3	.63	0	1	2.71	42.79	.24	2.04	535.28	.37	578.07	0.00	.11
615	15	35.7	28.4	.61	0	1	2.68	43.20	.26	2.01	536.71	.48	579.91	0.00	.11
615	18	33.0	30.0	.08	0	1	1.56	43.41	.18	1.17	537.22	.55	580.63	0.00	.11
615	21	18.9	28.7	0.00	0	1	0.00	43.36	.05	0.00	536.62	.50	579.97	0.00	.11
615	24	15.7	26.7	0.00	0	1	0.00	43.32	.04	0.00	536.09	.41	579.41	0.00	.11
615----------DAILY SUMS----------							9.32	43.32	.94	6.99	536.09	2.98	579.41	0.00	.87
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
616	3	13.0	20.0	0.00	0	1	0.00	43.29	.03	0.00	535.72	.26	579.01	0.00	.11
616	6	15.0	17.0	.09	0	1	.60	43.40	.04	.45	535.84	.22	579.25	0.00	.11
616	9	21.6	18.0	.39	0	1	1.60	43.73	.07	1.20	536.71	.23	580.44	0.00	.11
616	12	29.1	22.0	.63	0	1	3.17	44.38	.14	2.37	538.67	.31	583.05	0.00	.11
616	15	27.8	25.0	.61	0	1	3.25	45.07	.13	2.44	540.62	.37	585.69	0.00	.11
616	18	27.3	27.0	.08	0	1	1.77	45.39	.12	1.33	541.41	.43	586.80	0.00	.11
616	21	21.1	25.8	0.00	0	1	0.00	45.31	.07	0.00	540.93	.37	586.24	0.00	.11
616	24	16.0	22.0	0.00	0	1	0.00	45.27	.04	0.00	540.51	.31	585.78	0.00	.11
616----------DAILY SUMS----------							10.38	45.27	.64	7.79	540.51	2.50	585.78	0.00	.87

DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
717	3	18.7	29.5	0.00	-15	1	0.00	77.38	.08	0.00	720.64	.54	798.02	0.00	.15
717	6	16.6	28.1	.04	-14	1	1.60	77.63	.07	1.28	721.29	.48	798.92	0.00	.15
717	9	18.5	27.5	.15	-14	1	2.14	77.98	.08	1.72	722.41	.45	800.38	0.00	.15
717	12	26.0	27.4	.28	-13	1	3.84	78.55	.20	3.07	724.88	.45	803.43	0.00	.15
717	15	34.0	29.5	.54	-13	1	4.08	78.74	.63	3.26	727.46	.54	806.20	0.00	.15
717	18	25.0	29.7	.22	-13	1	2.49	79.05	.18	2.00	728.76	.55	807.81	0.00	.15
717	21	21.0	28.7	0.00	-13	1	0.00	78.93	.12	0.00	728.10	.51	807.03	0.00	.15
717	24	18.4	27.5	0.00	-13	1	0.00	78.85	.08	0.00	727.50	.46	806.34	0.00	.15
717----------DAILY SUMS----------							14.16	78.85	1.45	11.32	727.50	3.98	806.34	0.00	1.18
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
718	3	18.6	26.9	0.00	-13	1	0.00	78.76	.08	0.00	726.91	.43	805.68	0.00	.15
718	6	19.1	26.4	.04	-13	1	2.27	79.13	.09	1.82	728.17	.41	807.30	0.00	.15
718	9	25.7	26.8	.11	-13	1	2.53	79.44	.20	2.03	729.62	.43	809.06	0.00	.15
718	12	31.6	29.6	.22	-13	1	2.58	79.46	.50	2.07	730.99	.55	810.45	0.00	.15
718	15	36.1	32.4	.49	-13	1	3.89	79.46	.77	3.11	733.29	.66	812.75	0.00	.15
718	18	35.0	34.0	.22	-13	1	2.49	79.26	.70	1.99	734.40	.74	813.65	0.00	.15
718	21	24.7	32.8	0.00	-13	1	0.00	79.08	.18	0.00	733.56	.68	812.64	0.00	.15
718	24	22.5	31.1	0.00	-13	1	0.00	78.93	.14	0.00	732.80	.61	811.73	0.00	.15
718----------DAILY SUMS----------							13.77	78.93	2.67	11.01	732.80	4.52	811.73	0.00	1.19
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
719	3	17.4	29.6	0.00	-13	1	0.00	78.85	.08	0.00	732.10	.55	810.96	0.00	.15
719	6	16.8	28.1	.04	-13	1	1.68	79.12	.07	1.35	732.82	.49	811.93	0.00	.15
719	9	33.0	28.1	.11	-13	1	2.58	79.06	.57	2.06	734.24	.49	813.30	0.00	.15
719	12	39.6	32.1	.49	-13	1	3.47	78.75	1.00	2.78	736.22	.65	814.97	0.00	.15
719	15	38.3	35.3	.22	-13	1	2.18	78.28	.91	1.74	736.99	.82	815.27	0.00	.15
719	18	28.1	35.1	.21	-13	1	2.53	78.48	.30	2.03	736.06	.81	816.54	0.00	.15
719	21	21.2	30.1	0.00	-13	1	0.00	78.36	.12	0.00	737.34	.57	815.70	0.00	.15
719	24	19.1	31.3	0.00	-13	1	0.00	78.27	.09	0.00	736.56	.62	814.83	0.00	.15
719----------DAILY SUMS----------							12.45	78.27	3.15	9.96	736.56	5.01	814.83	0.00	1.19

DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
812	3	18.9	29.0	0.00	-29	2	0.00	71.36	.08	0.00	738.92	.53	810.29	0.00	.15
812	6	19.3	27.6	.03	-32	2	1.40	71.91	.08	.77	739.07	.47	810.98	0.00	.15
812	9	32.4	28.1	.36	-35	2	1.86	72.25	.49	1.02	739.45	.49	811.70	0.00	.15
812	12	39.1	31.5	.59	-37	2	1.79	72.08	.88	.99	739.65	.63	811.73	.09	.15
812	15	41.6	35.6	.51	-37	2	1.67	69.52	1.06	.92	739.58	.84	809.10	2.25	.15
812	18	37.2	36.7	.12	-38	2	1.37	69.39	.74	.75	739.27	.91	808.66	0.00	.15
812	21	27.1	30.4	0.00	-39	2	0.00	69.17	.22	0.00	738.53	.59	807.70	0.00	.15
812	24	23.6	32.1	0.00	-40	2	0.00	69.03	.14	0.00	737.72	.66	806.75	0.00	.15
812----------DAILY SUMS----------							8.08	69.03	3.70	4.45	737.72	5.13	806.75	2.34	1.20
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
813	3	20.1	30.4	0.00	-41	2	0.00	68.94	.09	0.00	736.99	.59	805.92	0.00	.15
813	6	18.4	28.8	.03	-42	2	1.27	69.44	.07	.70	737.02	.52	806.46	0.00	.15
813	9	32.4	28.1	.36	-43	2	1.79	69.77	.47	.99	737.36	.49	807.13	0.00	.15
813	12	39.1	31.5	.59	-44	2	1.73	69.61	.85	.95	737.53	.63	807.14	.09	.15
813	15	41.6	35.6	.51	-44	2	1.61	67.13	1.02	.89	737.43	.84	804.56	2.18	.15
813	18	37.2	36.7	.12	-45	2	1.32	67.01	.72	.73	737.10	.91	804.11	0.00	.15
813	21	27.1	30.4	0.00	-45	2	0.00	66.80	.21	0.00	736.36	.59	803.16	0.00	.15
813	24	23.6	32.1	0.00	-46	2	0.00	66.66	.14	0.00	735.56	.66	802.22	0.00	.15
813----------DAILY SUMS----------							7.73	66.66	3.58	4.25	735.56	5.22	802.22	2.26	1.20
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
814	3	20.1	30.4	0.00	-47	2	0.00	66.57	.09	0.00	734.82	.58	801.39	0.00	.15
814	6	18.4	28.8	.03	-48	2	1.23	67.05	.07	.68	734.83	.52	801.89	0.00	.15
814	9	32.4	28.1	.36	-49	2	1.73	67.37	.46	.95	735.14	.49	802.52	0.00	.15
814	12	39.1	31.5	.59	-50	2	1.49	66.87	1.09	.82	735.40	.42	802.27	.09	.15
814	15	40.0	35.6	.51	-50	2	1.47	65.54	1.16	.81	735.49	.57	801.03	.84	.15
814	18	37.2	36.7	.12	-50	2	.81	65.03	.88	.45	735.18	.61	800.20	0.00	.15
814	21	27.1	30.4	0.00	-50	2	0.00	64.68	.34	0.00	734.64	.39	799.32	0.00	.15
814	24	23.6	31.0	0.00	-50	2	0.00	64.45	.24	0.00	734.09	.40	798.53	0.00	.15
814----------DAILY SUMS----------							6.73	64.45	4.32	3.70	734.09	3.98	798.53	.92	1.19

DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
914	3	12.9	16.0	0.00	0	1	0.00	97.33	.07	0.00	896.22	.35	993.55	0.00	.18
914	6	10.4	13.0	.01	0	1	.19	97.30	.05	.16	895.91	.29	993.21	0.00	.18
914	9	22.4	12.0	.31	0	1	3.87	97.59	.18	3.40	898.86	.27	996.45	0.00	.18
914	12	28.0	13.0	.56	0	1	5.86	98.01	.28	5.16	903.54	.29	1001.55	0.00	.18
914	15	32.0	20.0	.45	0	1	6.19	98.37	.38	5.45	908.36	.44	1006.74	0.00	.18
914	18	27.1	22.0	.07	0	1	3.87	98.57	.26	3.41	911.07	.52	1009.64	0.00	.18
914	21	16.1	24.0	0.00	0	1	0.00	98.48	.09	0.00	910.29	.59	1008.77	0.00	.18
914	24	15.5	20.0	0.00	0	1	0.00	98.39	.09	0.00	909.66	.45	1008.05	0.00	.18
914	----------DAILY SUMS----------						19.98	98.39	1.41	17.58	909.66	3.20	1008.05	0.00	1.47
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
915	3	13.8	17.0	0.00	0	1	0.00	98.31	.07	0.00	909.10	.37	1007.42	0.00	.18
915	9	20.0	16.0	.38	0	1	3.06	98.54	.14	2.69	911.26	.35	1009.80	0.00	.18
915	6	13.2	15.0	.01	0	1	.81	98.57	.07	.71	911.45	.33	1010.02	0.00	.18
915	12	30.4	22.0	.55	0	1	6.11	98.96	.35	5.37	916.12	.52	1015.08	0.00	.18
915	15	32.8	27.0	.44	0	1	6.32	99.31	.40	5.56	920.76	.73	1020.07	0.00	.19
915	18	26.9	29.0	.07	0	1	3.92	99.52	.26	3.45	923.15	.87	1022.67	0.00	.19
915	21	14.1	22.0	0.00	0	1	0.00	99.44	.08	0.00	922.44	.53	1021.88	0.00	.19
915	24	12.4	20.0	0.00	0	1	0.00	99.38	.06	0.00	921.80	.45	1021.18	0.00	.19
915	----------DAILY SUMS----------						20.20	99.38	1.44	17.78	921.80	4.15	1021.18	0.00	1.49
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
916	3	14.9	17.0	0.00	-1	1	0.00	99.36	.08	0.00	921.32	.29	1020.62	0.00	.19
916	6	13.0	15.0	.01	-1	1	.73	99.32	.07	.64	921.52	.26	1020.84	0.00	.19
916	9	29.1	16.0	.33	-1	1	4.69	99.43	.45	4.13	925.18	.28	1024.61	0.00	.19
916	12	34.4	20.0	.56	-1	1	5.11	99.22	.83	4.50	929.13	.35	1028.35	0.00	.19
916	15	35.5	27.0	.45	-1	1	4.94	98.89	.92	4.35	932.73	.56	1031.63	0.00	.19
916	18	30.0	32.0	.08	-1	1	3.21	98.77	.51	2.82	934.54	.83	1033.31	0.00	.19
916	21	16.2	30.0	0.00	-1	1	0.00	98.68	.09	0.00	933.63	.72	1032.31	0.00	.19
916	24	16.5	21.0	0.00	-1	1	0.00	98.59	.09	0.00	933.06	.38	1031.65	0.00	.19
916	----------DAILY SUMS----------						18.68	98.59	3.03	16.44	933.06	3.67	1031.65	0.00	1.51

DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
1014	3	7.4	14.2	0.00	-5	1	0.00	6.30	.00	0.00	953.88	.25	960.18	0.00	.19
1014	6	4.7	13.2	0.00	-5	1	0.00	6.30	.00	0.00	953.45	.24	959.75	0.00	.19
1014	9	4.9	12.4	.07	-5	1	.00	6.29	.00	.00	953.04	.22	959.33	0.00	.19
1014	12	7.6	12.8	.22	-5	1	.00	6.29	.00	.00	952.62	.23	958.91	0.00	.19
1014	15	7.7	13.3	.11	-5	1	.00	6.29	.00	.00	952.19	.24	958.48	0.00	.19
1014	18	5.5	13.1	.01	-5	1	.00	6.29	.00	.00	951.76	.23	958.05	0.00	.19
1014	21	4.8	12.4	0.00	-5	1	0.00	6.29	.00	0.00	951.35	.22	957.63	0.00	.19
1014	24	3.2	11.6	0.00	-5	1	0.00	6.03	.00	0.00	950.95	.21	956.98	.25	.19
1014----------DAILY SUMS----------							.01	6.03	.02	.01	950.95	1.84	956.98	.25	1.55
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
1015	3	1.5	11.1	0.00	-5	1	0.00	5.28	.00	0.00	950.55	.20	955.83	.75	.19
1015	6	-1.7	10.0	0.00	-5	1	0.00	3.77	.00	0.00	950.17	.19	953.94	1.50	.19
1015	9	7.7	9.9	.14	-5	1	.00	3.77	.00	.00	949.79	.19	953.56	0.00	.19
1015	12	17.8	12.2	.31	-5	1	.12	3.78	.00	.11	949.49	.22	953.27	0.00	.19
1015	15	25.0	15.6	.35	-5	1	.18	3.79	.01	.16	949.18	.28	952.98	0.00	.19
1015	18	17.1	16.3	.00	-5	1	.09	3.80	.00	.07	948.78	.29	952.58	0.00	.19
1015	21	14.1	15.4	0.00	-5	1	0.00	3.80	.00	0.00	948.31	.27	952.11	0.00	.19
1015	24	10.3	14.5	0.00	-5	1	0.00	3.80	.00	0.00	947.86	.26	951.66	0.00	.19
1015----------DAILY SUMS----------							.39	3.80	.03	.35	947.86	1.89	951.66	2.26	1.54
DATE	TIME	AIR TEMP	SOIL TEMP	LIGHT	WATER	PHENO	PHOTO	AGB	AG RESP	TRANS	BGB	ROOT RESP	TOTBIO	AG LIT	BG LIT
1016	3	4.8	13.5	0.00	-5	1	0.00	3.79	.00	0.00	947.43	.24	951.22	0.00	.19
1016	6	5.2	12.3	0.00	-5	1	0.00	3.79	.00	0.00	947.02	.22	950.81	0.00	.19
1016	9	17.1	12.4	.25	-5	1	.09	3.80	.00	.07	946.68	.22	950.48	0.00	.19
1016	12	21.8	15.2	.42	-5	1	.16	3.81	.01	.14	946.36	.27	950.17	0.00	.19
1016	15	22.8	16.8	.26	-5	1	.12	3.82	.01	.10	945.98	.30	949.80	0.00	.19
1016	18	16.3	16.8	.01	-5	1	.07	3.82	.00	.07	945.55	.30	949.38	0.00	.19
1016	21	12.8	15.6	0.00	-5	1	0.00	3.82	.00	0.00	945.09	.28	948.91	0.00	.19
1016	24	9.6	14.5	0.00	-5	1	0.00	3.82	.00	0.00	944.64	.26	948.46	0.00	.19
1016----------DAILY SUMS----------							.44	3.82	.03	.39	944.64	2.07	948.46	0.00	1.54
----------TOTALS FOR 154 DAYS ARE----------							1412.58	3.82	224.36	1083.47	944.64	474.00	948.46	115.43	1482.33