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PHOTOSYNTHETIC TIME RESPONSE OF THREE GRASSLAND SPECIES

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GRASSLAND BIOME

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ABSTRACT

The timed response of photosynthesis as a function of changing leaf temperatures and irradiation intensities were determined for three grassland species: *Gutierrezia sarothrae*, *Sphaeralcea coccinea*, and *Agropyron smithii*. All three species responded very rapidly to increases in irradiation intensity and underwent light saturation of photosynthesis at approximately 3.5×10^4 $\mu w\ cm^{-2}$ (400 to 700 nm). Photosynthetic response to slowly increasing temperatures (1°C increase per 5 min) were quite similar for individuals of the same species although there were marked differences among the three species. All three species performed optimally between 18° and 30°C. Intracacies in the photosynthetic response to temperature are discussed. Photosynthetic data for *Gutierrezia sarothrae* in the field suggested that absolute rates of photosynthesis are highly dependent upon the phenological status of the plants. Qualifications in the interpretation and incorporation of these data into the Grassland Biome modelling effort are discussed.

INTRODUCTION

In order to facilitate the interpretation of CO_2 exchange data being derived by the integrated "dome" system at the Pawnee Site, this project was undertaken in the late spring, 1971. The objective of the project was to determine the photosynthetic time response characteristics of *Gutierrezia sarothrae*, *Sphaeralcea coccinea*, and *Agropyron smithii* to changes in leaf temperature and irradiation intensity. The characteristic photosynthetic activity curves were monitored as leaf temperature and irradiation intensity were altered independently. A wide range of temperatures and irradiation intensities were chosen to represent field conditions. Although most of this work was performed in the laboratory, some field measurements for *Gutierrezia sarothrae* were also carried out.

LOCATION

Laboratory studies were carried out on the Utah State University campus using plant material collected in the Logan environs; field studies were carried out immediately north of Logan, Utah, in an undisturbed site where *Gutierrezia sarothrae* exists in a sagebrush-grass community.

METHODS

In order to minimize errors in the determination of these photosynthetic time response curves, most of the gas exchange analyses were performed in the laboratory. In this situation, leaf temperature and irradiation could be precisely controlled while time lags in the system were minimized. Plants of *Gutierrezia sarothrae* (Pursh) Britton and Rusby, *Agropyron smithii* Rydb., and *Sphaeralcea coccinea* (Pursh) Rydb. were located in the immediate environs of Logan, Utah, excavated, and placed in large pots for establishment. They were then transported to a transplant garden near the USU campus to establish for several weeks before gas exchange determinations were carried out.

Two fully climatized micro-gas exchange chambers (Siemens Corp.) with complete temperature, humidity, and air movement control were used for both the field and laboratory measurements of photosynthesis (Koch, Klein, and Walz, 1968). The temperature and humidity environment inside the chambers was automatically adjusted to follow either predetermined or ambient conditions. Temperature and humidity control was exerted by Peltier heat exchangers and dew point control systems. Carbon dioxide concentrations in the system were measured by infrared gas analysis (Beckman Co.), and water vapor concentrations were measured by lithium chloride sensors (Siemens Corp.). Air temperatures were measured with platinum resistance thermometers. Leaf temperatures were measured by fine-wire thermocouples. Artificial irradiation was supplied with high intensity incandescent lamps ("Cool-lux," Sylvania Co.). Photosynthetically active irradiation between 400 and 700 nm was determined by a photocell calibrated against an ISCO spectroradiometer. In the field, solar radiation intensities were measured with an Eppley pyranometer. Plant moisture potential was determined by the "pressure bomb" technique (Waring and Cleary, 1967). Gas exchange rates are represented on a leaf dry weight or leaf area basis. Leaf area determinations were determined using a photoelectric planimeter (Caldwell and Moore, 1971). All data were recorded on strip chart recorders and were also directly converted to perforated tape. Perforated tape data were then converted to other computer-compatible formats and further reduced and analyzed.

All data being submitted to the Grassland Biome laboratory have been reduced and represented in meaningful units. These data sets contain not only plant gas exchange rates but also all pertinent abiotic data, sampling dates, phenological status of the plant samples, plant water potential values, and time sequences. Identification of all elements in these data sets may be found in Appendices I and II.

Laboratory measurements of photosynthetic time response curves were carried out between July 1 and September 15, 1971. Specific dates for each determination are cited with the graphical presentations.

In the determination of temperature response curves, temperatures were gradually increased from approximately 5° to 20°C, and in a second series from 20° to 45°C. Temperatures were increased at the rate of 1°C per 5 min. This allowed for a smooth transition in temperature increments as might be expected under field conditions. This is a deviation from the original proposal which suggested that only three temperature levels would be used. We felt this was a decided improvement in the research design despite the added time and effort involved. Irradiation intensities were held constant at 2.3×10^4 μw cm^{-2} (400 to 700 nm) as temperature was allowed to vary. Plant water potential was determined by the pressure bomb technique at the conclusion of each run. Since 1971 was an exceptionally moist year in the Logan environs, a wide distribution of plant water potentials was not attained as was originally anticipated. Technical difficulties precluded determination of water potentials for *Agropyron smithii*. For the determination of photosynthetic response to changes in irradiation intensity, a constant leaf temperature of 20°C was maintained. Irradiation intensity was increased in a series of six increments rather than the three proposed earlier. By using six increments, we feel we have more closely approached the gradual increase in irradiation intensities that would be expected in nature.

Field determinations of photosynthetic rates for *Gutierrezia sarothrae* were carried out on August 26 and 27 and September 24, 1971. Other field work which has been carried out in this same area on the gas exchange of *Artemisia tridentata* will be reported in the 1971 progress report of the Desert Biome.

In these field determinations, photosynthesis of *Gutierrezia sarothrae* was measured in response to ambient environmental conditions. These data should allow comparison with similar measurements being carried out at the Pawnee Site. In addition, a few determinations were also carried out in which leaf temperature was held constant at 20°C, and photosynthetic rates were measured in response to changes in the normal solar irradiation throughout the course of a day.

RESULTS

The photosynthetic time response of each of the three primary species as a function of changing temperature or irradiation conditions are represented in Fig. 1 through 9. These constitute the laboratory determinations. Irradiation intensities are reported as $\mu w\ cm^{-2}$ in the wavelength band 400 to 700 nm, which is generally considered as photosynthetically active irradiation.

For the field measurements, the response of *Gutierrezia sarothrae* to changes in the normal ambient environment is represented in Fig. 10 to 12. The response of the same species to changes in the normal solar irradiation intensities with a constant leaf temperature of 20°C is represented in Fig. 13 and 14. The phenological status of the plants, water potential vlaues when available, and dates of determinations are given in each figure

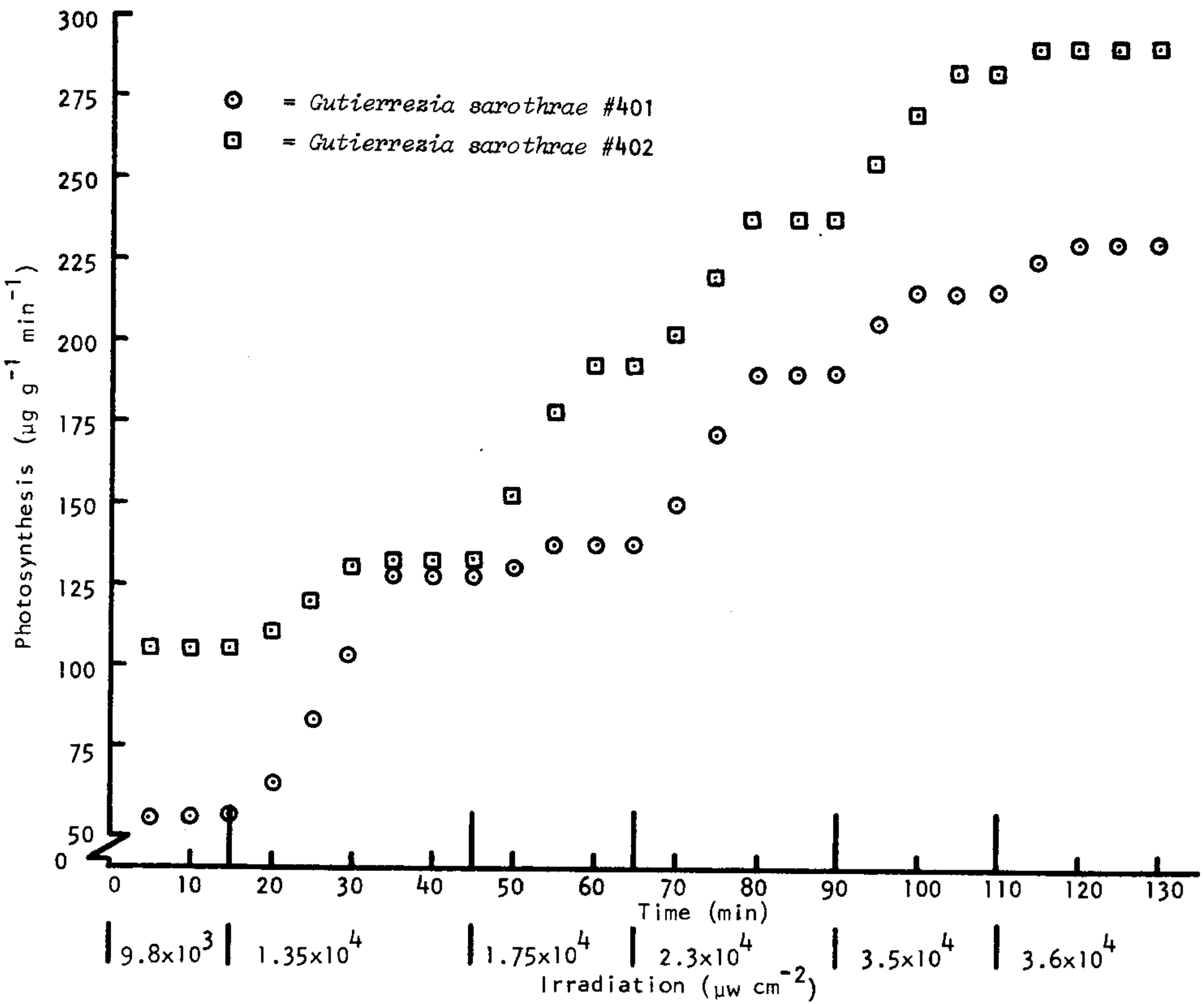

Fig. 1. Time response of photosynthesis of *Gutierrezia sarothrae* with increasing irradiation. Leaf temperature was held constant at 20°C. All plants were in the early vegetative growth phenological stage. Determinations were made on July 10, 1971, for plant #401 and on July 9, 1971, for plant #402. Water potential was 23 bars for plant #401 and 21.5 bars for plant

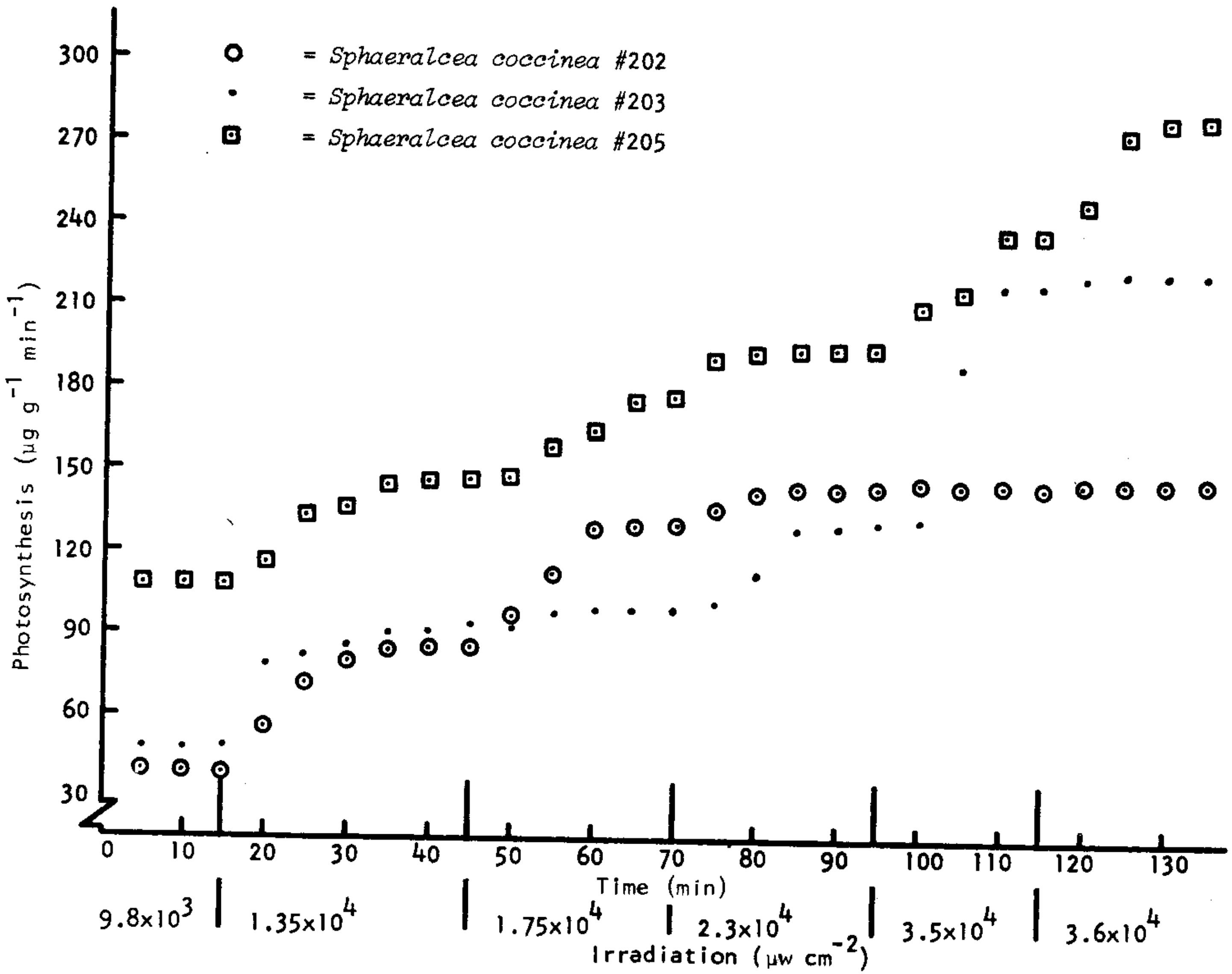

Fig. 2. Time response of photosynthesis of *Sphaeralcea coccinea* with increasing irradiation. Leaf temperature was held constant at 20°C. All plants were in the flowering phenological stage. Determinations were made on July 6, 1971, for plant #202; on July 7, 1971, for plant #203; and on July 15, 1971, for plant #205. Water potential was 12 bars for plant #202, 12 bars for plant #203, and 13 bars for plant #205.

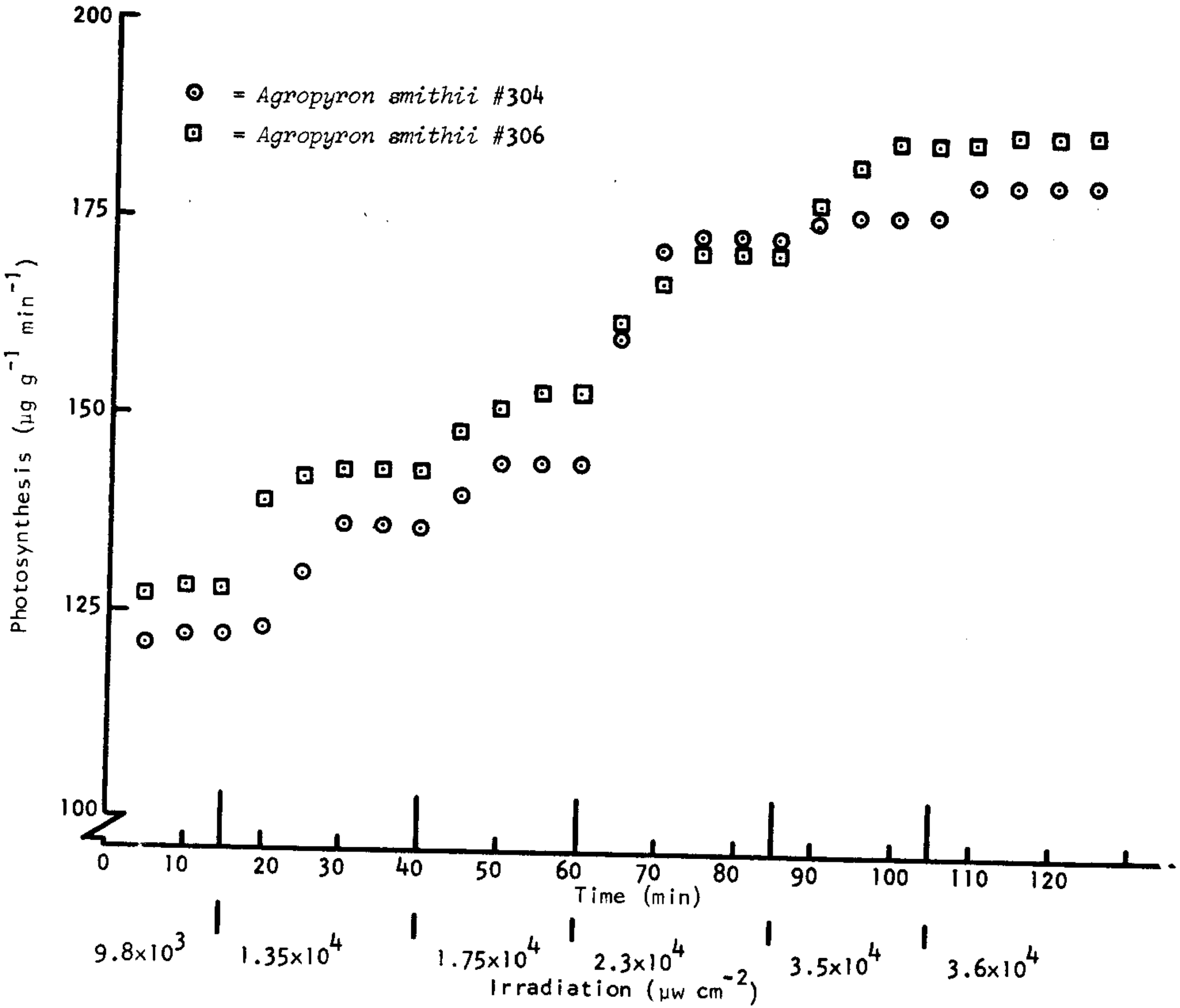

Fig. 3. Time response of photosynthesis of *Agropyron smithii* with increasing irradiation. Leaf temperature was held constant at 20°C. All plants were in the well-developed seed head phenological stage. Determinations were made on August 16, 1971, for plant #304 and on September 14, 1971, for plant #306.

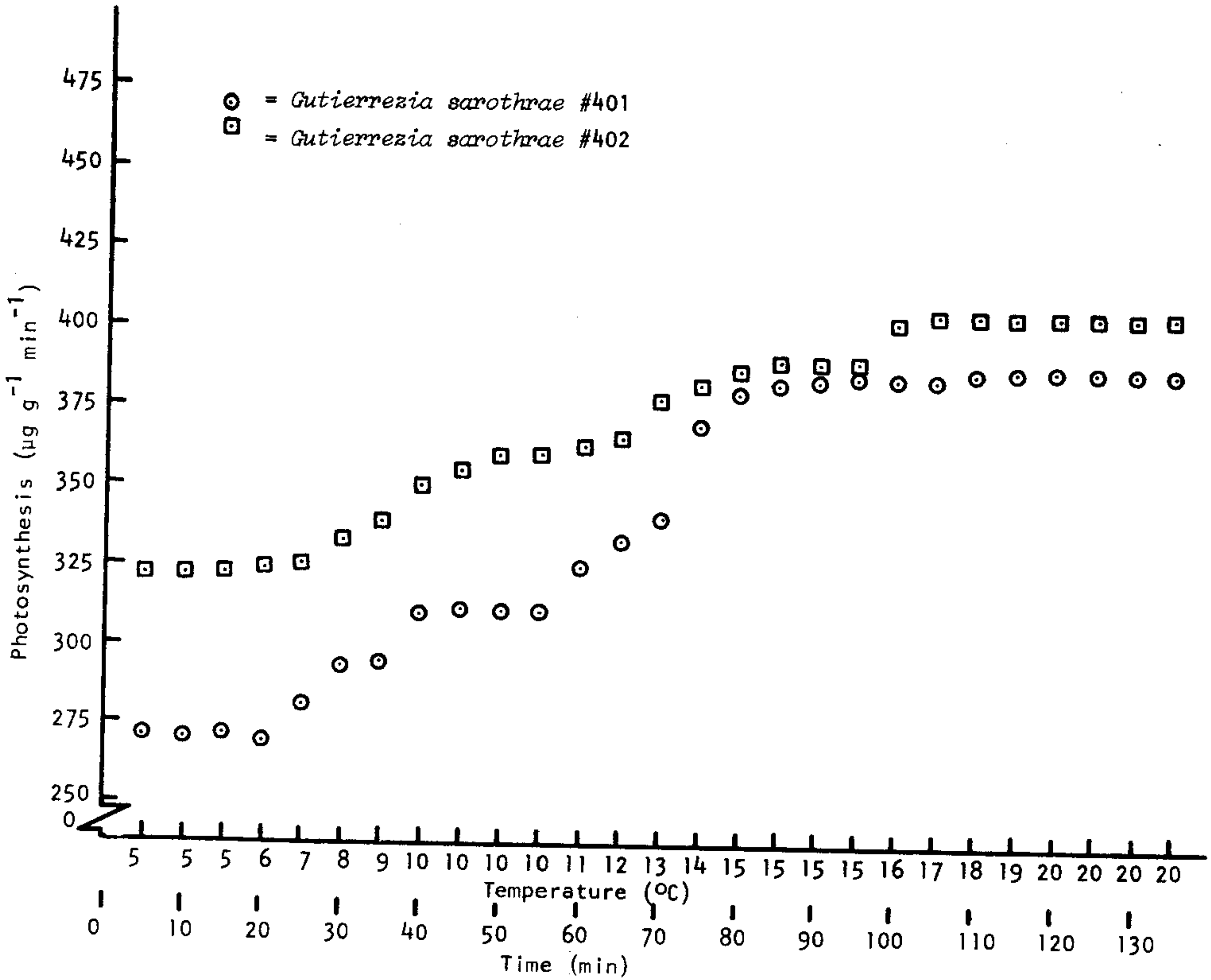

Fig. 4. Time response of photosynthesis of *Gutierrezia sarothrae* with increasing leaf temperature. Irradiation intensity was maintained at 2.3×10^4 μw cm^{-2} (400 to 700 nm). All plants were in the early vegetative growth phenological stage. Determinations were made on July 9, 1971, for plant #401 and on July 10, 1971, for plant #402. Water potential was 23 bars for plant #401 and 21.5 bars for plant #402.

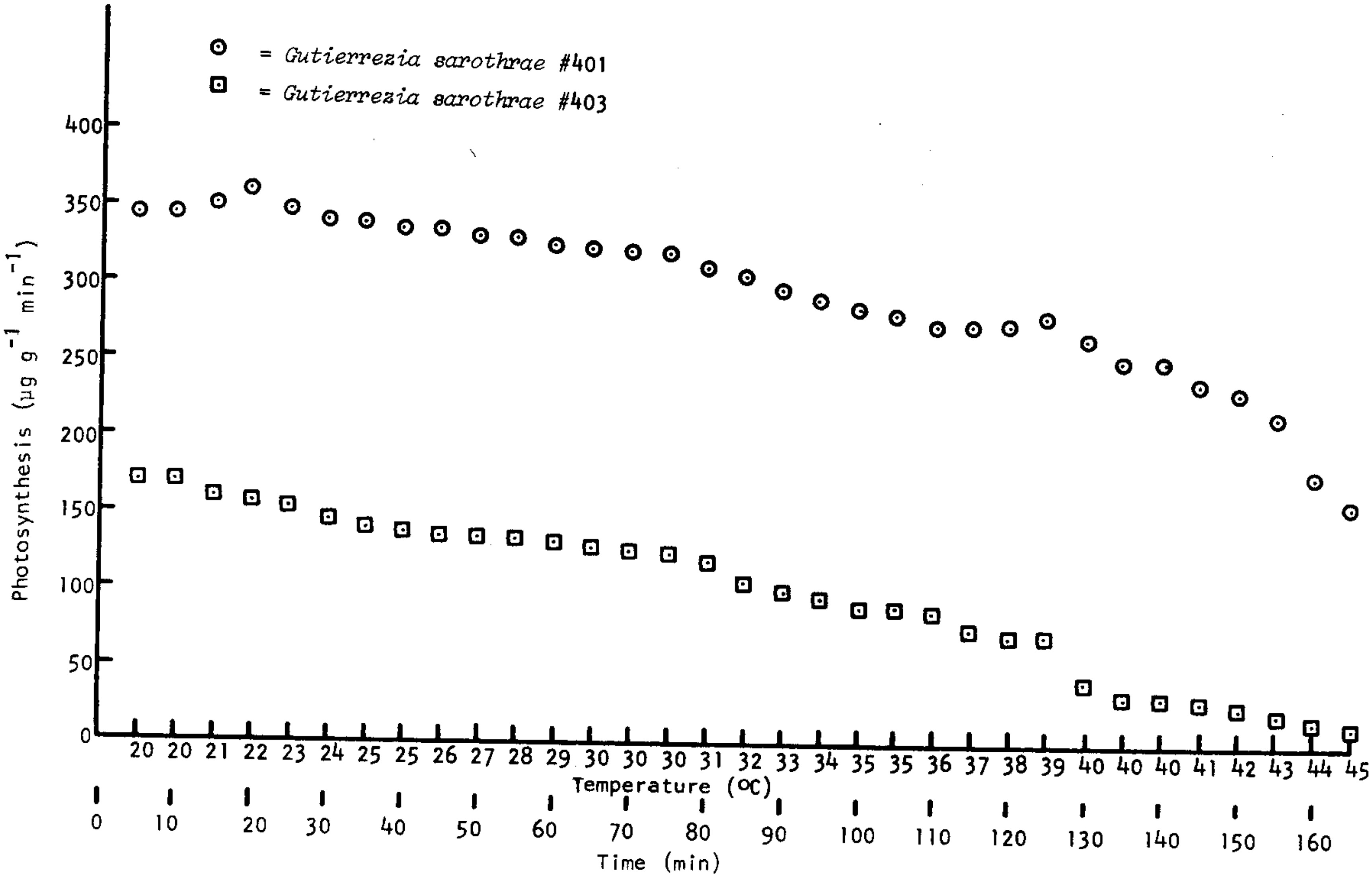

Fig. 5. Time response of photosynthesis of *Gutierrezia sarothrae* with increasing leaf temperature. Irradiation intensity was maintained at 2.3×10^4 μw cm^{-2} (400 to 700 nm). All plants were in the early vegetative growth phenological stage. Determinations were made on July 12, 1971, for plant #401 and on July 13, 1971, for plant #403. Water potential was 23 bars for plant #401 and 27.2 bars for plant #403.

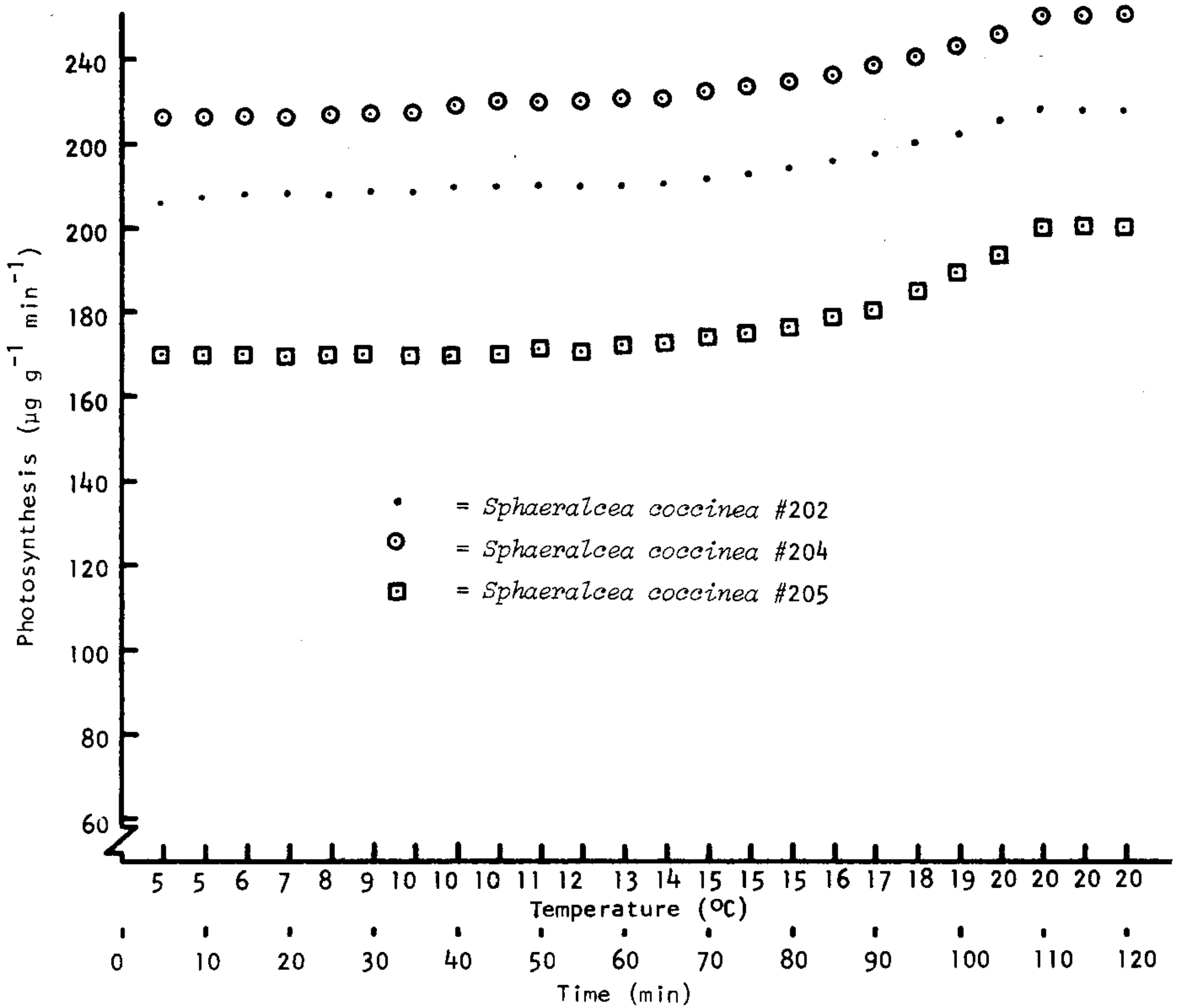

Fig. 6. Time response of photosynthesis of *Sphaeralcea coccinea* with increasing leaf temperature. Irradiation intensity was maintained at 2.3×10^4 µw cm^{-2} (400 to 700 nm). All plants were in the flowering phenological stage. Determinations were made on July 7, 1971, for plant #202; on July 14, 1971, for plant #204; and on July 15, 1971, for plant #205. Water potential ... 10 bars for plant #202, 14 bars for plant #204, and 13 bars for plant #205.

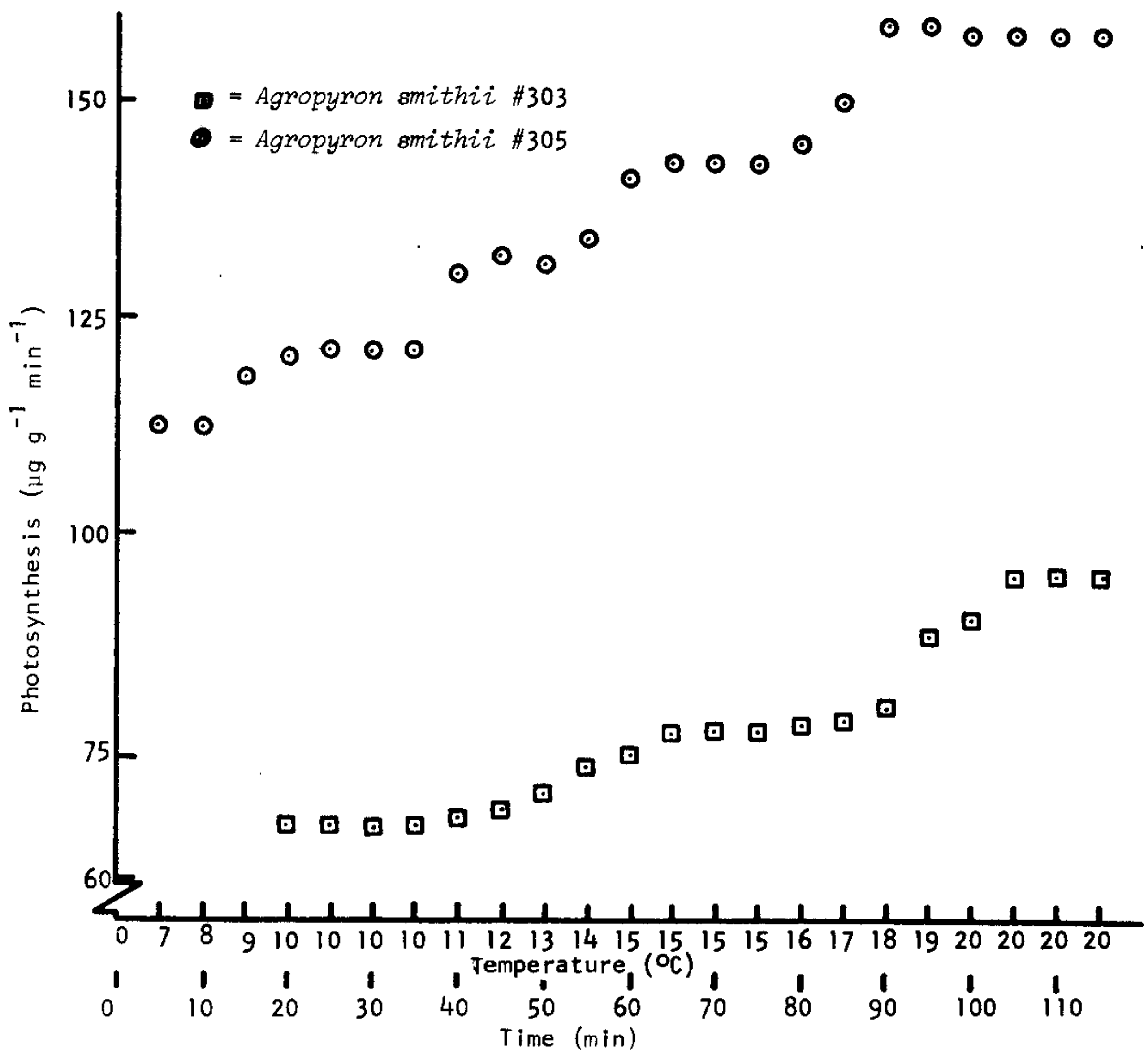

Fig. 8. Time response of photosynthesis of *Agropyron smithii* with increasing leaf temperature. Irradiation intensity was maintained at 2.3×10^4 μw cm^{-2} (400 to 700 nm). All plants were in the well-developed seed head phenological stage. Determinations were made on August 17.

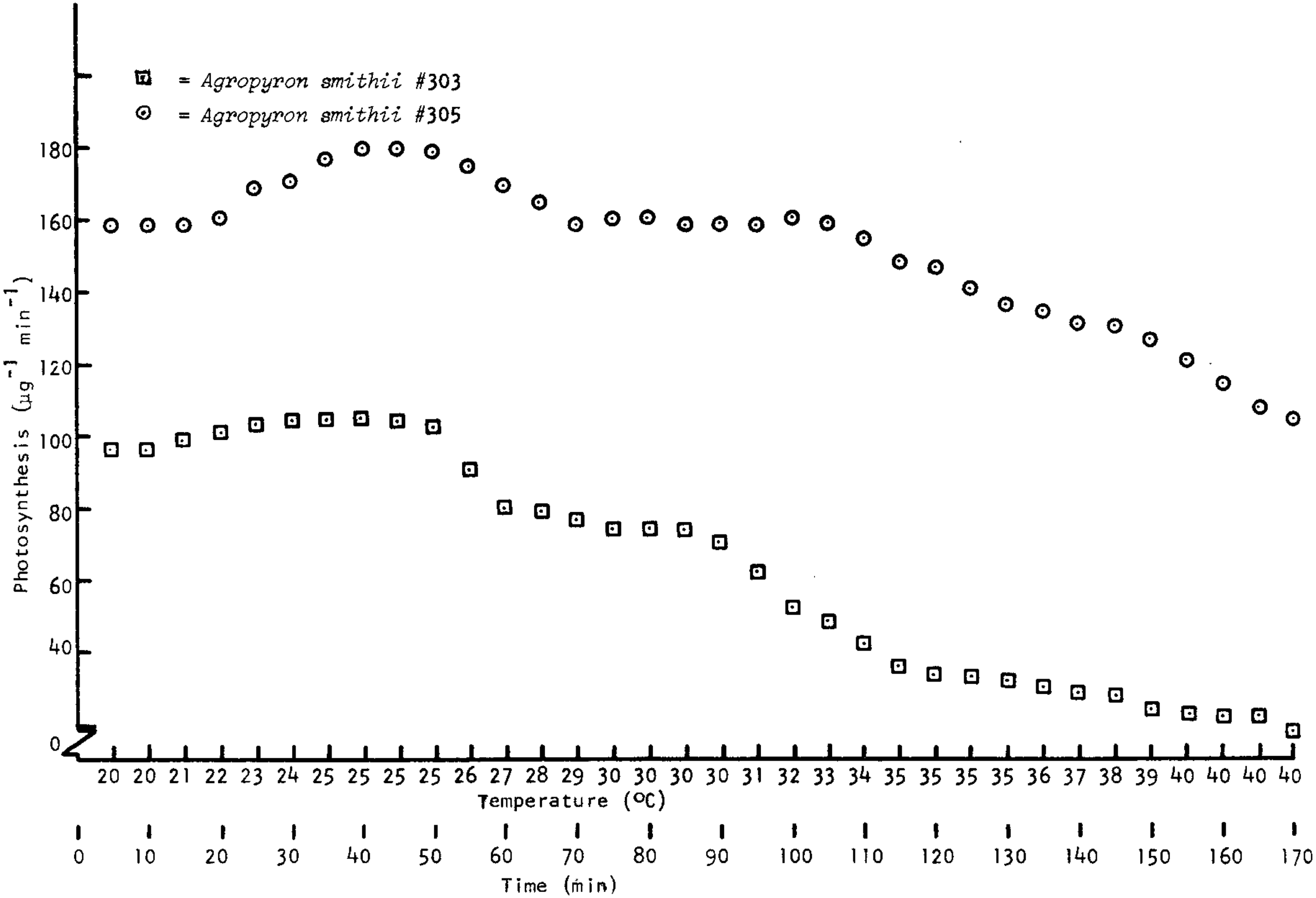

Fig. 9. Time response of photosynthesis of *Agropyron smithii* with increasing leaf temperature. Irradiation intensity was maintained at 2.3×10^4 μw cm^{-2} (400 to 700 nm). All plants were in the well-developed seed head phenological stage. Determinations were made on August 18,

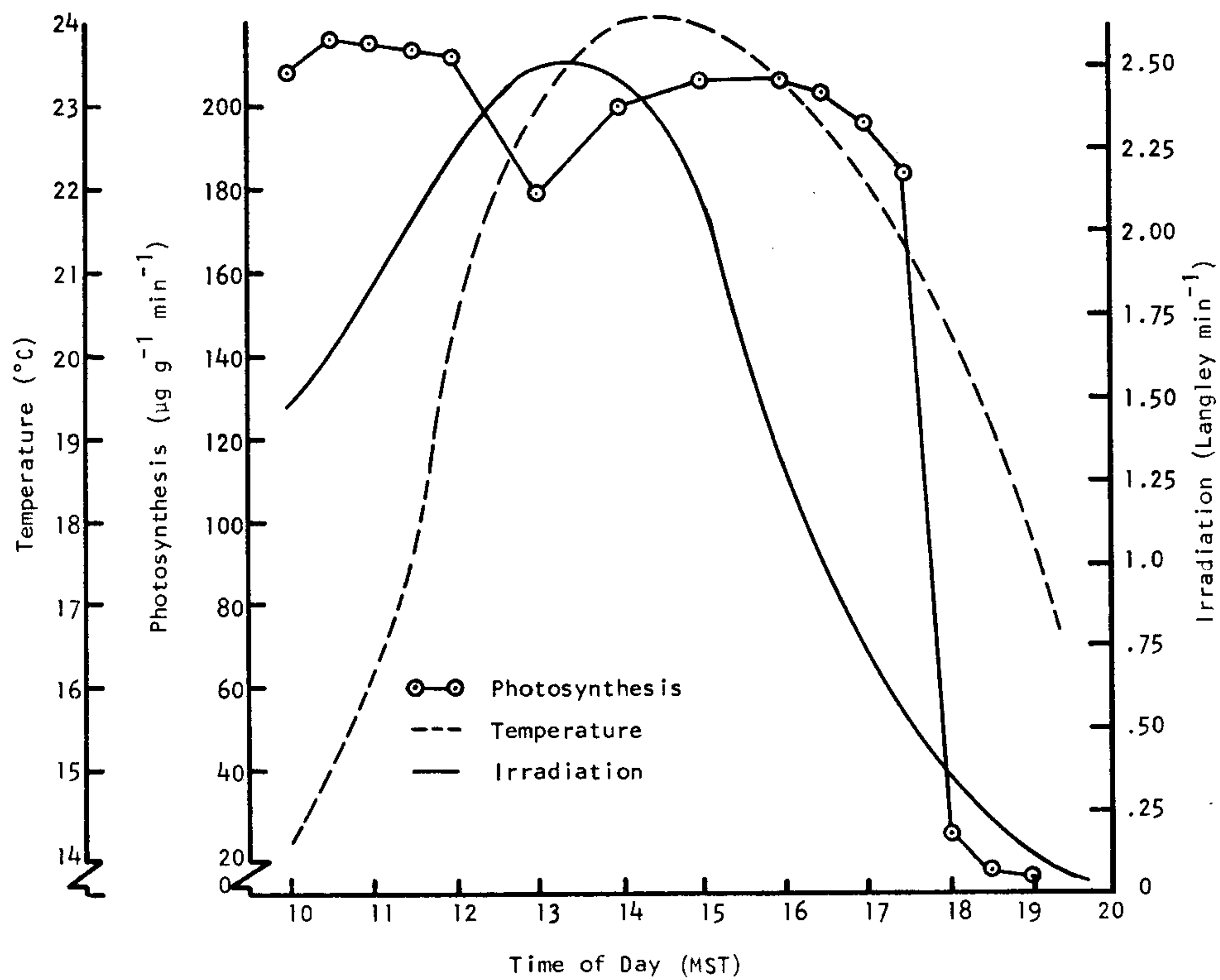

Fig. 10. Photosynthesis of *Gutierrezia sarothrae* (plant #410) in the field under ambient irradiation and temperature conditions. Determination was made on September 24, 1971, when the plant was in the flowering phenological stage. The water potential of plant #410 was 28.9 bars.

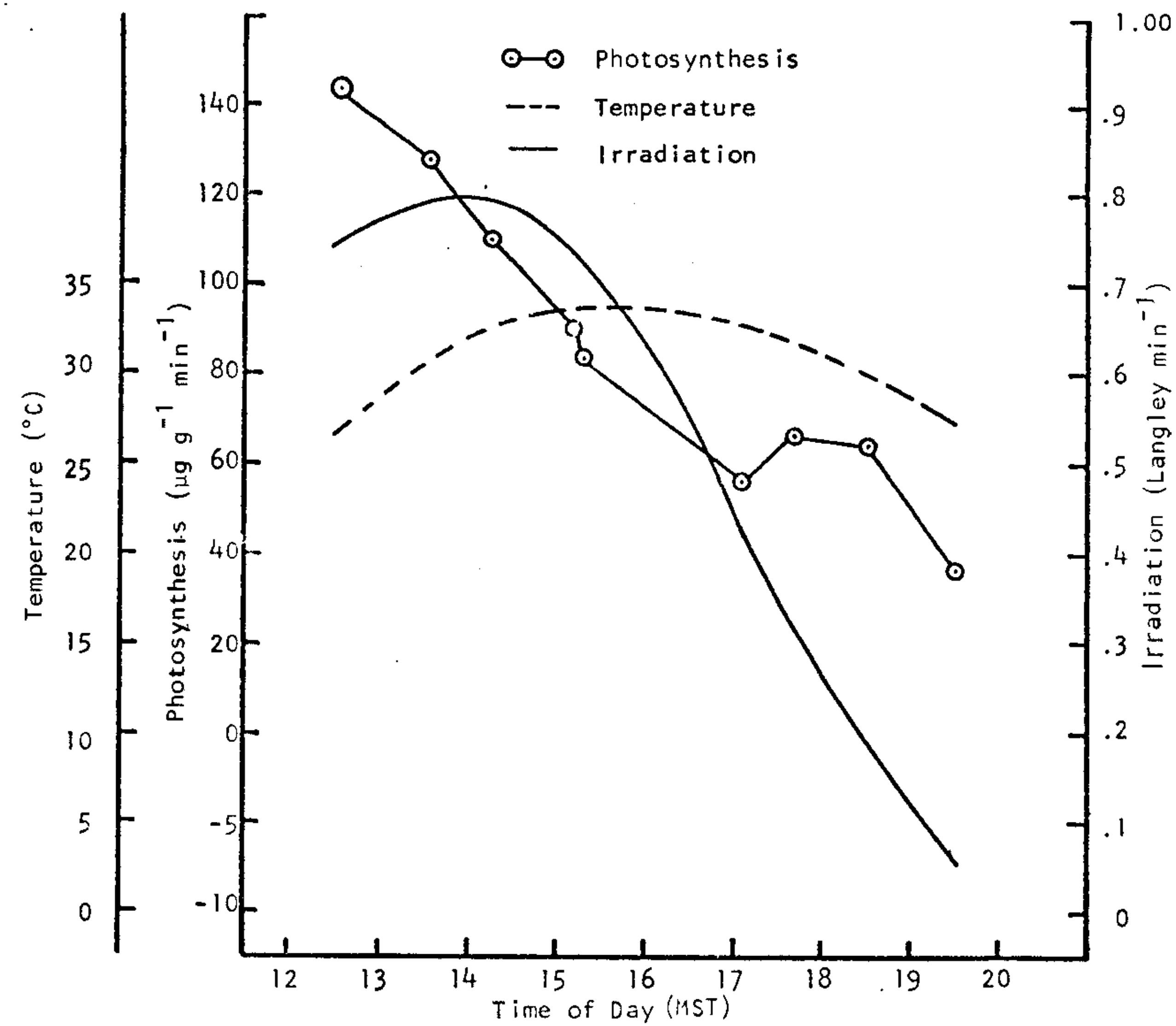

Fig. 11. Photosynthesis of *Gutierrezia sarothrae* (plant #406) in the field under ambient irradiation and temperature conditions. Determination was made on August 27, 1971, when the plant was in the flowering phenological stage. The water potential of plant #406 was 23.1 bars.

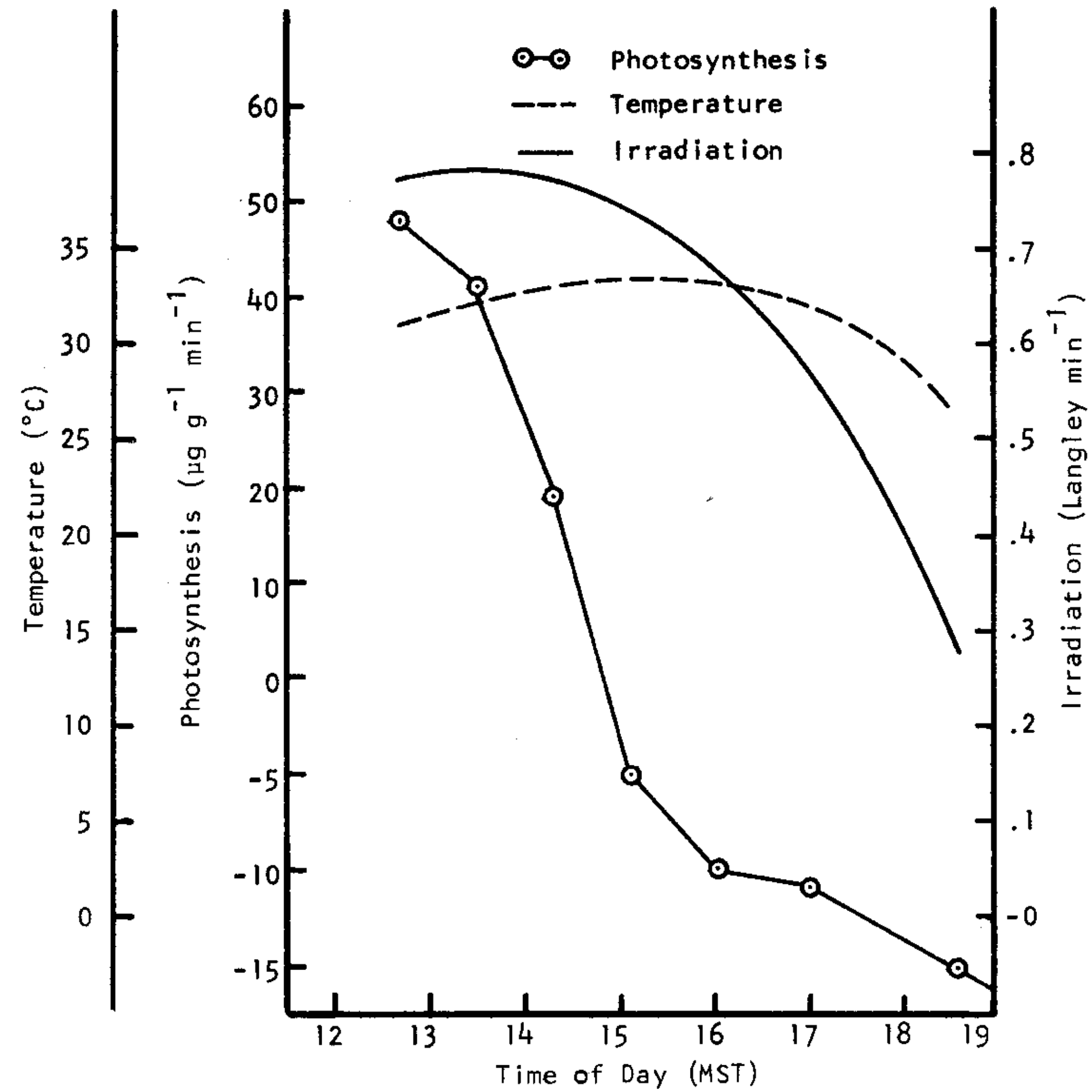

Fig. 12. Photosynthesis of *Gutierrezia sarothrae* (plant #407) in the field under ambient irradiation and temperature conditions. Determination was made on August 27, 1971, when the plant was in the flowering phenological stage. The water potential of plant #407 was 20.7 bars.

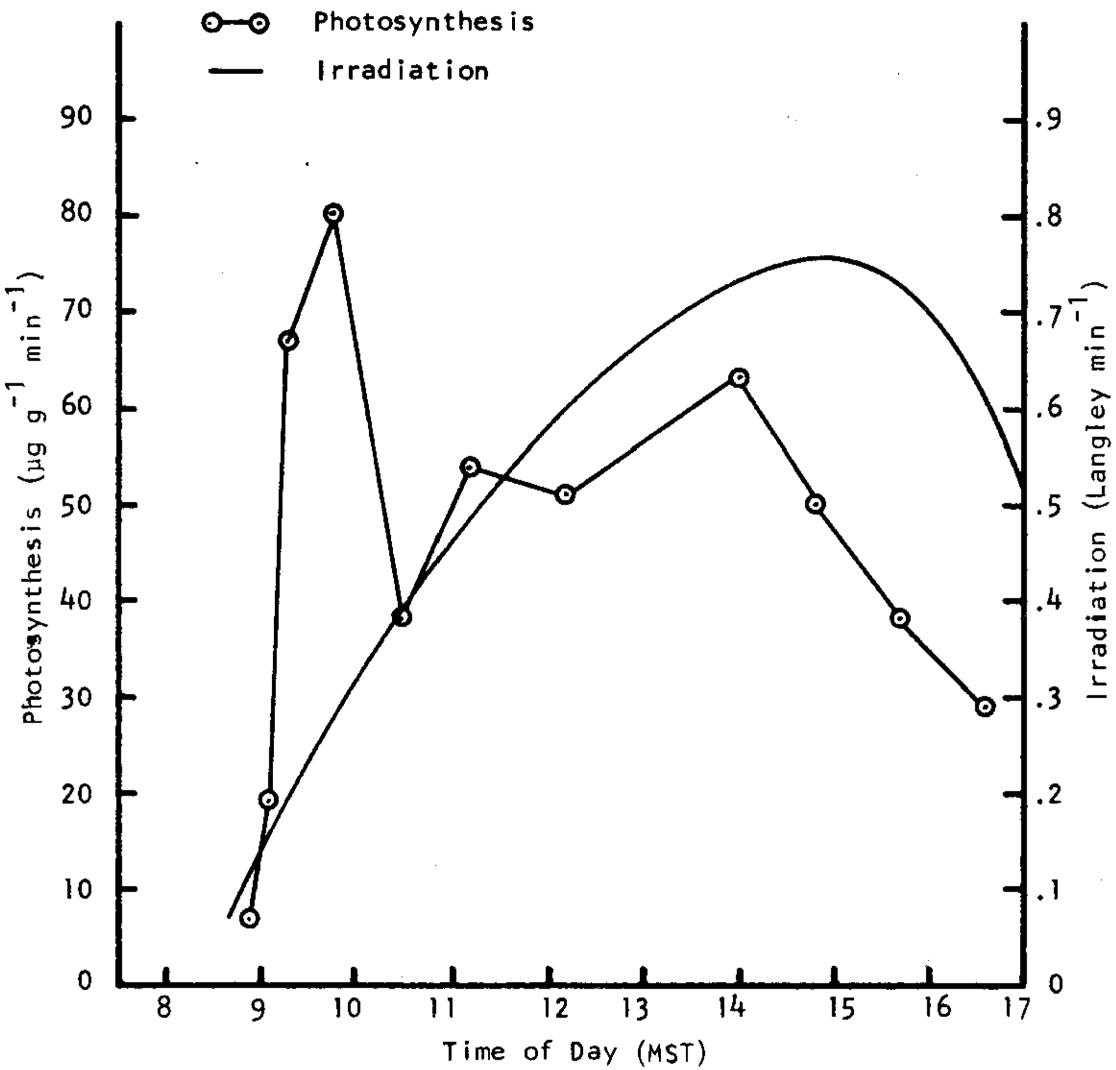

Fig. 13. Photosynthesis of *Gutierrezia sarothrae* (plant #406) in the field under ambient irradiation conditions with a constant leaf temperature of 20°C. Determination was made on September 26, 1971. The water potential of plant #406 was 23.1 bars.

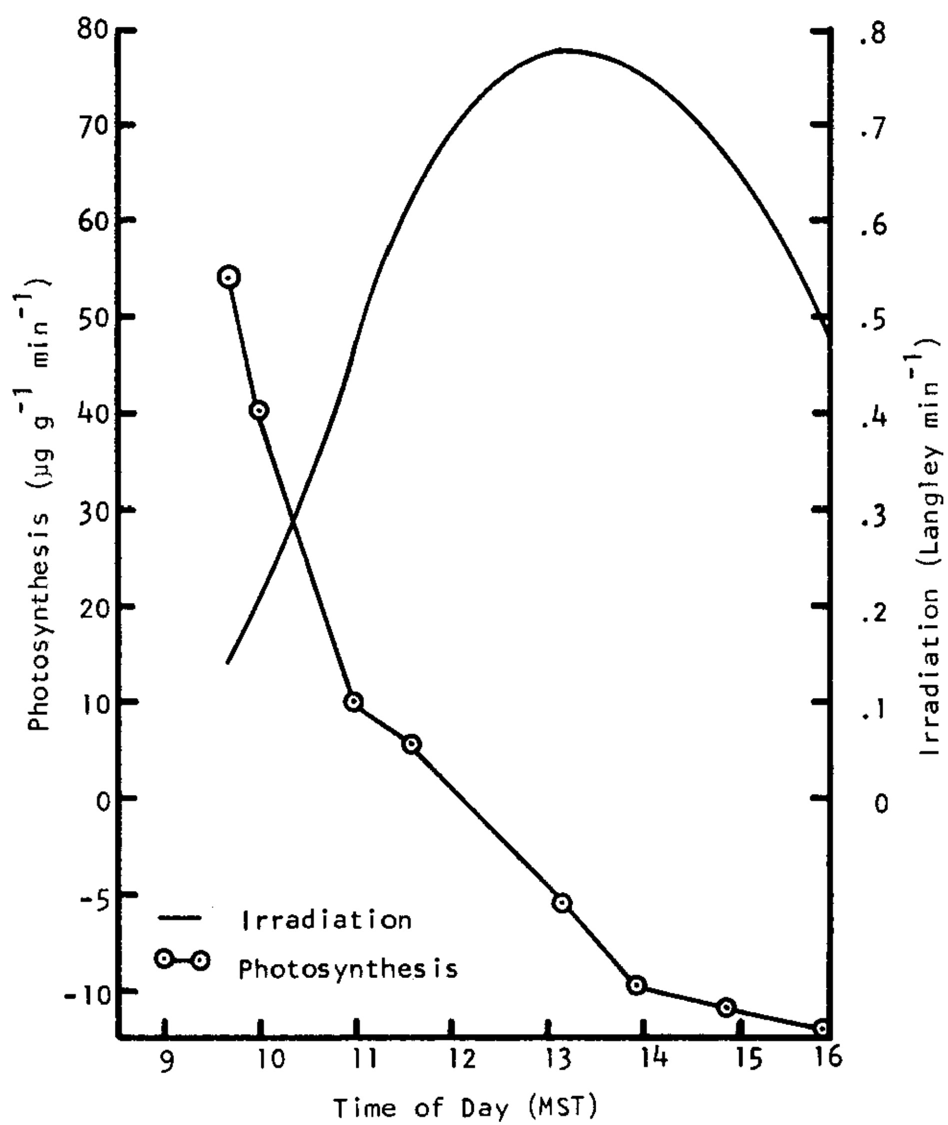

Fig. 14. Photosynthesis of *Gutierrezia sarothrae* (plant #407) in the field under ambient irradiation conditions with a constant leaf temperature of 20°C. Determination was made on September 26, 1971. The water potential of plant #407 was 20.7 bars.

weight basis. If photosynthetic rates per unit leaf area are desired, conversion coefficients are provided for each individual plant in Appendix III.

DISCUSSION

This process study was specifically contracted by the Grassland Biome directorate to aid in the interpretation of integrated CO_2 gas exchange data being gathered at the Pawnee Site using the "dome" system (J. Trlica, project leader). By documenting the time response of photosynthesis as environmental parameters were changed independently, data were to be provided which should lend insight into the characteristic time response of the CO_2 exchange of small vegetation-soil test plots which were measured under the "dome" system at the Pawnee Site.

When comparing the photosynthetic time response of individual plants of the same species (see Fig. 1 to 9), there is a remarkable similarity in the rates of response and also in the photosynthetic performance at different temperature and irradiation levels. For example, temperature optima for photosynthesis of plants of the same species closely coincide, and light saturation values for photosynthesis are also similar. Absolute rates of photosynthesis do differ among plants of the same species. This might be accounted for by small geometric differences in the manner in which photosynthetic tissue is displayed to the incoming radiation. This would naturally vary slightly from plant to plant and could account for the differences in absolute photosynthetic rates. However, the correspondence in the shapes and slopes of the relative photosynthetic curves for individuals within any species is quite close.

When comparing the photosynthetic behavior of the three species as a function of irradiation intensity, it is readily apparent that all three species behave very similarly. All seemed to reach a saturation of photosynthesis around 3.5 to 3.6 × 10^4 μw cm^{-2} (400 to 700 nm) except for one individual of *Sphaeralcea coccinea* which underwent saturation at only 2.3 × 10^4 μw cm^{-2}. Also, the time response characteristics of all three species were quite similar. As irradiation intensities were increased, photosynthetic rates increased and reached 90% of the new equilibrium level within 10 to 15 min. Some of this lag is in the physical gas exchange system as will be discussed later. The irradiation intensities required for maximal photosynthesis (3.5 to 3.6 × 10^4 μw cm^{-2}) are still below maximum solar intensities which might be expected to occur at this latitude (5 × 10^4 μw cm^{-2}). This is quite characteristic of most species which possess the normal Calvin C_3 photosynthetic pathway.

In respect to the photosynthetic response to changing temperatures, these three species showed greater variability than in the case of photosynthetic behavior as a function of changing irradiation intensities. *Agropyron smithii* exhibited a pronounced temperature optimum for photosynthesis around 24° to 26°C. However, photosynthesis did not undergo a significant reduction unless temperatures were below 18° or above 30°C. For *Sphaeralcea coccinea* the optimum temperatures for photosynthesis ranged between 20° and 21°C. Above 21°C, photosynthesis rates dropped off appreciably with increased temperature. However, below 20° there was only a slight drop in photosynthetic rates; and between 5° and 15°C, there was virtually no apparent effect of temperature on photosynthesis. *Gutierrezia sarothrae* behaved more like *Agropyron smithii*. Photosynthetic rates were maximal between 18° and 30°C, although there was no well-defined peak as with *Agropyron*. Below 18° or above 30°C, photosynthetic rates dropped off appreciably as was the case for *Agropyron*. As far as the time response characteristics of photosynthesis, in most cases changes in photosynthetic rates followed a rather smooth trend as temperatures were steadily increased at the rate of 1°C per 5 min. However, individual plants of all three species did occasionally exhibit erratic changes in photosynthetic rates with increasing temperature. Occasionally, photosynthetic rates would be accelerated rather quickly over short increments in temperature and, in other temperature ranges, would experience very little change as temperature increased. In most cases, this behavior seemed to be surprisingly consistent among individuals of the same species, i.e., rapid acceleration or deceleration or plateaus of photosynthesis seemed to occur in roughly the same temperature ranges for members of the same species. These uneven rates of change of photosynthesis in response to changing temperatures present perplexing physiological questions. Conventionally, graphs relating photosynthesis to temperature for most plant species reveal a broad, bell-shaped curve without sharp breaks or changes in slope. However, most temperature response curves for plant photosynthesis have been determined by allowing the plant to equilibrate in photosynthetic activity at several temperatures. Usually 5° or even 10° increments are used in the determination of these relationships. By using 1° increments at regular time intervals (5 min), a more intricate curve results. Although there does appear to be a fair degree of consistency in the details of these curves for plants of the same species, more experimentation would be required to determine if identical curves would result for a large number of individuals of the same species under a variety of circumstances such as various phenological stages and for different rates of temperature increase or decrease.

Although the field portion of this study was necessarily limited by commitments to other research projects, photosynthetic data collected for *Gutierrezia sarothrae* should be valuable when making comparisons with photosynthetic information from the Pawnee Site. Photosynthetic activity in response to ambient environmental conditions are reported in Fig. 10 to 12. In both situations, nearly cloudless weather prevailed. In Fig. 10 the progression of photosynthesis of *Gutierrezia sarothrae* throughout the entire daylight period is shown. A characteristic midday depression of photosynthesis occurred which is quite common for many arid land species. The rates of increase and decrease of photosynthetic activity with the onset and the end of day were quite rapid and probably reflect the influence of irradiation intensity more than leaf temperature. Fig. 11 and 12, which only include data for the last half of August 27, depict photosynthesis for two *Gutierrezia* plants in different phenological stages. Although the shapes of these curves are very similar, it is evident that the plant in the flowering stage exhibited much lower positive rates of net photosynthesis in the early afternoon, and after approximately 3 PM finally exhibited net CO_2 efflux. In contrast to this, the plant in the earlier phenological stage maintained favorable rates of positive net photosynthesis until late in the day. The response of these same individuals is illustrated in Fig. 13 and 14 in which leaf temperatures were held constant at 20°C while solar radiation intensities varied with the progression of the day. Again, as in Fig. 11 and 12, the basic shapes of the photosynthetic response curves are reasonably similar; however, the plant in the earlier phenological stage exhibited higher rates of positive net photosynthesis throughout the day. For the plant in flowering, net photosynthesis rates became negative around noon.

In the interpretation of these timed response relationships, consideration must be given to lag times in the measuring system. Physical lag times would depend upon the absolute photosynthetic activity of the plant material, the amount of plant material in the gas exchange chamber, the internal volume of the chamber and associated pneumatic leads, and the flow rates employed. For the measurements reported in this study, lag rates of 1 to 3 min can be accounted for by the pneumatic leads employed in both the field and laboratory. As far as lags involved in the plant chamber, it is impossible to exactly predict these values because of the different amounts of photosynthetic tissue used for each individual plant determination. However, lags were estimated to be on the order of 1 to 3 min for the plant gas exchange chamber. A total estimated lag time of approximately 5 min should be attributed to the physical system in the interpretation of the time response curves. For any given determination, however, the lag time would be constant since the same flow rates and the same amount of photosynthetic tissue would be employed. Having observed the "dome" system in operation at the Pawnee Site, I would estimate that lags in this system would be rather similar to those experienced in the Siemens' systems used in our study.

Care should be exercised in the interpretation and incorporation of these data in the Biome modelling efforts. It was not within the scope of this research project to evaluate the change in photosynthetic behavior of these three species throughout the progression of the growing season. It is well known that irradiation intensities required for light saturation of photosynthesis and the optimal temperatures for maximum photosynthesis can shift with environmental pre-treatments of progression of phenology for the same individual plants (Mooney and Shropshire, 1967; Hellmuth, 1971; White, Moore, and Caldwell, 1971). In addition, it would not be unreasonable to expect that the time response characteristics of photosynthesis would also undergo changes with the progression of the growing season. Although the photosynthetic time response curves reported in this study may indeed be reasonably representative of the behavior of these three species throughout the growing season, there may be considerable variance in behavior at certain times of the year. Also, since optimal temperatures for photosynthesis may shift with irradiation intensity and irradiation intensity required for light saturation of photosynthesis may shift with different temperatures, these factor interactions should also be considered in the final refinement of the primary productivity model.

Finally, since it is well known that different ecotypes of the same species may exhibit different photosynthetic behavior under the same environmental conditions, ecotypes of these three species from northern Utah might be expected to differ somewhat in their photosynthetic time response relationships as compared to populations at the Pawnee Site.

ACKNOWLEDGEMENTS

This project was funded as a subcontract from the U.S. International Biological Program Grassland Biome, National Science Foundation Grant GB-13096 and GB-31862X, for "Analysis of Structure, Function, and Utilization of Grassland Ecosystems." The technical assistance and computer programming by Mr. Richard S. White and Mr. Edward DePuit are gratefully acknowledged.

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APPENDIX I

BASIC LABORATORY DATA

Data for the laboratory measurements are on two cards: the first card of the set is labeled GSR in columns 73 to 75; the second card of the set is labeled CON in columns 73 to 75. The set is identified in columns 76 to 80.

Laboratory measurements for cards labeled GSR in columns 73 to 75.

Column Number	Parameter	Units
1- 2	Format identification number	
3- 4	Type of laboratory measurement	See laboratory measurement code
5- 7	Time of day	hours
8-11	Transpiration (per unit leaf weight)	mg HOH g^{-1} min^{-1}
12-16	Transpiration (per unit leaf area)	μg HOH cm^{-2} min^{-1}
17-21	Photosynthesis (per unit leaf weight)	μg CO_2 g^{-1} min^{-1}
22-26	Photosynthesis (per unit leaf area)	μg CO_2 dm^{-2} min^{-1}
27-30	Leaf temperature	°C
31-34	Leaf temperature	°C
35-38	Leaf temperature	°C
39-42	Outgoing chamber humidity	mg $liter^{-1}$
43-46	Outgoing chamber humidity	Vapor pressure deficit
47-50	Ambient temperature	°C
51-54	Chamber temperature	°C
55-58	Soil temperature at ~6 inches	°C
59-62	Soil temperature at ~12 inches	°C
63-66	Irradiation	Langley min^{-1}
67-71	Date	month/day/year
72	Chamber number	
73-75	Data card identification	
76-80	Card set identification number	

Laboratory measurement for cards labeled CON in columns 73 to 75.

Column Number	Parameter	Units
1- 2	Format identification number	
3- 4	Type of laboratory measurement	See laboratory measurement code
5-10	Date	month/day/year
11	Chamber number	
12-14	Plant identification number	
15	Species identification number	See species code
16	Unused column	
17-19	Phenology	See phenology code
20	Unused column	
21-25	Leaf area	cm^2
26-30	Leaf weight	g
31-32	Unused columns	
33-40	Total plant area	cm^2
41-48	Total plant weight	g
49-50	Unused columns	
51-53	CO_2 concentration in incoming air stream	ppm
54-63	Unused columns	
64-65	Time of day	hours
66	Unused column	
67-70	Pressure bomb measurement	bars
71-72	Unused columns	
73-75	Data card identification	
76-80	Card set identification number	

Note: Missing data are indicated by 9 in each column.

APPENDIX II

BASIC FIELD DATA

Data for the field measurements are on two cards: the first card of the set is labeled GLD in columns 73 to 75; the second card of the set is labeled AMB in columns 73 to 75. The set is identified in columns 76 to 80.

Field measurements for cards labeled GLD in columns 73 to 75.

Column Number	Parameter	Units
1- 2	Format identification number	
3- 7	Time of day	hours and minutes
8-11	Transpiration (per unit leaf weight)	mg HOH g^{-1} min^{-1}
12-16	Transpiration (per unit leaf area)	µg HOH cm^{-2} min^{-1}
17-22	Photosynthesis (per unit leaf weight)	µg CO_2 g^{-1} min^{-1}
23-26	Photosynthesis (per unit leaf area)	µg CO_2 dm^{-2} min^{-1}
27-30	Leaf temperature	°C
31-34	Leaf temperature	°C
35-38	Leaf temperature	°C
39-42	Outgoing humidity	mg $liter^{-1}$
43-46	Outgoing humidity	Vapor pressure deficit
47-50	Ambient temperature	°C
51-54	Chamber temperature	°C
55-58	Soil temperature at ~6 inches	°C
59-62	Soil temperature at ~12 inches	°C
63-66	Irradiation	Langley min^{-1}
67-71	Date	month/day/year
72	Chamber number	
73-75	Data card identification	
76-80	Card set identification number	

Field measurements for cards labeled AMB in columns 73 to 75.

Column Number	Parameter	Units
1- 2	Format identification number	
3- 8	Date	month/day/year
9	Chamber number	
10-12	Plant identification number	
13	Species identification	See species code
14	Unused column	
15-17	Phenology	See phenology code
18	Unused column	
19-23	Leaf area	cm^2
24-28	Leaf weight	g
29-30	Unused columns	
31-38	Total plant area	cm^2
39-46	Total plant weight	g
47-48	Unused columns	
49-51	CO_2 concentration in incoming air stream	ppm
52-64	Unused columns	
65-72	Pressure bomb measurement	bars
73-75	Data card identification	
76-80	Card set number	

Note: Missing data are indicated by 9 in each column.

APPENDIX III

CONVERSION RATES

Coefficients for converting photosynthetic rates from μg CO_2 g^{-1} min^{-1} to μg CO_2 cm^{-2} min^{-1}.

Species	Plant Number	Factor
Sphaeralcea coccinea	202	.0474
	203	.0216
	204	.0253
	205	.0238
Gutierrezia sarothrae	401	.0119
	402	.0109
	403	.0080
	406	.0099
	407	.0210
	410	.0229

APPENDIX IV

SPECIES, PHENOLOGY, AND LABORATORY MEASUREMENTS CODES

Species Code

02 *Sphaeralcea coccinea*
03 *Agropyron smithii*
04 *Gutierrezia sarothrae*

Phenology Code

Species	Number	Phenology
Sphaeralcea coccinea	03	Early vegetative growth
	04	Flowering
Agropyron smithii	03	Early vegetative growth
	04	Well-developed seed heads
Gutierrezia sarothrae	03	Early vegetative growth
	04	Floral bud stage
	05	Flowering

Laboratory Measurements Code

Number	Explanation
40	2.3×10^4 μw cm^{-2} (400 to 700 nm) light intensity with the temperature varied from 5° to 20°C.
41	Temperature constant at 20°C, light varied in intensity from 9.8×10^3 μw cm^{-2} (400 to 700 nm) to 3.6×10^4 μw cm^{-2} (400 to 700 nm).
42	2.3×10^4 μw cm^{-2} (400 to 700 nm) light intensity with the temperature varied from 20° to 45°C.