

AN ABSTRACT OF THE THESIS OF

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Title: SEASONAL CHANGES IN THE CO₂ GAS EXCHANGE OF
RED FESCUE (*Festuca rubra* L.) IN A MONTANE
MEADOW COMMUNITY IN NORTHERN GERMANY

Abstract approved: Signature redacted for privacy.
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Completely climatized cuvettes were used to follow the CO₂ gas exchange of red fescue (*Festuca rubra* L.), growing on a fertilized and an unfertilized plot, during a growing season from May through October. Objective of the study was to determine the effect of environmental factors on the seasonal CO₂ gas exchange.

Gas exchange rates were calculated on the basis of leaf dry weight, surface area and chlorophyll. There was close correlation between leaf dry weight and area. Photosynthetic rates differed between the fertilized and unfertilized plants when based on leaf dry weight or leaf surface area but were similar when based on chlorophyll.

Multiple regression analysis was used to relate photosynthetic rates to radiation, temperature, vapor pressure deficit, chlorophyll

content and time. A cubic regression equation based on daily radiation alone explained 75% to 88% of the variation in total daily photosynthesis for the season for the three reference bases.

During the growing season the unfertilized plants had a continual decline in their photosynthetic rates until the end of the growing season. On a dry weight basis the fertilized plants had 24% higher photosynthetic rates for the growing season period; on a leaf area basis the rates were only 16% higher.

Light response curves indicated greater photosynthetic rates at light saturation as well as in the light limited portion of the photosynthetic light curve for the fertilized plants. Photosynthetic rates of fertilized plants were generally depressed during periods of warm temperature and high light intensity in June and July.

Photosynthetic rates declined at temperatures above 24° C. The decline was greater for the fertilized plants. A similar response was noted to increasing vapor pressure deficit, although it was difficult to separate from the temperature effect. A temperature increase to 32° C decreased photosynthetic rates 50% and a decrease in temperature to 12.5° C decreased photosynthesis by 12% for the fertilized plants in July.

Maximum photosynthetic rates were found between 14° and 22° C, although there was considerable variation in the photosynthetic rates.

The effects of cutting (mowing) on the gas exchange were difficult to determine due to the interaction of the environmental factors.

Chlorophyll content showed significant correlation with photosynthetic rates.

Seasonal Changes in the CO₂ Gas Exchange of Red
Fescue (Festuca rubra L.) in a Montane Meadow
Community in Northern Germany

by

Wolfhard Friedrich Ruetz

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Lastly I thank the Solling weather, whose adverse conditions made it possible for me to meet Gerda.

The cyclic alliance of soil and living things keeps on unfolding . . . if there is to be new life tomorrow, going back to the earth is a necessary link in the order that surrounds us. The process saddens us and frightens us . . . because we cannot recall what went before and we are uncertain about what happens next. We are gifted with abilities far beyond those held by other living things . . . but we spend a lot of time not seeing, not thinking. We are almost, but not quite, masters of all that comes to mind. Could it be that we have gone too far?

from

"Thoughts from the Charlottes"

by B. J. Pauls

LIST OF ABBREVIATIONS

- (NPK) ----Fertilized
- (0) ----Unfertilized
- VPD ----Vapor pressure deficit. Difference between water vapor saturation at leaf temperature and water vapor of ambient air (mg H₂O/liter).
- PS_n ----Net photosynthesis, the CO₂ uptake, no correction for respiration.
- RAD ----Radiation (cal/cm² or klx)
- TEMP ----Temperature °C
- CHL ----Chlorophyll (mg chlorophyll/g dry weight)
- IRGA ----Infra-red gas analyzer
- R ----Multiple correlation coefficient
- R² ----Coefficient of multiple determination
- PhAR ----Photosynthetically active radiation
- TIME ----Day of year (i. e. January 1 equals day 1)

TABLE OF CONTENTS

INTRODUCTION	1
METHODS	4
Study Area and Field Measurements	4
Area Description	4
General Methodology	7
Selection of Plants	7
Bases of Reference	8
Measurements of CO ₂ Gas Exchange	9
Temperature Control	14
Humidity Control and Transpiration Measurement	17
Leaf Temperature Measurement	19
Light Intensity Measurement	19
Registration of Measurements	21
Statistical Treatment	26
Laboratory Measurements	26
Phenology and Weather During the Growing Season in 1970	27
RESULTS AND DISCUSSION	28
Reference Basis for Photosynthesis	28
Daily Photosynthetic Patterns on Clear Days	35
Changes in Daily Net Photosynthesis from June until October	38
Photosynthesis Based on Radiation Regression for Three Reference Bases	39
Regression Fit for <u>Festuca</u> (0) Based on Radiation	44
Regression Fit for <u>Festuca</u> (0) Based on Radiation, Temperature, Vapor Pressure Deficit, Chlorophyll and Time	48
Regression Fit for <u>Festuca</u> (NPK) Based on Radiation	52
Regression Fit for <u>Festuca</u> (NPK) Based on Radiation, Temperature, Vapor Pressure Deficit, Chlorophyll and Time	57
Seasonal Differences in Photosynthetic Rate between <u>Festuca</u> (0) and <u>Festuca</u> (NPK) Based on Leaf Dry Weight, Area and Chlorophyll	60
CO ₂ Fixed by <u>Festuca</u> (NPK) and <u>Festuca</u> (0) from June until October	63
Photosynthetic Efficiency on a Monthly Basis for <u>Festuca</u> (0) and <u>Festuca</u> (NPK)	65

Analysis of Specific Factors Affecting the Photosynthetic Rate of <u>Festuca rubra</u>	68
Photosynthetic Response to Light	68
The Effect of Temperature and Vapor Pressure Deficit	72
Field Measurements	72
Laboratory Measurements	80
The Effect of Time since Cutting	84
The Effect of Chlorophyll Content	87
 FINAL CONSIDERATIONS AND CONCLUSIONS	 93
Environmental Considerations	93
Methodological Considerations	101
 BIBLIOGRAPHY	 103
 APPENDIX	 109

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Average daily temperature and total daily precipitation in the Solling during the measurement period of 1970.	5
2. View of experimental site with mobile field laboratory.	10
3. Diagram of gas exchange apparatus.	12
4. Close-up view of cuvette.	16
5. Clamp and thermocouple for leaf temperature measurement.	20
6. Schematic diagram of data gathering system.	23
7. Net photosynthetic rates (based on dry weight) for <u>Festuca rubra</u> fertilized (NPK) and unfertilized (0) on select clear days at various times of the year.	30
8. Net photosynthetic rates (based on leaf area) for <u>Festuca rubra</u> fertilized (NPK) and unfertilized (0) on select clear days at various times of the year.	31
9. Net photosynthetic rates (based on chlorophyll) for <u>Festuca rubra</u> fertilized (NPK) and unfertilized (0) on select clear days at various times of the year.	32
10. Net photosynthetic rates (based on dry weight) for <u>Festuca rubra</u> fertilized (NPK) in relation to several environmental parameters on three select clear days.	37
11. Seasonal response curve of net photosynthesis to radiation. Photosynthesis based on leaf dry weight, area and chlorophyll.	40
12. Predicted and observed photosynthetic rates for <u>Festuca</u> (0) for the season. The predicted values were obtained from the multiple linear regression equation: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \epsilon$.	46

13. Predicted and observed photosynthetic rates for Festuca (0) for the season. The predicted values were obtained from the multiple linear regression equation: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (TEMP) + \beta_4 (TEMP)^2 + \beta_5 (VPD) + \beta_6 (CHL) + \beta_7 (TIME) + \beta_8 (TEMP \times VPD) + \beta_9 (RAD \times TEMP) + \epsilon$. 47
14. Predicted and observed photosynthetic rates for Festuca (NPK) for the season. The predicted values were obtained from the multiple linear regression equation: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \epsilon$. 55
15. Predicted and observed photosynthetic rates for Festuca (NPK) for the season. The predicted values were obtained from the multiple linear regression equation: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \beta_4 (TEMP) + \beta_5 (TEMP)^2 + \beta_6 (VPD) + \beta_7 (CHL) + \beta_8 (TIME) + \beta_9 (TEMP \times VPD) + \epsilon$. 56
16. Seasonal changes in daily net photosynthesis for Festuca (NPK) and Festuca (0). Photosynthetic rate is expressed on a leaf dry weight, surface area and chlorophyll basis. 61
17. Seasonal changes in the photosynthetic response to light for Festuca (NPK) and Festuca (0). Each curve represents a regression fit to 45 to 80 hourly means. 70
18. Changes in temperature (T) and vapor pressure deficit (VPD). 74
19. Photosynthetic response to temperature and vapor pressure deficit for Festuca (NPK) and Festuca (0) for the period June 17 to 22. 77
20. Photosynthetic response to temperature and vapor pressure deficit for Festuca (NPK) and Festuca (0) for the period July 8 to 13. 78
21. Photosynthetic response to temperature and vapor pressure deficit for Festuca (NPK) and Festuca (0) for the period August 25 to September 8. 79

<u>Figure</u>	<u>Page</u>
22. Photosynthetic response of <u>Festuca</u> (NPK) (5 and 10 weeks since cut) and <u>Festuca</u> (0) (13 weeks since cut) on September 24, following a light frost.	81
23. Changes in the photosynthetic rates of <u>Festuca</u> (NPK) and <u>Festuca</u> (0) with temperature from September until November, as measured on cut samples under laboratory conditions at 48 Klx.	83
24. Seasonal changes in leaf chlorophyll content and maximum photosynthetic rate for <u>Festuca</u> (NPK) and <u>Festuca</u> (0). The numbers denote weeks since that portion of the meadow was mown (cutting).	92
25. Changes in the aboveground and root biomass on the fertilized and unfertilized plot during the growing season in 1970.	97
26. Relationship between leaf dry weight (g), surface area (cm ²) and chlorophyll content (mg), for <u>Festuca rubra</u> leaves from fertilized and unfertilized plots.	111
27. Comparison of regression fitted to 6-minute values and the respective hourly means for two days in June.	112
28. Comparison of photosynthetic response to light for <u>Festuca rubra</u> (NPK) based on hourly mean rates in the morning (until 12:00) and in the afternoon. The data covers hourly means in a one-week period from September 1 to 8.	113
29. Changes in leaf respiration rates of <u>Festuca rubra</u> fertilized (NPK) and unfertilized (0) with temperature during various months of the year. Rates measured in the laboratory.	116
30. The relation between % of maximum photosynthetic rate to % of maximum chlorophyll content (mg Chl/g dry weight) for <u>Festuca</u> (0) and <u>Festuca</u> (NPK).	118
31. Daily pattern of CO ₂ and H ₂ O gas exchange of <u>Festuca</u> (NPK) and <u>Festuca</u> (0) on August 13, 1970.	119

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Plants found on the research plots, Solling 1970.	6
2. Comparison of temperatures inside and outside the cuvette at full solar insolation between 12:00 and 14:00 on June 18, 1970 for <u>Festuca rubra</u> fertilized and <u>Festuca rubra</u> unfertilized.	15
3. Data registered on the 12 channel - 6 range recorder.	22
4. Values calculated and printed out by the computer	25
5. Some environmental factors measured on the days depicted in Figures 7, 8 and 9.	33
6. Coefficients, t-significance and R^2 values for the seasonal photosynthetic regression based on radiation for three reference bases for <u>Festuca</u> (0).	41
7. Coefficients, t-significance and R^2 values for the seasonal photosynthetic regression based on radiation for three reference bases for <u>Festuca</u> (NPK).	42
8. Coefficients, t-significance and R^2 values for the seasonal regression based on radiation for <u>Festuca</u> (0) (plotted in Figure 12).	45
9. Radiation and temperatures for July 1, 2 and for October 22 and 23.	48
10. Coefficients, t-significance and R^2 values for the seasonal photosynthetic regressions for <u>Festuca</u> (0) using parameters of radiation, temperature, vapor pressure deficit, chlorophyll and time.	50
11. Radiation and temperatures (average daily and maximum hourly) for June 22, July 2 and July 26.	54
12. Coefficients, t-significance and R^2 values for the seasonal photosynthetic regressions for <u>Festuca</u> (NPK) using parameters of radiation, temperature, vapor pressure deficit, chlorophyll and time.	58

<u>Table</u>		<u>Page</u>
13.	Comparison of monthly solar radiation and monthly net photosynthesis of <u>Festuca</u> (NPK) and <u>Festuca</u> (0) based on leaf dry weight and leaf surface area.	64
14.	Computed photosynthetic efficiency of <u>Festuca</u> (NPK) and <u>Festuca</u> (0).	66
15.	Daily photosynthesis for <u>Festuca</u> (NPK) measured at different times since cutting of the meadow. Percentage photosynthetic rates are also given.	85
16.	Coefficients, F-significance and R^2 values for the regression equations relating leaf dry weight to leaf area and mg chlorophyll.	111
17.	Daily respiration rates of <u>Festuca</u> (NPK) computed from laboratory data and as measured in the field. Previous day photosynthesis and night temperature are also listed.	117

SEASONAL CHANGES IN THE CO₂ GAS EXCHANGE OF RED
FESCUE (*Festuca rubra* L.) IN A MONTANE
MEADOW COMMUNITY IN
NORTHERN GERMANY

INTRODUCTION

As increasing pressure is put on our environment to produce more food and fiber, the importance of understanding the environmental limits upon photosynthesis becomes more critical. Man owes a long time debt to the process of photosynthesis. This was well summed up by Meyer, Anderson and Böhning (1960, p. 190) who wrote:

A goodly share of what economists term wealth originates directly or indirectly as a consequence of photosynthesis. This is true not only of all plant and animal products but also of our heritage of coal oil and gas from past geological ages. These latter products all derive from the remains of living organisms and also represent photosynthetic capital. The energy released from them upon combustion represents sunlight of past geological ages which was captured and converted into chemical energy by the photosynthesis of plants which flourished during geological epochs long antedating the advent of man.

Man's stake in photosynthesis is thus even greater than that of any other living organism. Not only is he, like plants and all other animals, dependent for his very existence upon this process, but he is also indebted to it for many of the goods and most of the energy which contribute to the maintenance of his standard of living above a mere subsistence level.

Photosynthesis has attracted the attention of investigators ever since Priestley's "Observations on Different Kinds of Air" in 1772 (Gabriel and Fogel, 1955). Since that time many studies have related

environmental parameters, primarily light, temperature, air and soil moisture and CO₂ content of the air to photosynthesis. Most of these experiments were carried out under closely controlled laboratory conditions. Such studies laid the foundation for much of our present understanding of the photosynthetic process.

Another common experimental approach was to measure photosynthetic rates under natural conditions with little or no control over environment and then to explain observed rate changes in terms of measured ambient parameters. Such studies were usually extended over short time periods of one to several days. Although an insight is gained into the plant's current photosynthetic behavior, long term environmental effects are often not detected.

With the development of more sophisticated field data gathering equipment it has become easier to simultaneously measure, record and control the various environmental parameters as well as the photosynthetic process. Furthermore the development of mobile field laboratories such as described by Koch, Lange and Schulze (1971) and Mooney *et al.* (1971), have made it possible to measure a plant's photosynthetic behavior in a wide variety of natural environments.

Such measurements are being conducted as part of the German International Biological Program (IBP) known as the "Sollingprojekt" where various investigations into the functioning of a beech (Fagus

silvatica), spruce (Picea abies) and meadow community, where red fescue (Festuca rubra) is the primary component, have been carried out since 1966 (Ellenberg, 1971).

In the work reported here, photosynthesis of Festuca rubra was monitored through an entire growing season and related to light, temperature and vapor pressure deficit. Measurements were made on both fertilized and unfertilized plots.

In the following pages the results of the experimental program are synthesized and predictive empirical equations developed to estimate net photosynthesis throughout the growing season. The importance of each measured environmental variable is evaluated. Furthermore, the three classic bases of reference for photosynthesis, leaf dry weight, surface area and concentration of chlorophyll, are compared. Special characteristics of the meadow production process in northern Germany are identified and suggestions for future studies offered.

METHODS

Study Area and Field Measurements

Area Description

The research was carried out on a meadow in the Solling area of Lower Saxony in the Federal Republic of Germany as a part of the "Sollingprojekt" of the Deutsche Forschungsgemeinschaft. The Solling project is part of the International Biological Program (IBP) (Ellenberg, 1968).

The meadow, in the forest district Neuhaus, lies at an elevation of 475 meters with a 3° north-westerly slope. The soil is composed of a loess layer overlying a soil with a high clay content derived from the colored sandstone which is found at a depth of 1.5-2.0 m. (Benecke and Mayer, 1971). The soil belongs to the class of oligotrophic brown soils. The weather during the growing season is characterized by frequent rains, with daily average temperatures only rarely above 20° C (Figure 1).

The vegetation of the meadow belongs to the red fescue facies of the golden oat meadow (Speidel and Weiss, 1971). A list of plant species found in the meadow appears in Table 1. Various parts of the meadow have been subjected to differing degrees of fertilization. For this study, measurements were made on an unfertilized and an

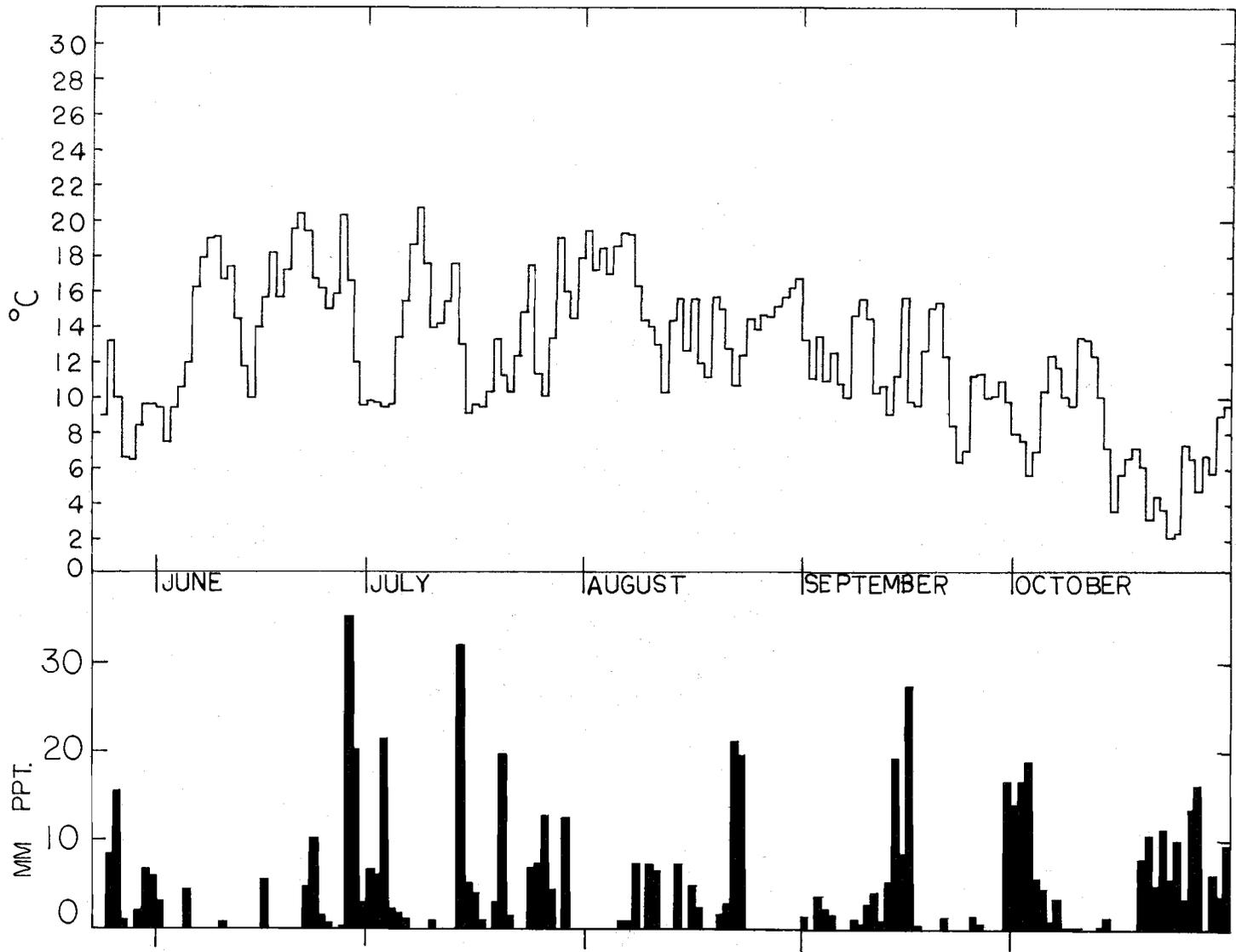


Figure 1. Average daily temperature and total daily precipitation in the Solling during the measurement period of 1970.

Table 1. Plants found on the research plots, Solling 1970 (Speidel, personal communication).

Date of sample:	<u>Unfertilized</u>	<u>Fertilized</u>
	June 15, 1970	May 29, 1970
Grasses	85 ^a	80
Legumes	2	+
Herbs	13	20
<i>Festuca rubra</i>	55	63
<i>Anthoxanthum odoratum</i>	15	1
<i>Holcus lanatus</i>	5	3
<i>Trisetum flavescens</i>	1	1
<i>Agrostis tenuis</i>	8	+
<i>Dactylis glomerata</i>	+	7
<i>Poa pratensis</i>	1	5
<i>Poa trivialis</i>	+	+
<i>Trifolium pratense</i>	2	+
<i>Trifolium repens</i>	+	+
<i>Lathyrus montanus</i>	+	+
<i>Lotus corniculatus</i>	+	+
<i>Taraxacum officinale</i>	7	12
<i>Plantago lanceolata</i>	4	1
<i>Ranunculus acer</i>	2	3
<i>Rumex acetosa</i>	+	2
<i>Anemone nemorosa</i>	+	2
<i>Ajuga reptans</i>	+	+
<i>Chrysanthemum leucanthemum</i>	+	+
<i>Veronica chamaedrys</i>	+	+
<i>Cardamine pratensis</i>	+	+
<i>Leontodon autumnalis</i>	+	+
<i>Luzula campestris</i>	+	
<i>Hypochaeris radicata</i>	+	
<i>Phyteuma spicatum</i>	+	
<i>Cerastium caespitosum</i>	+	
<i>Campanula rotundifolia</i>	+	
<i>Hypericum maculatum</i>	+	
<i>Phyteuma nigrum</i>		+
<i>Achillea millefolium</i>		+
Number of species:	28	24

^aThe numbers give the estimate amount by proportion of each species in % of the total amount.

A + means that the species makes up less than 1%. The fertilized plot was fertilized with 120 kg/ha P₂O₅, 240 kg/ha K₂O and 200 kg/ha N. (Speidel and Weiss, 1971).

NPK fertilized portion of the meadow.

General Methodology

The measurement of the climatic factors and of the gas exchange was done with a portable field laboratory of the Botanical Institute II of the University of Würzburg (Lange and Schulze, 1971; Koch, Lange and Schulze, 1971). Similar equipment for measuring gas exchange in the field has been described by Cernusca and Moser (1969) and by Mooney et al. (1970). An excellent description of methodology used in measurements of CO₂ gas exchange, including methods used in this study, is given by Šesták, Čatský and Jarvis (1971). Photosynthesis, respiration, transpiration and various climatic factors were measured from the beginning of the growing season in May until the first week of November, with measurements being virtually continuous throughout this period.

Selection of Plants

Two basic factors were considered in choosing the type of plant to be measured. First, it had to be relatively abundant on the meadow to be important in the overall productivity and secondly, it had to be of sufficient size to enable it to be sealed into the cuvette. Festuca rubra qualified as the most common species on the meadow, comprising 55% of the unfertilized and 63% of the fertilized plots

(estimated by proportion of individual species, Speidel and Weiss, 1971). Measurements were made throughout the growing season on both the fertilized and unfertilized plots. Other species were measured on the fertilized plot but will not be considered here.

Because the meadow was mowed periodically, various stages of growth also had to be considered; consequently the photosynthetic rate of leaves of newly mowed grass was compared with that of the unmowed grass whenever possible. This was done on the fertilized plot where there was rapid regrowth.

Bases of Reference

Photosynthesis and respiration were calculated on three reference bases: leaf dry weight, surface area and chlorophyll content. Dry weight is most important in determining the productivity of the plant in terms of biomass and is perhaps the easiest to determine of the three reference bases. Leaf surface area is important in terms of area exposed to solar radiation, while chlorophyll content gives an indication of the efficiency of the photosynthetic apparatus. Photosynthesis based on chlorophyll has frequently been termed the assimilation number (Heath, 1969).

The computation of leaf surface area was done by Dr. E. Geyger who has done extensive work on determining the leaf area indices of grassland communities (Geyger, 1971). The determination of surface

area was particularly difficult for Festuca rubra since it is a roll-leaf grass. In this case the area of the outer cylinder was considered. The dry weight was obtained by drying at 105° C for 48 hours. Chlorophyll samples were taken by grinding a portion of the plant material with quartz sand and extracting the chlorophyll with 80% acetone and then determining the chlorophyll content photometrically according to the methods of Arnon (1949).

Measurement of CO₂ Gas Exchange

The gas exchange measurements were made using completely climatized plexiglass cuvettes (Siemens A. G.) (Koch, Klein and Walz, 1968). The cuvettes had a volume of 7 liters with the usable inside space being 28 x 20 x 8 cm. The temperature and relative humidity could be controlled to follow ambient conditions, or in the case of temperature could be set to remain at a selected value. Three such cuvettes were in operation the entire season.

The instrumentation was located in a trailer 25 meters from the gas exchange chambers. Cables and tubing were adequate to increase the sampling distance to a radius of 50 meters from the trailer (Figure 2).

Surrounding air was drawn from a point two meters above the meadow. Initially the air was drawn at plant height, but fluctuations



Figure 2. View of experimental site with mobile field laboratory.

in CO₂ concentration during the night hours when there was little turbulence made it difficult to obtain a reliable CO₂ reading on the sensitive differential infra-red gas analyzer (Janáč, 1970). Thus a fluctuation of 2 ppm CO₂ could obscure a change in respiration rate of 2-4 ppm CO₂. During the day, turbulence normally was sufficient to prevent large, short term fluctuations.

A portion of this air (measuring gas) was drawn through the cuvette, while the other portion (comparison gas) went directly to the differential infra-red gas analyzer (IRGA)¹ (URAS-Ultra-Rot-Absorbptions-Schreiber, Hartman and Braun) (Figure 3). Several buffer bottles (B) were attached to the comparison gas line so that the volume would correspond to that of the cuvette; thus the measuring and comparison gas would arrive at the analyzer at the same time. This was done to further minimize any possible CO₂ fluctuations. The difference between the comparison gas and measuring gas was considered as being the CO₂ gas exchange of the enclosed plant.

The CO₂ content of the air from each plant chamber was registered once every six minutes. This was accomplished by a program timer (PT) with gas multi-way switches (AMV). The switches allowed

¹ Abbreviations refer to Figure 3 (page 12) and are described on the page facing Figure 3.

Description of abbreviations used in Figure 3.

CUV	-Cuvette with radial fan
B	-Buffer bottles
Th	-Pt-100 resistance thermometer
TR	-Temperature regulator
IHS	-Ingoing humidity sensor
OHS	-Outgoing humidity sensor
BPHS	-By-pass humidity sensor
P	-Pump
V	-Valve to control flow rate
FM	-Flow meter
WVT	-Water vapor trap
HC	-Humidity controller
VR	-Voltage regulator
AMV	-Automatic magnetic valves ^a
PT	-Program timer
CR	-Chart recorder
ADC	-Analog-digital converter
T	-Teletype
IRGA	-Infra-red gas analyzer
Hi, Hbp, Ho	-Data from humidity sensors entering chart recorder
ati, ato	-Data from temperature sensors entering chart recorder
ΔCO_2	-Differential CO_2 content between ambient and cuvette air

^aThe numbers denote positions where gas lines from other cuvettes may be attached.

The narrow lines represent electrical connections and the thick lines with arrows represent pneumatic tubing.

the gas to be measured to pass into the gas analyzer for one minute, representing the time necessary to flush the analyzer of any gas remaining from the previous sample. When not passing into the gas analyzer, the air was released into the atmosphere through a valve having the same resistance as that encountered by air passing through the gas analyzer. This system permitted a continuous flow of air through the cuvette.

Every six minutes the ambient (comparison gas) air was passed through both tubes of the differential gas analyzer giving the zero differential CO_2 value of the analyzing system. This value was stored on a millivolt recorder (Minicomp, Hartman and Braun) and was used as the zero point of CO_2 gas exchange for each cuvette for every six minute period.

The gas analyzer was calibrated every 7-10 days with bottled gas of a known CO_2 concentration. Although there was some drift of the zero point during this time, the magnitude of the output was not changed noticeably. The analyzer was always recalibrated after power failures due to thunderstorm activity or after the power was shut off. The calibration allowed for a scale range of plus or minus 75 ppm CO_2 on a scale of 25 cm. An analysis of errors in CO_2 measurements of this kind is discussed in detail by Koch, Lange and Schulze (1971).

To eliminate the effects of water vapor in the air being measured

in the gas analyzer, a light filter was built into the analyzer to eliminate the light absorption band of water which is very similar to that of CO₂.

Immediately after leaving the infra-red gas analyzer the flow of the air was measured. Flow rates for the CO₂ measurements varied from 50-200 liters per hour, depending upon the size and gas exchange activity of the plant material within the cuvette. The flow rates were also kept sufficiently high to avoid any significant buildup or decrease in the CO₂ content of the air in the cuvette.

Temperature Control

Temperature control of the air inside the plant chamber was achieved through the use of Peltier heat exchange elements on the base of the cuvette (Bosian, 1964). These were connected to Pt-100 resistance thermometers (Th) located inside and outside the cuvette. If a temperature difference exists between the ambient air and that in the cuvette, a signal is sent to the electronic temperature regulator (TR) which then results in the cooling or heating of the Peltier elements, thus maintaining the desired temperature in the cuvette. Alternatively a constant temperature can be maintained in the cuvette.

A radial fan located inside the cuvette allows a wind velocity of from .5-2.0 m/second. This velocity is sufficient to adequately mix the air such that the temperature in the center of the cuvette

does not fluctuate more than plus or minus .5° C from the desired temperature. The radial fan also serves the function of "drawing" the air over the leaf, thus breaking the boundary layer (Figure 4).

In Table 2, the air and leaf temperatures inside and outside the cuvette are compared during a two hour period (20 measurements) of full insolation on June 18. The air temperatures inside the cuvette are all within .5° C of air temperatures outside the cuvette. The variance is slightly greater outside the cuvette as might be expected. Leaf temperature is only slightly (1-2° C) higher than ambient for the Festuca rubra leaves inside the cuvette whereas outside there is hardly any difference.

Table 2. Comparison of temperatures inside and outside the cuvette at full solar insolation between 12:00 and 14:00 on June 18, 1970 for Festuca rubra fertilized and Festuca rubra unfertilized.

Festuca rubra fertilized

	Air temperature inside cuvette	Air temperature outside cuvette	Leaf temperature inside cuvette	Leaf temperature outside cuvette
Mean temp.	22.6°C	23.0°C	23.8°C	22.7°C
Variance s ²	.234	.276	.168	.346

Festuca rubra unfertilized

Mean temp.	23.1°C	22.9°C	25.1°C	23.4°C
Variance s ²	.185	.334	.111	.876

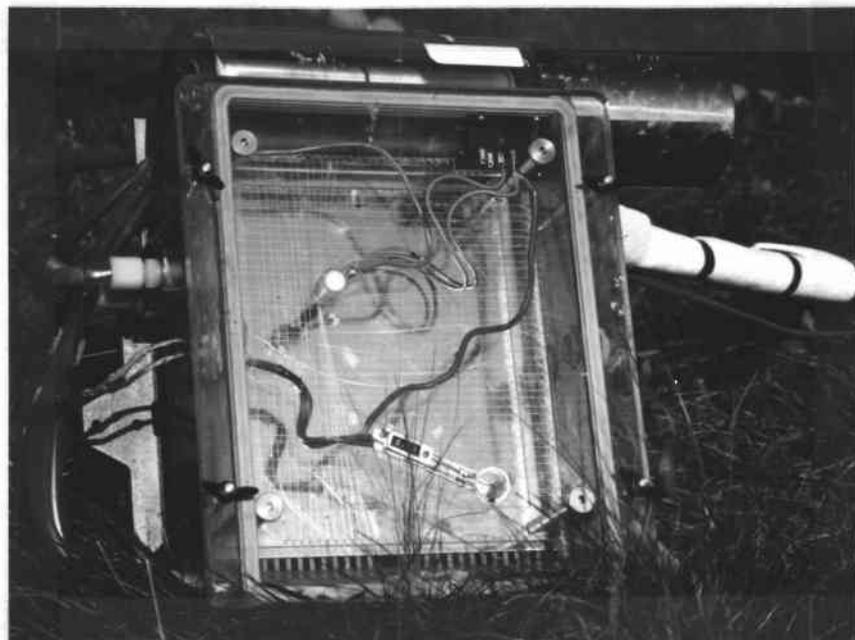


Figure 4. Close up view of cuvette.

It is possible to obtain any desired temperature up to 30° C above ambient in the cuvette. Furthermore, it is possible to obtain temperatures 8° C below ambient at full insolation; however, in that case one would have to cool the Peltier elements with water.

Another thermometer is located directly above the Peltier elements inside the cuvette, this can be used to check if the elements are colder than the dew point. If so, condensation would occur inside the cuvette making invalid the transpiration measurement described below.

Humidity Control and Transpiration Measurement

The humidity is controlled by the use of a by-pass system connected to a water vapor trap. The humidity of the air is measured just before entering the cuvette (Lithium chloride humidity sensors) (IHS) and just after leaving the cuvette (OHS) before going to the infra-red gas analyzer. If the exit air has a higher humidity than the entering air, meaning that the plant is transpiring, a certain amount of water would have to be taken out of the air in the cuvette to maintain a humidity equal to the ambient. This removal of excess moisture is done by the by-pass system.

In this separate, closed system, air is pumped out of the cuvette at a rate up to 10 times greater (2-10 liters per minute) than the CO₂ measuring air flow. This is necessary to assure rapid

control and also to remove excess water from the air. The air is drawn from the cuvette and forced through a water vapor trap (WVT) and flow meter (FM) with a differential pressure regulator to assure even flow rates. The air then passes through a humidity sensor (BPHS) (identical to IHS and OHS) and back to the cuvette. The humidity sensors, water vapor trap, pump and flow meter are located in a box adjacent to the cuvettes (Figure 2).

The intensity of the cooling of the Peltier element water vapor trap is proportional to the amount of water given off by the plant. In other words, the electronic humidity controller is set to maintain identical entry and exit humidities. Thus the water vapor content of the air returning to the cuvette from the by-pass is lower than the entry (i. e. exit) humidity by the amount of water the plant is transpiring. Transpiration values can then be calculated by multiplying the flow rate (in the by-pass) times the difference between exit water vapor content and by-pass water vapor content ($\text{mg H}_2\text{O/liter}$). In this way follow-up control of humidity is achieved. In order to maintain a constant selected humidity one needs to attach a water vapor trap in front of the entry humidity sensor.

In moist climates it is possible that considerable condensation may occur in the tubing. Condensation is common when the tubing is placed unprotected on the ground where temperatures quite often are below the dew point, especially on clear nights. In most cases

the condensed water in the tubing will have evaporated by midmorning if the ambient humidity is less than 85%. The error that might be expected in this case is partially compensated for by the fact that dew frequently remained on the grass outside the cuvette for a time comparable to the condensed water in the tubing.

The problem can be partially avoided by heating the PVC tubing or by placing a water vapor trap or some drying agent at the air intake to maintain a dew point slightly below ambient.

The lithium chloride humidity sensors had to be soaked with a lithium chloride solution every 14 to 35 days depending upon the moisture conditions encountered.

Leaf Temperature Measurement

Copper-constantan thermocouples .05 mm in diameter were used to measure leaf temperature both inside and outside the cuvette. The thermocouples were attached to leaf clamps as described by Lange (1965). The clamps held the leaf and pressed the thermocouple junction against the underside of the leaf (Figure 5). The reference junctions for the thermocouples were kept at 0° C in a Peltier cooled oil bath (Thermonullstelle, Siemens A. G.).

Light Intensity Measurement

Silicon light cells were placed in each cuvette. They were

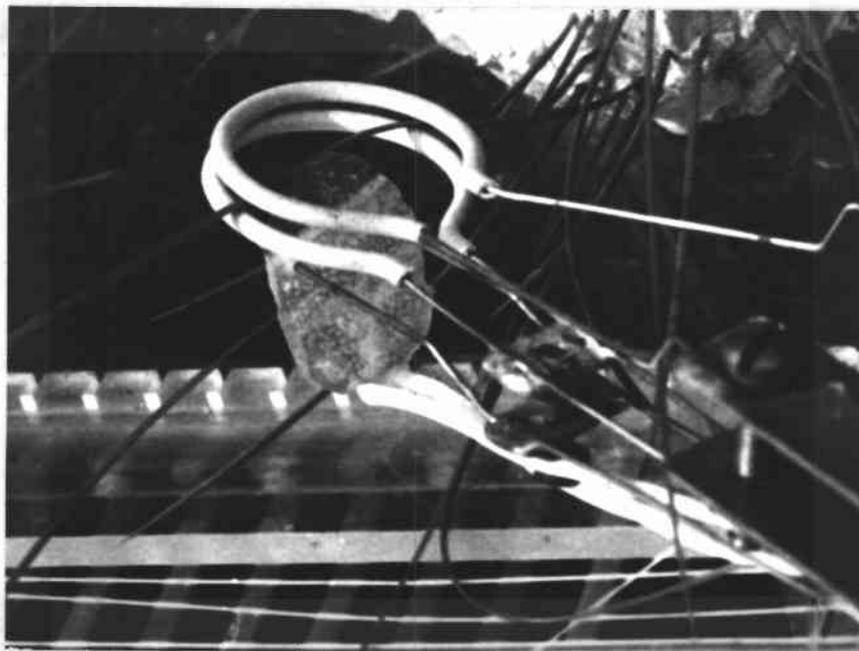


Figure 5. Clamp and thermocouple for leaf temperature measurement.

located parallel to the lid of the cuvette so that the exposure was the same as for the cuvette. Silicon photocells have the advantage that they do not fatigue with time and have a greater output than the selenium photocells. Measurement of illumination was in lux.

Total solar radiation data were obtained by O. Kiese of the Meteorological Institute in Hannover. These values were in terms of $\text{cal/cm}^2/\text{hour}$; however, since the cuvettes were tilted these values could not be directly related to the light available to the plant in the cuvette. Daily radiation values, however, were used and related to daily net photosynthesis.

Registration of Measurements

To register the data for the three cuvettes, three chart recorders, one for each cuvette, were available; data (Table 3) were registered on the Polycomp (Hartman and Braun) 12 channel, 6 range recorders. The data were registered once every six minutes for each cuvette, with a time of one minute required to print out the data. In addition to being registered on the chart recorder the data were converted via a follow-up potentiometer and analog-digital converter (ADC) to a teletype print out. Here the data were printed out in millivolt readings and the same data transferred to 5 channel paper punch tape (Figure 6).

By registering data in three different forms it was easier to

Table 3. Data registered on the 12 channel - 6 range recorder.

Parameter measured	measuring range	method
Light inside the cuvette	0-50 mV	Si light cells (0-100 k1x)
Air temperature inside the cuvette	-30-60°C	Pt 100 resistance thermometers
Air temperature outside the cuvette	-30-60°C	Pt 100 resistance thermometers
Leaf temperature inside the cuvette	0-2.5 mV	Cu-constantan thermocouples (0-50°C)
Leaf temperature outside the cuvette	0-2.5 mV	Cu-constantan thermocouples (0-50°C)
Entering humidity (dew point)	-10-40°C	Pt 100 resistance thermometers + LiCl
Exiting humidity (dew point)	-10-40°C	Pt 100 resistance thermometers + LiCl
By-pass humidity (dew point)	-10-40°C	Pt 100 resistance thermometers + LiCl
Zero CO ₂	0-5 mV	Differential gas analyzer + 75 ppm CO ₂
Delta CO ₂	0-5 mV	Differential gas analyzer + 75 ppm CO ₂
Peltier element temp. in cuvette	-30-60°C	Pt 100 resistance thermometers
Dew point of water vapor trap	-30-60°C	Pt 100 resistance thermometers

Data registered on two of the recorders in place of the dew point of the water vapor trap.

Reference junction of thermocouples	-10-60°C	Cu-constantan in peltier cooled oil bath
Light outside the cuvette (horizontal)	0-50 mV	Si light cells (0-100 k1x)

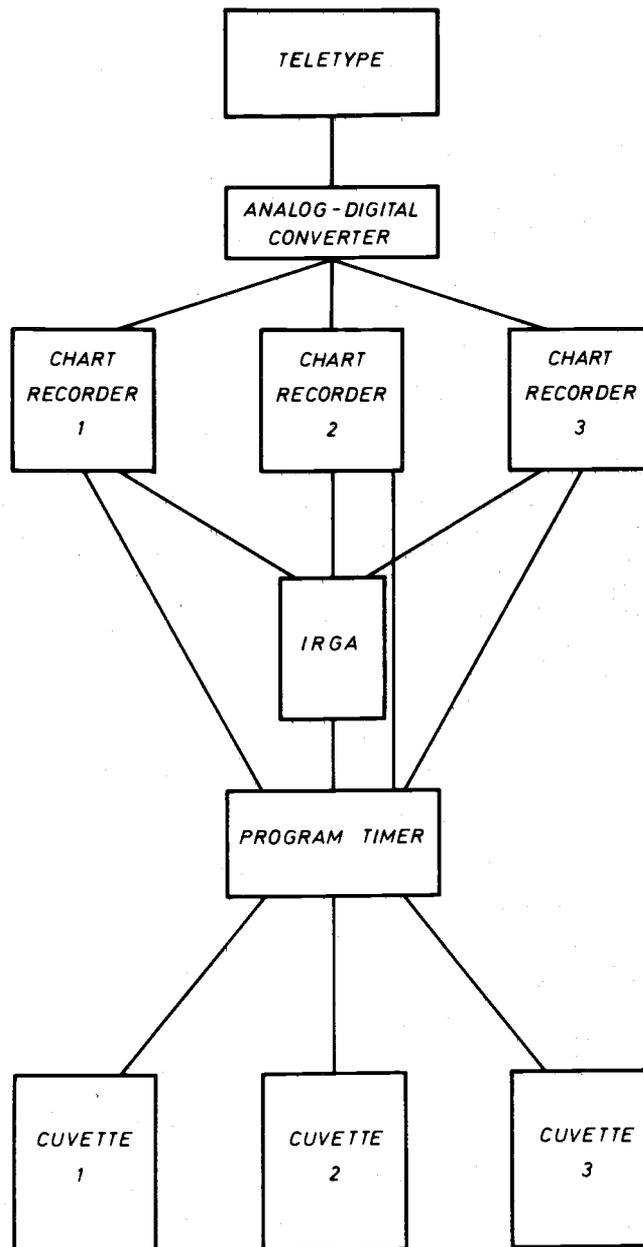


Figure 6. Schematic diagram of data gathering system.

check for errors. For example, on the chart recorder the measured parameters were plotted with respect to time for each cuvette. Although the reference values were not taken into account one could see from the shape of the curves if all systems were functioning correctly. From the teletype printout alone it would have been difficult to determine possible errors.

The punch tape was read into an EXL 8 computer at the computer center of the University of Würzburg for the data conversion. The first step consisted of adding all the reference values and flow rates and then computing the various parameters from the millivolt readings (Table 4). Once the daily values were printed out they were rechecked for possible errors which were then erased from the disc. Hourly means were also computed and printed out.

Initially it was hoped that the entire data as collected could be analyzed on the computer; however, due to the many printout errors it was not possible to do this directly. Consequently, data desired for the various analyses were read from the printout and typed back into the computer. This was a very time-consuming step and considerably lengthened the time for analysis of data.

During the six month measuring period 70 punch tapes (360 m each) were used with each tape having 20,000 individual measurements. However, from these individual measurements various other parameters were computed, thus a printout of 21 different parameters

Table 4. Values calculated and printed out by the computer.

Parameter calculated	Units
Time	hours, minutes
Light	klux
Air Temp. in the cuvette	°C
Air Temp. outside the cuvette	°C
Leaf Temp. in the cuvette	°C
Leaf Temp. outside the cuvette	°C
Entering humidity	°C dewpoint
Outgoing humidity	°C dewpoint
Outgoing humidity	mg H ₂ O liter ⁻¹
Outgoing minus by-pass humidity	mg H ₂ O liter ⁻¹
Change in ppm CO ₂	ppm CO ₂
CO ₂ gas exchange/dry weight	mg CO ₂ g ⁻¹ hr ⁻¹
CO ₂ gas exchange/leaf surface area	mg CO ₂ dm ⁻² hr ⁻¹
CO ₂ gas exchange/chlorophyll	mg CO ₂ mg Chl ⁻¹ hr ⁻¹
Transpiration/dry weight	mg H ₂ O g ⁻¹ hr ⁻¹
Transpiration/surface area	mg H ₂ O dm ⁻² hr ⁻¹
Vapor pressure deficit (VPD) inside the cuvette	mg H ₂ O liter ⁻¹
Vapor pressure deficit (VPD) outside the cuvette	mg H ₂ O liter ⁻¹
Diffusion resistance to H ₂ O of enclosed leaf material	sec. dm ⁻¹
Relative humidity inside the cuvette	%
Relative humidity outside the cuvette	%
Relative humidity based on leaf temperature (inside)	%

was obtained in addition to the hourly means (Table 4).

Statistical Treatment

Further analysis of the data was carried out at the computer center at Oregon State University. Programs used were *STEP for stepwise multiple linear regression, *NANOVA for analysis of variance, *WALTB for plotting of data, and *SIPS for additional multiple linear regression and analysis of residuals.

Laboratory Measurements

After the field measurements were begun it was found that there were periodic large fluctuations in the ambient CO₂ concentration at night which made it difficult to determine plant respiration. Furthermore, the fluctuating light conditions as well as the low light levels which were encountered during the latter part of the growing season made it difficult to determine photosynthetic response to temperature at a constant high light level. Thus, portions of the meadow were dug up periodically and brought to the laboratory in Würzburg where CO₂ gas exchange was measured on cut leaf segments.

An open system similar to that used in the field, but using smaller cuvettes submerged in a water bath were used for the CO₂ gas exchange measurements. CO₂ gas exchange was measured over a temperature range of 5° to 30° C. Illumination was 48 klx for the

photosynthesis measurement.

Phenology and Weather During the Growing Season in 1970

The winter of 1969-1970 was unusually long in the Solling area, with snow remaining on the meadow until the beginning of May. The last light frost occurred on June 3. Precipitation was frequent throughout the growing season (Figure 1), the driest month being August with 83 mm precipitation (Precipitation data were obtained by Prof. Dr. Ulrich, Institut für Bodenkunde, Hann-Münden).

Gas exchange measurements were begun in the latter part of May. Growth proceeded rapidly in the month of June, which was characterized by moderate temperatures, many clear days and occasional rain. The first mowing of the meadow occurred on June 22. July was characterized by frequent rains and primarily low temperatures, although the warmest day of the year also occurred in July (maximum temperature for one hour at .2 m above ground 31 °C (27 °C at 2 m)). August was quite warm with frequent rain. The meadow was mowed for the second time on August 15. During the month of September temperatures were moderate with the latter part of the month being warm and sunny. During this time the unfertilized grass (Festuca (0))² became brown

²Throughout the text (NPK) will refer to the fertilized and (0) to the unfertilized plot.

near the tips and no further height growth was apparent. The first moderate frost occurred on September 23-24 (-1°C at plant height). The meadow was mowed for the last time in October.

In October the grass blades of the unfertilized Festuca became increasingly brown whereas on the fertilized plots they remained green and continued to increase in length despite the cool temperatures. The first intensive frost occurred on October 24 (-1°C at 2 m and -4°C at plant height). By the end of October radiation and temperature decreased to such an extent that on many days respiration exceeded photosynthesis. The measurements were terminated on November 3.

RESULTS AND DISCUSSION

Reference Basis for Photosynthesis

Photosynthesis has been expressed on various bases, most notably leaf dry weight, surface area and chlorophyll. In this study all three were determined, but due to the vast amounts of data, only leaf dry weight was used in all aspects of data analysis. However, since much of the work involving primary productivity, of which photosynthesis is the underlying process, is based on dry matter production, leaf area indices and the amount of chlorophyll, it is necessary to include the relations between the three reference values. As stated by Šesták, Čatský and Jarvis (1971): "To get the maximum possible information out of measurements of photosynthesis in different environmental conditions, it is clearly advantageous to have the information available to calculate the rate of photosynthesis on the basis of several plant characteristics."

Figures 7, 8 and 9 depict the photosynthetic rates based on leaf dry weight, leaf surface area and chlorophyll content for Festuca rubra fertilized (NPK) and unfertilized (0) on various clear days of the same dates from June until October. It should be recognized that the curves represent widely differing conditions with respect to age, phenology, temperature and humidity. The leaf and air temperature, relative humidity and vapor pressure deficit (VPD) for those days are listed in Table 5.

The photosynthetic rates of Festuca (NPK) show considerably greater variability than the rates of Festuca (0). This variability

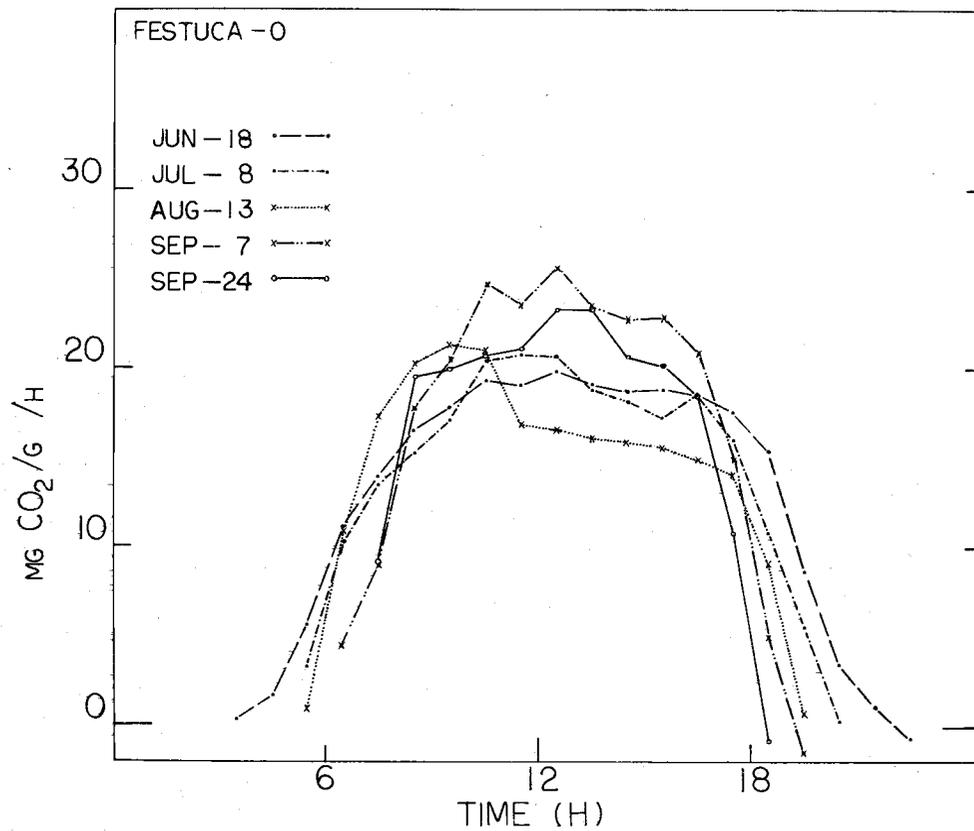
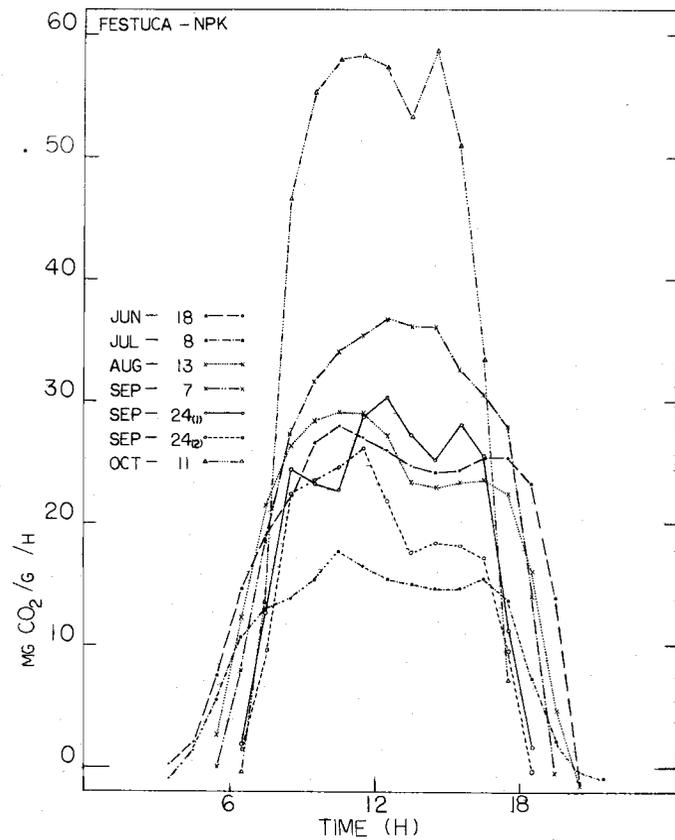


Figure 7. Net photosynthetic rates (based on dry weight) for *Festuca rubra* fertilized (NPK) and unfertilized (0) on select clear days at various times of the year.

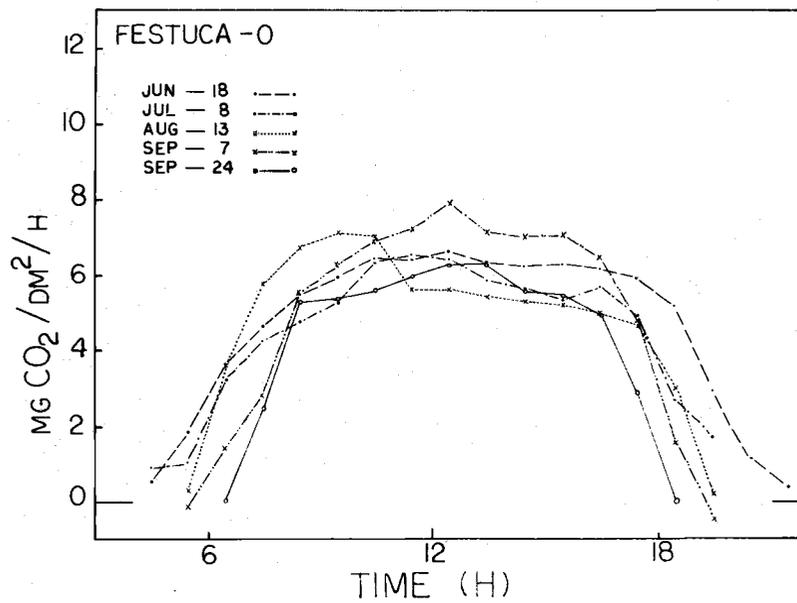
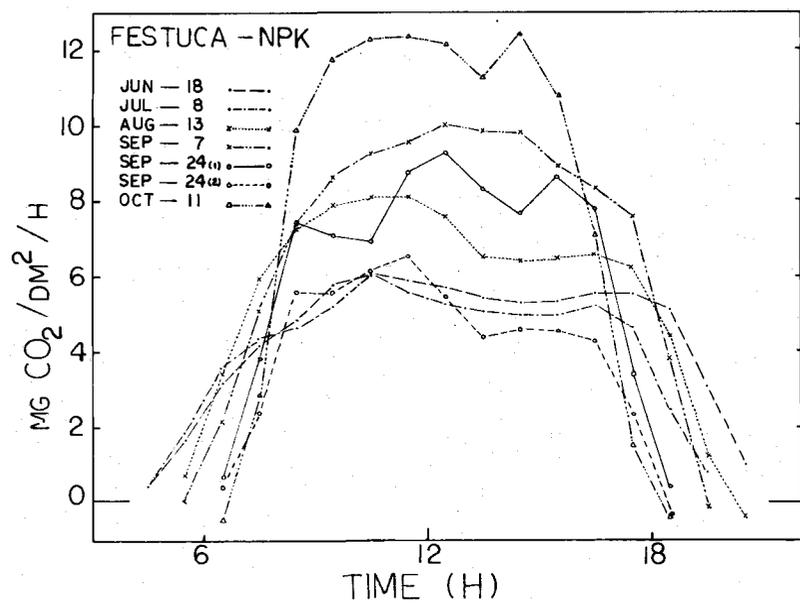


Figure 8. Net photosynthetic rates (based on leaf area) for *Festuca rubra* fertilized (NPK) and unfertilized (0) on select clear days at various times of the year.

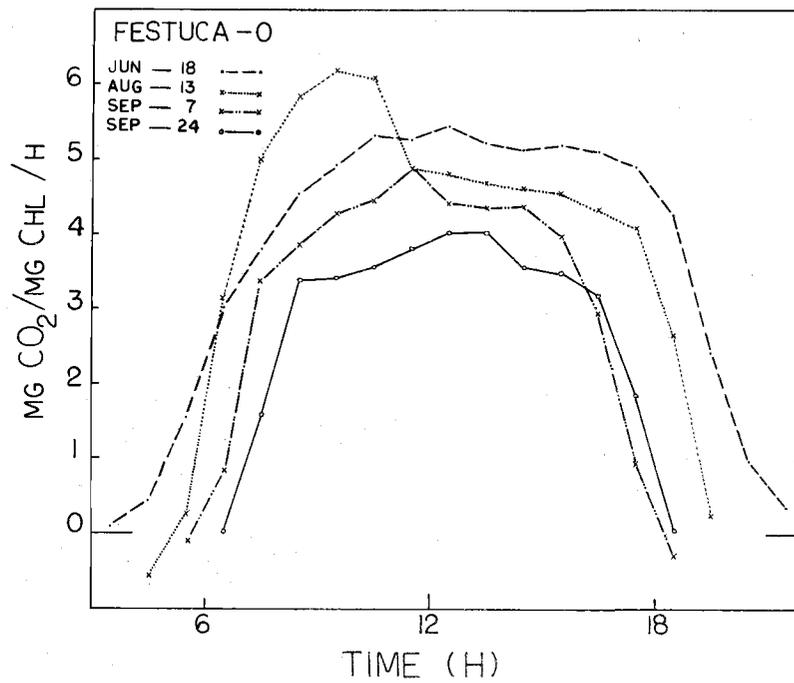
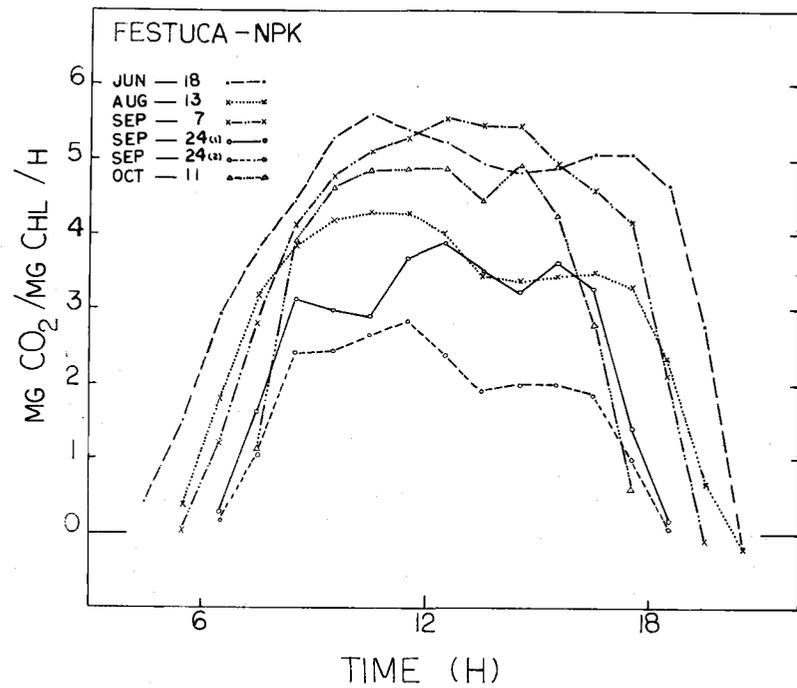


Figure 9. Net photosynthetic rates (based on chlorophyll) for *Festuca rubra* fertilized (NPK) and unfertilized (0) on select clear days at various times of the year.

Table 5. Some environmental factors measured on the days depicted in Figures 7, 8 and 9.

Day	Max. Temp. air ° C	Max Temp. leaf ° C	Min. Rel. Humidity %	Max VPD mg H ₂ O/l
June 18	23.2	24.9	41%	14.09
July 8	29.7	30.1	36%	15.77
Aug. 13	25.2	26.7	45%	15.10
Sept. 7	21.6	20.7	45%	9.06
Sept. 24	17.1	18.1	52%	7.74
Oct. 11	20.1	20.0	87%	2.36

remains fairly constant regardless of the reference basis used.

On the basis of dry weight and area, the photosynthetic rates of the fertilized grass are generally above that of the unfertilized. On a chlorophyll basis, however, the rates are virtually the same; indicating equal photosynthetic efficiency based on a unit chlorophyll.

Similarly the curves generally maintain the same relation to each other when expressed on a leaf dry weight or area basis. However, when based on chlorophyll the relative magnitudes vary considerably. This change in magnitude is most notable for the October 11 rate on the fertilized plot.

That the photosynthetic rates of Festuca (NPK) are greater than those of Festuca (0) based on leaf dry weight and leaf area, while nearly the same based on chlorophyll is due primarily to fluctuations in the relationship between the reference values. The relationship between leaf dry weight and area remained essentially the same during the year. The coefficient of multiple determination (R^2) of a regression relating dry weight to area was .72 for the May-August period and .80 for the August-November period for the fertilized Festuca and .95 and .93 for the unfertilized Festuca respectively. The unfertilized grass had a slightly higher dry weight per unit area than the fertilized grass (Appendix, Figure 26, Table 16).

The chlorophyll content per unit dry weight on the other hand showed considerable variation. This finding is consistent with that of Medina and Lieth (1964) and others who suggest that the chlorophyll

content changes rapidly during the growing period, being very sensitive to environmental changes. The R^2 value of a regression relating dry weight to chlorophyll content was .67 for the fertilized and .34 for the unfertilized grass, the latter being statistically insignificant at the 5% probability level based on an F test.

Daily Photosynthetic Patterns on Clear Days

Restricting ourselves to photosynthetic rates based on dry weight (Figure 7) several response patterns are discernible. Afternoon depressions with a slight recovery are visible on June 18, July 8, August 13, and on September 24 (2). All except the latter occurred on days of relatively warm temperatures and high VPD (Table 5), which are rare in the Solling area. The September 24 (1 and 2) patterns which are from leaves 5 and 10 weeks after cutting respectively, show rather erratic behavior which will be discussed in greater detail under the heading "The Effects of Temperature and Vapor Pressure Deficit."

The days of moderate temperatures, September 7 and October 11 show the highest photosynthetic rates with no afternoon depression (the depression on October 11 was due to partial cloudcover). The highest rates of photosynthesis (based on dry weight) during the growing season for Festuca rubra (NPK) were recorded on October 11 (60 mg CO₂/g/hr), although rates nearly this high were also found

in late May.

Similar behavior was observed for Festuca rubra (0), although there was no visible photosynthetic depression on June 18 and no data were obtained on October 11. Stocker (1967) working with middle European grasses, found such double peaked curves a rarity except during the spring when the grasses were in a more succulent, sensitive stage. Festuca (NPK) was probably more comparable to this condition than Festuca (0).

The apparent action of the environmental factors, light, temperature and VPD on photosynthesis is depicted in Figure 10 for Festuca rubra (NPK) on three widely differing days. On June 18, a day with moderate temperatures (maximum air temperature inside the cuvette being 23° C), the photosynthetic depression coincides with the maximum temperature and VPD which could cause considerable plant water stress. The August 13 pattern shows a gradual temperature increase to 26° C with a dramatic increase in the VPD around 11 am and a corresponding decrease in the photosynthetic rate. Late in the afternoon as VPD drops there is again an increase in photosynthesis before light becomes limiting. October 11 depicts a rather cool day with a maximum temperature of 21° C and low VPD. Light and photosynthesis are closely related, with temperature and VPD also fluctuating with the light levels.

The general photosynthetic patterns discussed above suggest

Festuca rubra (NPK) June 18 Solling 1970 Festuca rubra (NPK) August 13 Solling 1970 Festuca rubra (NPK) October 11 Solling 1970

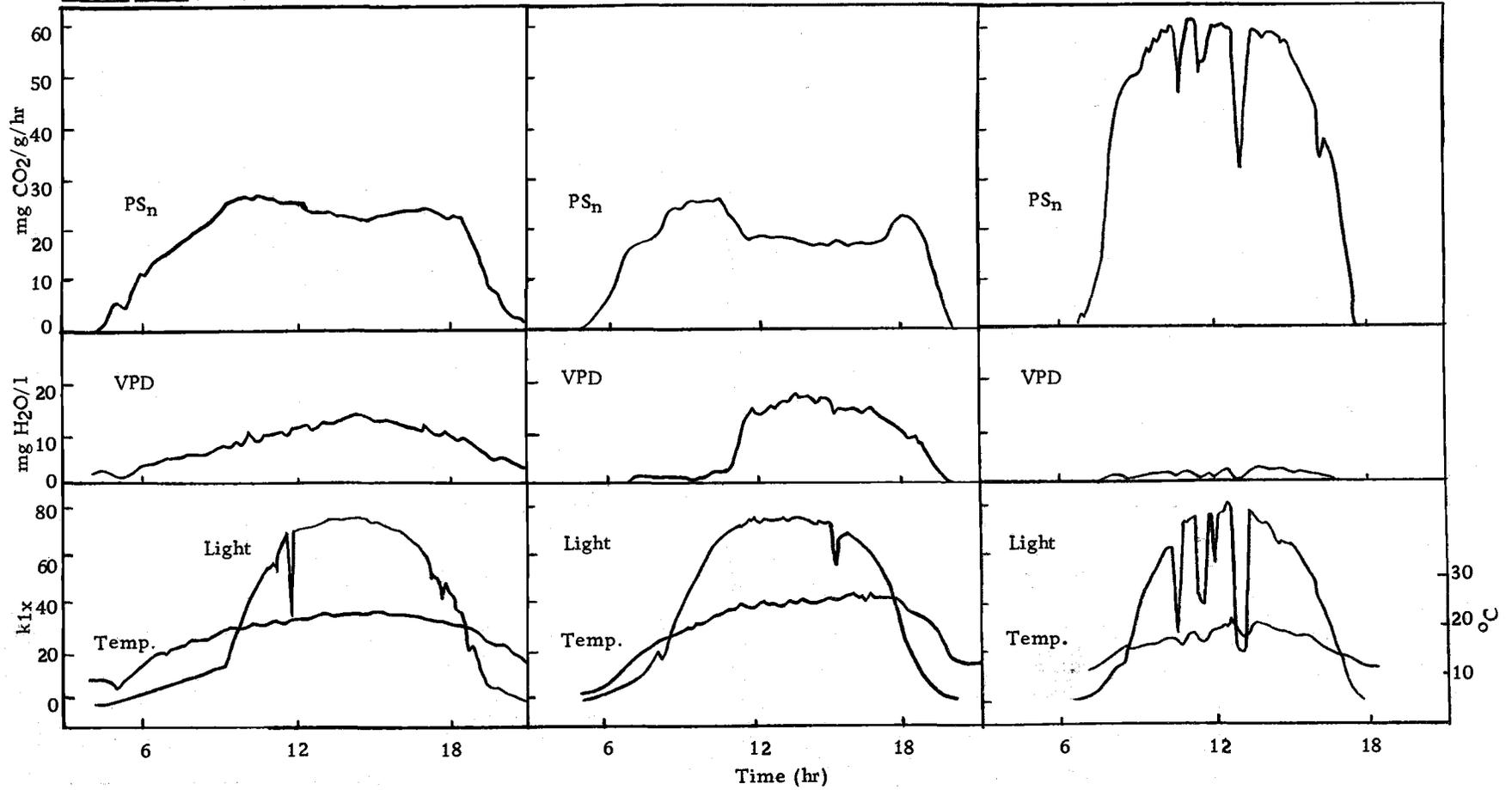


Figure 10. Net photosynthetic rates (based on dry weight) for Festuca rubra fertilized (NPK) in relation to several environmental parameters on three select clear days.

that they are closely tied to light with temperature and VPD playing a secondary role in limiting photosynthesis. These are similar to the findings of Schulze (1970) who studied the beech in the Solling area and found light to be the principal limiting factor.

Consequently further analyses were made by examining the light factor first and then the other parameters in explaining the photosynthetic rates. This was done using daily net photosynthetic values as a function of total daily radiation, and then adding other parameters, such as maximum daily temperature, maximum daily VPD (hourly means), time (day of year) and chlorophyll content of the foliage to the regression equation.

Changes in Daily Net Photosynthesis from June until October

Measurements of long term or seasonal change of primary productivity either on the basis of dry matter accumulation or on the CO_2 gas exchange have been made as early as Gregory's work with barley (1926) in which dry weight increase per unit leaf area per unit time was studied. He related dry weight increase to such environmental parameters as average day and night temperature, total radiation and the evaporative power of the air. Thomas and Hill (1937) followed the CO_2 gas exchange of alfalfa and wheat growing under field conditions for extended periods using a six foot square celluloid-covered plant chamber. Kaben (1959) followed CO_2 assimilation of

the shade plant Lamium galeobdolon over a year, finding that ambient CO₂ content best explained variation in the CO₂ gas exchange. Other studies such as those of Helms (1965) on Douglas-fir found no single factor to be the principal component in explaining photosynthetic rates.

Photosynthesis Based on Radiation Regression for three Reference Bases

The changes in total daily net photosynthesis³ in relation to total daily radiation are depicted in Figure 11 for the three reference bases of photosynthesis (covering a minimum of 85 days throughout the growing season). The curves were determined from the stepwise multiple linear regression model: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \epsilon$ (Tables 6 and 7). This model was used to allow maximum flexibility in fitting the curve.

For Festuca (NPK) leaves the maximum daily photosynthetic production is reached at a radiation level of approximately 300 cal/cm²/day. The R² values for the regressions vary from .87 based on dry weight to .75 when based on leaf surface area. Part of this variation is probably due to the greater error involved in leaf surface measurements of the roll-leaved grass Festuca rubra. For Festuca (0) virtually the same amount of variation was explained regardless of the reference basis used; the R² values being .87 to .88.

³Daily net photosynthesis is defined here as the CO₂ uptake during the day with no correction made for night respiration.

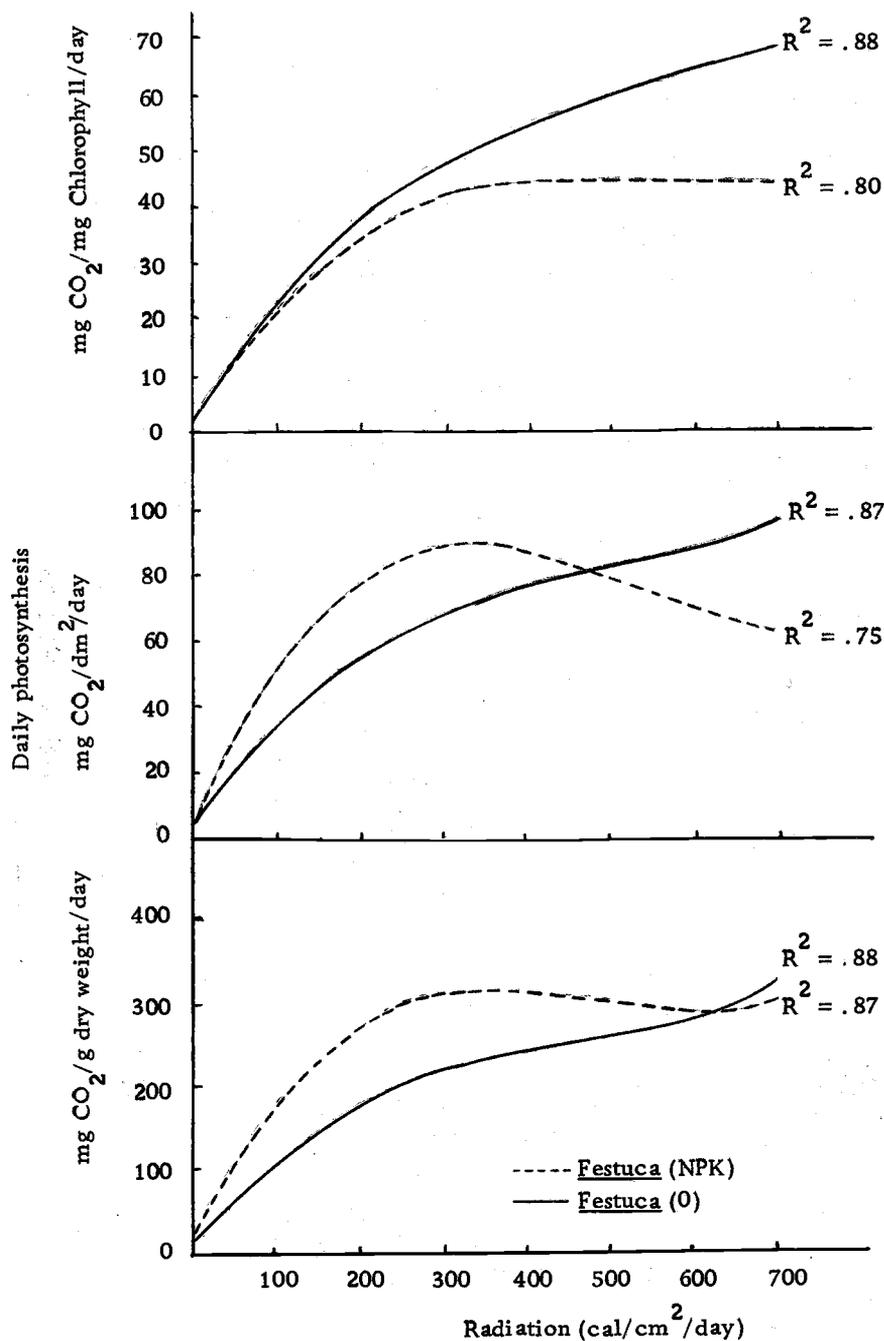


Figure 11. Seasonal response curve of net photosynthesis to radiation. Photosynthesis based on leaf dry weight, area and chlorophyll. The curves were obtained from the regression model: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \epsilon$. Coefficients of regression equations are listed in Tables 6 and 7.

Table 6. Coefficients, t-significance and R^2 values for the seasonal photosynthetic regression based on radiation for three reference bases for *Festuca* (0). $PS_n = \beta_0 + \beta_1 (\text{RAD}) + \beta_2 (\text{RAD})^2 + \beta_3 (\text{RAD})^3 + \epsilon$.

Photosynthesis based on leaf dry weight			
Variable	β Coefficient	t-signif. ^a	R^2
Constant	4.97623	----	----
(radiation)	1.32601	**	.79
(radiation) ²	-.00275	**	.85
(radiation) ³	2.17E-6 ^b	**	.88
Photosynthesis based on leaf surface area			
Variable	β Coefficient	t-signif.	R^2
Constant	2.48241	----	----
(radiation)	.38173	**	.79
(radiation) ²	-.00071	**	.86
(radiation) ³	5.23E-7	**	.87
Photosynthesis based on mg chlorophyll			
Variable	β Coefficient	t-signif.	R^2
Constant	1.07022	----	----
(radiation) ₂	.25500	**	.81
(radiation) ₃	-.00039	**	.88
(radiation)	2.42E-7	----	.88

^a** significant 1%

* significant 5%

^bExponential notation, equivalent to $2.17 \cdot 10^{-6}$

Table 7. Coefficients, t-significance and R^2 values for the seasonal photosynthetic regression based on radiation for three reference bases for *Festuca* (NPK). $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \epsilon$.

Photosynthesis based on leaf dry weight			
Variable	β Coefficient	t-signif. ^a	R^2
Constant	5.98507	----	----
(radiation)	2.11231	**	.60
(radiation) ²	-.00471	**	.84
(radiation) ³	3.28E-6 ^b	**	.87
Photosynthesis based on leaf surface area			
Variable	β Coefficient	t-signif.	R^2
Constant	1.17421	----	----
(radiation)	.61243	**	.43
(radiation) ²	-.00132	**	.73
(radiation) ³	8.30E-7	**	.75
Photosynthesis based on mg chlorophyll			
Variable	β Coefficient	t-signif.	R^2
Constant	1.07085	----	----
(radiation)	.24039	**	.65
(radiation) ²	-.00043	**	.79
(radiation) ³	2.49E-7	----	.80

^a** significant 1%

* significant 5%

^bExponential notation, equivalent to $3.28 \cdot 10^{-6}$

On the basis of dry weight and area the increase in the daily photosynthetic rate with radiation was greater for the fertilized than the unfertilized grass. This would indicate a more efficient utilization of light at lower light intensities. When based on chlorophyll the photosynthetic rates for Festuca (0) and Festuca (NPK) were identical at lower light intensities. This is expressed by the greater regression coefficients for the (radiation) term for Festuca (NPK) when based on dry weight and area, while on a chlorophyll basis the coefficient for Festuca (0) was slightly greater (Tables 6 and 7).

On the basis of chlorophyll however, the unfertilized Festuca had higher daily photosynthetic rates, particularly at radiation values above $300 \text{ cal/cm}^2/\text{day}$. These higher rates can largely be explained by the fact that in June and July when daily radiation values were high the leaf chlorophyll content was low, possibly due to photo-inactivation of the chlorophyll. Thus, the fact that the photosynthetic rates of Festuca (0) based on chlorophyll continue to increase is primarily due to the changing chlorophyll concentrations in the leaf.

The drop in total daily photosynthesis associated with Festuca (NPK) at higher radiation values indicates that it is probably more sensitive than Festuca (0) to environmental factors such as temperature and moisture when light is optimum. Part of the differential response at high radiation values between the two grasses is also due to the changing photosynthetic rate with time. Festuca (NPK)

had relatively high photosynthetic rates throughout the year, particularly during the latter part of the growing season in September when many days occurred during which the total daily radiation was between 200 and 300 cal/cm². For Festuca (0) on the other hand the photosynthetic rate declined during the latter part of the growing season reflecting the lower production at intermediate daily radiation values. This decline in photosynthetic rate will be covered in more detail in a later section.

Regression Fit for Restuca (0) Based on Radiation

A total of 84 days was selected, covering the entire growing season, for relating the daily photosynthetic rate to the environmental parameter radiation.

Figure 12 depicts the observed and predicted values of photosynthesis based on the regression model: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \epsilon$. The model explains 87% of the variation (Table 8). Maximum daily photosynthesis was approximately 300 mg CO₂/g dry weight; this declined gradually to less than 10 mg CO₂/g dry weight/day toward the end of October. The majority of the deviations of observed from predicted occurred in the early part of the season (June and July). From August until October there was little deviation of predicted from observed values. This would indicate that toward the latter part of the season light became the principal

factor in explaining daily photosynthesis.

Table 8. Coefficients, t-significance and R^2 values for the seasonal regression based on radiation for *Festuca* (0), (plotted in Figure 12).

Variable	Coefficient	t-significance ^a	R^2
Constant	6.90036	----	
(radiation) ₂	1.28149	**	.78
(radiation) ₃	-.00258	**	.85
(radiation) ₃	1.99E-6	**	.87

^a** 1% level, * 5% level

The period from mid-June until July, where the predicted exceeded the observed values, follows the period of maximum insolation. Then from mid to late July followed a period where the observed photosynthetic rates exceeded the predicted. Apparently the photosynthetic apparatus recovered during July, which was characterized by low temperatures and low light levels at the beginning of the month followed by high light intensity days interspersed with cloudy days with considerable amounts of precipitation. There were no extended periods of high temperatures and light as in June which could reduce photosynthesis by limiting the production (or hastening the destruction) of chlorophyll and photosynthetic enzymes (Björkman and Holmgren, 1963),

Several days on which temperature was probably limiting are depicted by July 2 and October 23, whose radiation and average and

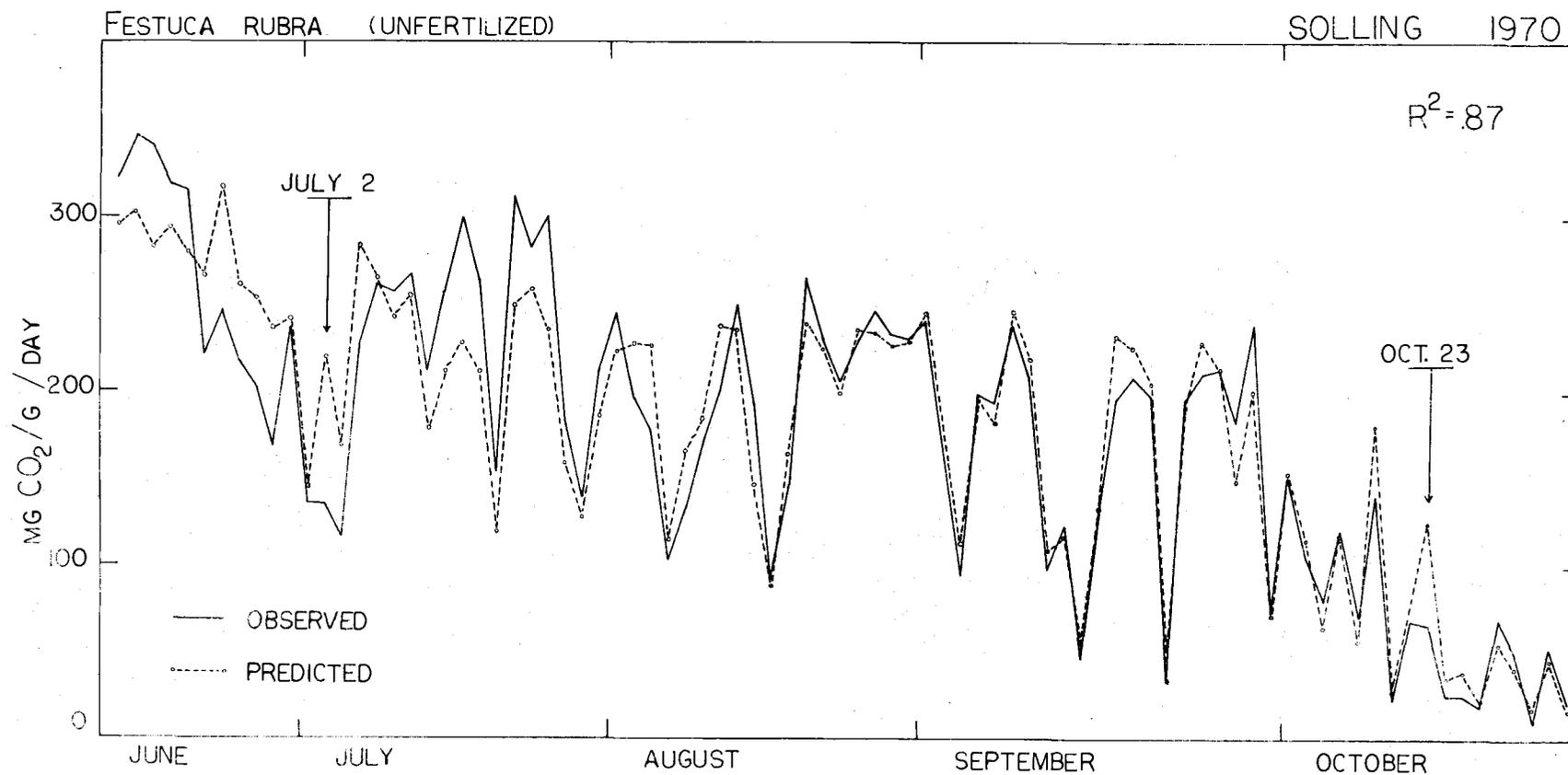


Figure 12. Predicted and observed photosynthetic rates for *Festuca* (0) for the season. The predicted values were obtained from the multiple linear regression equation: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \epsilon$.

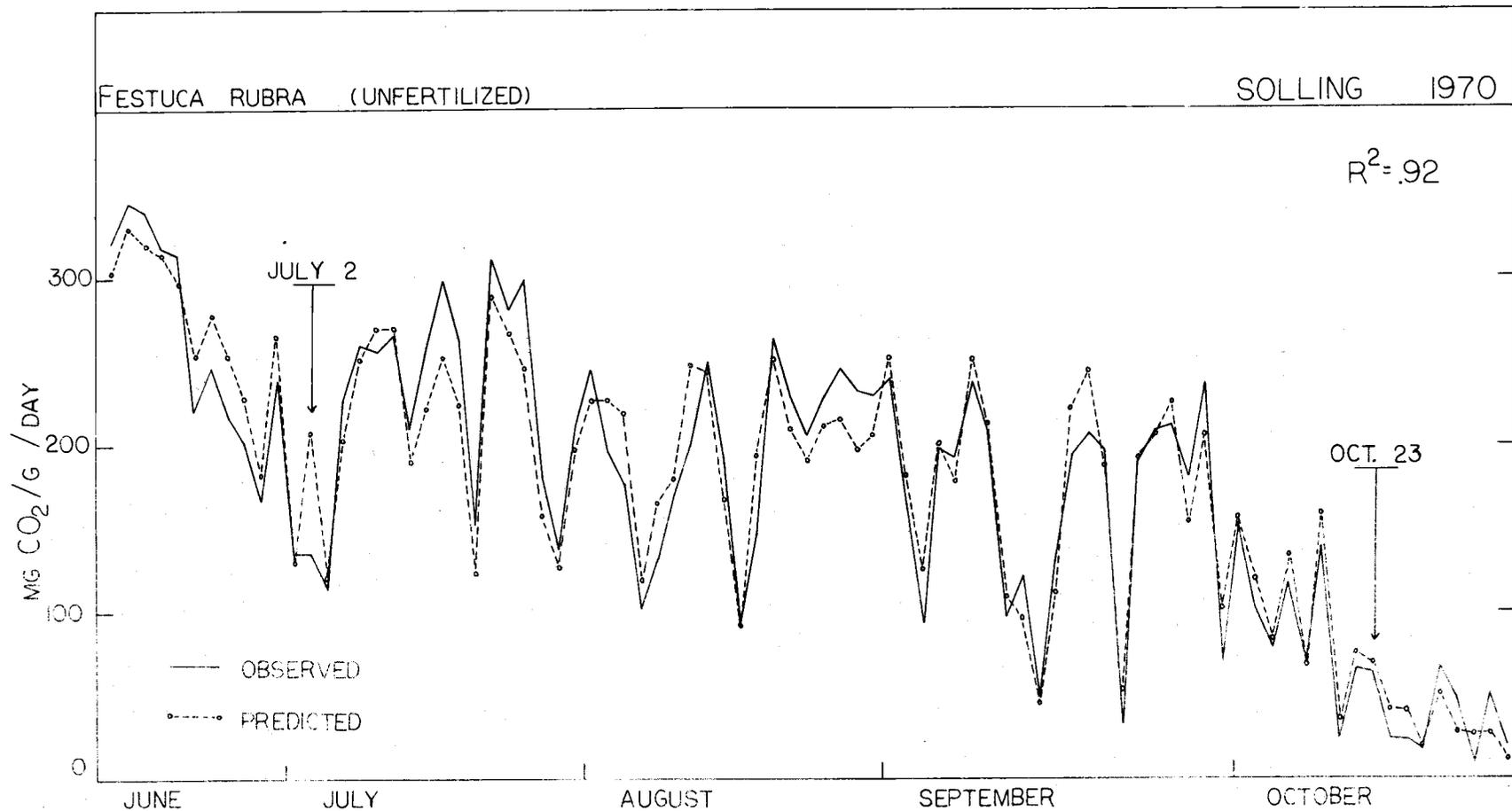


Figure 13. Predicted and observed photosynthetic rates for *Festuca* (0) for the season. The predicted values were obtained from the multiple linear regression equation: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (TEMP) + \beta_4 (TEMP)^2 + \beta_5 (VPD) + \beta_6 (CHL) + \beta_7 (TIME) + \beta_8 (TEMP \times VPD) + \beta_9 (RAD \times TEMP) + \epsilon$.

maximum temperature values appear in Table 9. On July 2 the temperature remained largely unchanged from the previous day while radiation more than doubled; thus the regression equation considerably overestimated the daily photosynthesis. A similar situation occurred on October 22 and 23 where the radiation increased slightly on October 23 but temperature dropped from the previous day.

Table 9. Radiation and temperatures for July 1, 2 and October 22 and 23.

Date	Radiation cal/cm ² /day	Average Temperature °C	Maximum Temperature °C
July 1	145.1	9.4	10.6
July 2	329.8	9.7	13.1
October 22	102.9	4.2	6.8
October 23	118.3	2.5	5.0

Regression Fit for *Festuca* (0) Based on
Radiation, Temperature, Vapor Pressure
Deficit, Chlorophyll and Time

Observed and predicted values of daily photosynthesis based on the expanded regression model are depicted in Figure 13. All days were chosen for which data on radiation (cal/cm²/day), temperature (maximum daily one hour average), VPD (maximum daily one hour average), chlorophyll (mg chlorophyll/g dry weight) and time (day of year) were available for both *Festuca* (0) and *Festuca* (NPK). The regression model used was: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (TEMP) +$

β_3 (VPD) + β_4 (TIME) + β_5 (CHL) + β_6 (RAD)² + β_7 (TEMP x VPD) + β_8 (TEMP)² + β_9 (RAD x TEMP) + ϵ . This model was chosen to include as many terms as possible to determine which ones were most significant and to determine the maximum R² that could be expected. The regression explains 92% of the variation, an increase of only 5% over the regression model based solely on radiation. However, (RAD), (VPD), (TIME) and (CHL) were all significant at the 1% level based on a t-test. All other terms except the (RAD x TEMP) interaction were significant at the 5% level. The regression fit based on the R² values was not improved by the addition of (TEMP)² or (RAD x TEMP) terms (Table 10A).

The regression containing the additional parameters has considerably improved the fit of the regression for the June-July period with the fit for the latter part of the growing season showing little change from the radiation regression fit. The portions of the curve which were overestimated by the regression equation based only on radiation were also overestimated by the regression equation based on the additional parameters although not as much.

Two days where it was suggested that temperature might be limiting, July 2 and October 23, have a slightly better fit with the expanded model. The October 23 predicted value shows slight deviation from the observed (Figure 13). For July 2 the fit was improved slightly but considerable deviation still existed. This might be due to

Table 10. Coefficients, t-significance and R^2 values for the seasonal photosynthetic regressions for *Festuca* (0) using parameters of radiation, temperature, vapor pressure deficit, chlorophyll and time. Parameters are listed in the order in which they entered the three regression equations (A, B, and C), t-significance is based on the full model.

A) Variable	Coefficient	t-significance ^a	R^2
Constant	139.7662	----	----
(RAD)	.6997	**	.78
(RAD) ²	-.0004	*	.85
(TEMP X VPD)	.9350	*	.87
(VPD)	23.0473	**	.89
(CHL)	15.3396	**	.90
(TIME)	-.5928	**	.92
(TEMP) ²	.4115	*	.92
(TEMP)	-8.7302	*	.92
(RAD X TEMP)	-.0082	-----	.92

B) Variable	Coefficient	t-significance	R^2
Constant	163.6339	----	----
(RAD) ₂	4.6077	**	.78
(RAD) ₂	-.0546	**	.85
(RAD) ₃	.4228	**	.88
(TIME)	-5.4855	**	.90
(TEMP X VPD)	-75.2292	*	.91
(VPD)	195.1601	**	.92
(CHL)	4.6439	----	.92
(TEMP) ²	20.8708	----	.92
(TEMP)	-53.0697	----	.92

C) Variable	Coefficient	t-significance	R^2
Constant	126.1997	----	----
(RAD)	6.4212	**	.78
(RAD) ²	-.0716	**	.85
(RAD) ³	1702	**	.88
(TIME)	-4.7171	**	.90
(TEMP X VPD)	-8.7470	**	.91
(CHL)	5.2121	----	.91

^a** Significant 1%

* Significant 5%

the relative magnitude of the temperature observed on those days. On July 2 the maximum temperature was 13.1° C which, although not very low, was probably limiting photosynthesis to some extent at the beginning of July since the plant had become acclimated to higher temperatures as a result of the warm sunny weather in June. However, when considered over the whole growing season 13.1° C is not unusually low since many days with such temperatures occur, particularly toward the latter part of the summer and early fall when the plants have become acclimated to them. However, 5° C is well below the optimum temperature, regardless of the time of growing season resulting in decreased photosynthesis which was fitted by the regression model.

The inclusion of many parameters in a regression equation often makes the interpretation of that equation difficult and the coefficients meaningless if the parameters are not significant. This is shown by the varying magnitudes of the regression coefficients and their sign (for example a negative (TEMP) and positive (TEMP)² coefficient) (Table 10A and 10B). To make the terms more realistic biologically, a regression was run using the basic radiation terms ((RAD), (RAD)², (RAD)³), a (TEMP x VPD) stress term, a physiological term (CHLOROPHYLL) and a (TIME) term (day of year) to consider possible seasonal or dormancy effects (Table 10C). All terms except chlorophyll were significant at the 1% level (t-test)

with 91% of the variation explained, which is nearly as high as the value obtained for the 9 term regression equation.

The signs of the regression coefficients are also more meaningful biologically in the 6 term regression equation. Coefficients for the (RAD), (RAD)², and (RAD)³ terms have the same sign as in the regression based only on radiation. The (TIME) and (TEMP x VPD) term coefficients are negative indicating decreasing photosynthetic rates during the growing season and with increasing temperature and VPD. The (CHLOROPHYLL) term is positive as expected.

Regression Fit for Festuca (NPK) Based on Radiation

The regression equation for Festuca (NPK) was based on the model: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \epsilon$, which is identical to the one used for Festuca (0). The regression was run once with the high values in July included and once with them excluded. It was felt that the high July values (5 days) represented a rather atypical response due to a unique combination of cutting date (age of the grass) and environment which will be discussed under the heading "The Effect of Time since Cutting." The regression equation, with the high July values omitted explains 85% of the variation with the observed and predicted values depicted in Figure 14. When the regression was run with the high values included the R² value dropped to .80.

In some cases replicate measurements were made on different age leaves (representing a different time since cutting (mowing)), these replicate measurements, which were made using the third cuvette, are indicated by the fine dotted lines in Figure 14 and 15. Generally there was only slight difference between the two measurements, except for the very high photosynthetic rates for one sample in July, mentioned above.

The maximum daily photosynthesis predicted by the regression equation was $300 \text{ mg CO}_2/\text{g dry weight/day}$. However, considerably greater rates did occur in August and September as shown by the observed values. In July the regression considerably overestimated predicted as compared to the observed values while in October there was little difference between observed and predicted values.

When high radiation days occurred in August and September, temperature and VPD were generally moderate, resulting in the regression underestimating the daily photosynthetic rate. At much higher radiation values in June and July photosynthesis was often inhibited by high temperatures and high VPD, or in a few cases by unseasonably low temperatures.

Such conditions possibly occurred on June 22, July 2 and July 26, where the regression overestimated the observed values. Radiation, average and maximum temperature for those days appear in Table 11.

Table 11. Radiation and temperatures (average daily and maximum hourly) for June 22, July 2, and July 26.

Date	Radiation cal/cm ² /day	Average Temperature °C	Maximum Temperature °C
June 22	407.6	19.4	26.7
July 2	329.8	9.7	13.1
July 26	119.8	10.1	10.8

June 22 was characterized by unusually high temperatures for the Solling, while the temperatures on July 2 and 26 were unusually low for the Solling for that time of year. Both of these temperature extremes undoubtedly contributed to the reduced photosynthesis occurring on those days.

The fit of the regression equation based on light for Festuca (NPK) is not as good as the fit of the radiation regression equation for Festuca (0), the R^2 values being .85 (.80 with high values included) and .87 respectively. For Festuca (0) the regression fit showed little difference between observed and predicted from August on, while for the Festuca (NPK) the fit was very good from October on, while during August and September the regression consistently underestimated photosynthesis on the high radiation days.

There was an apparent depression in the photosynthetic rate during the July period with the exception of one sample which showed

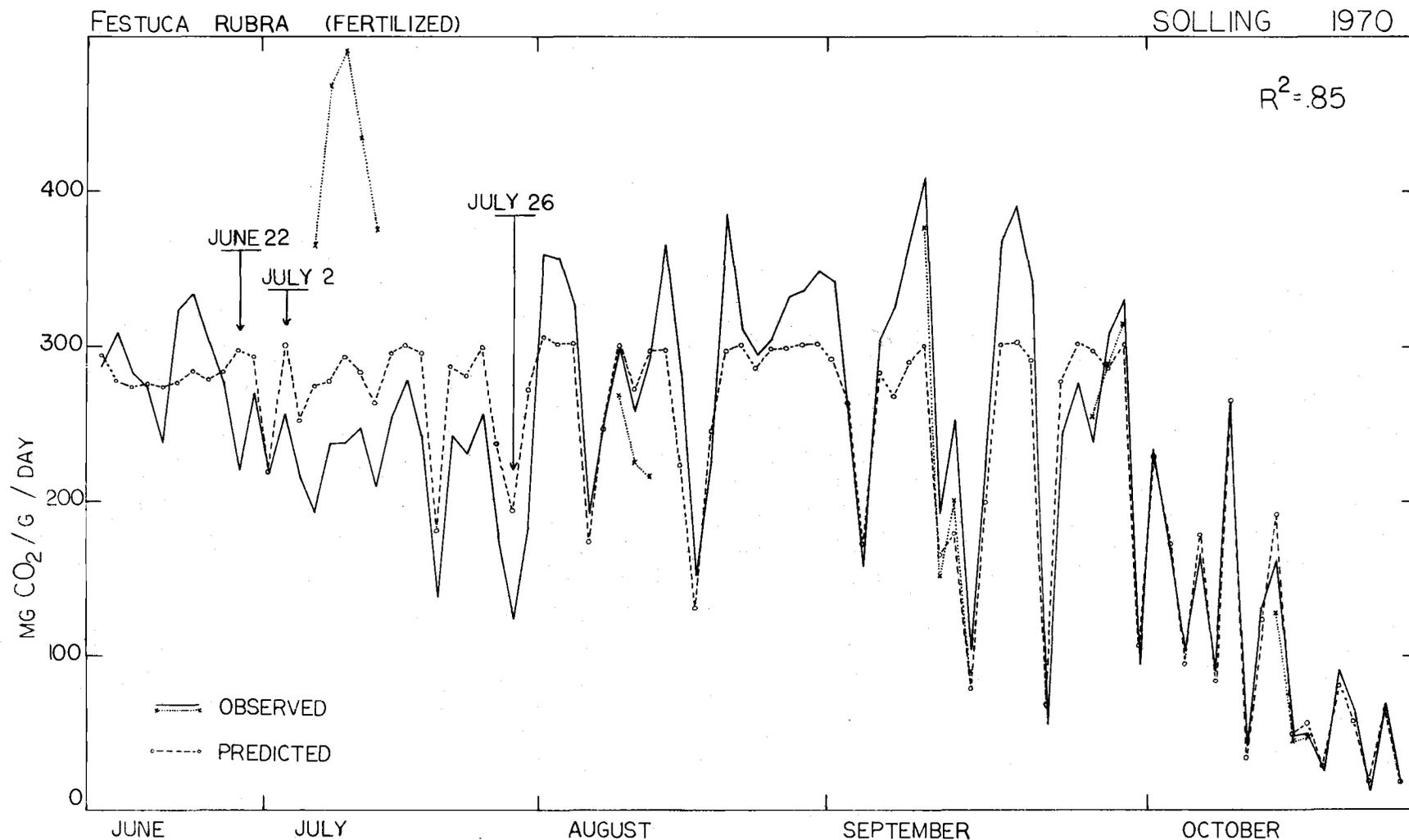


Figure 14. Predicted and observed photosynthetic rates for *Festuca* (NPK) for the season. The predicted values were obtained from the multiple linear regression equation: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \epsilon$.

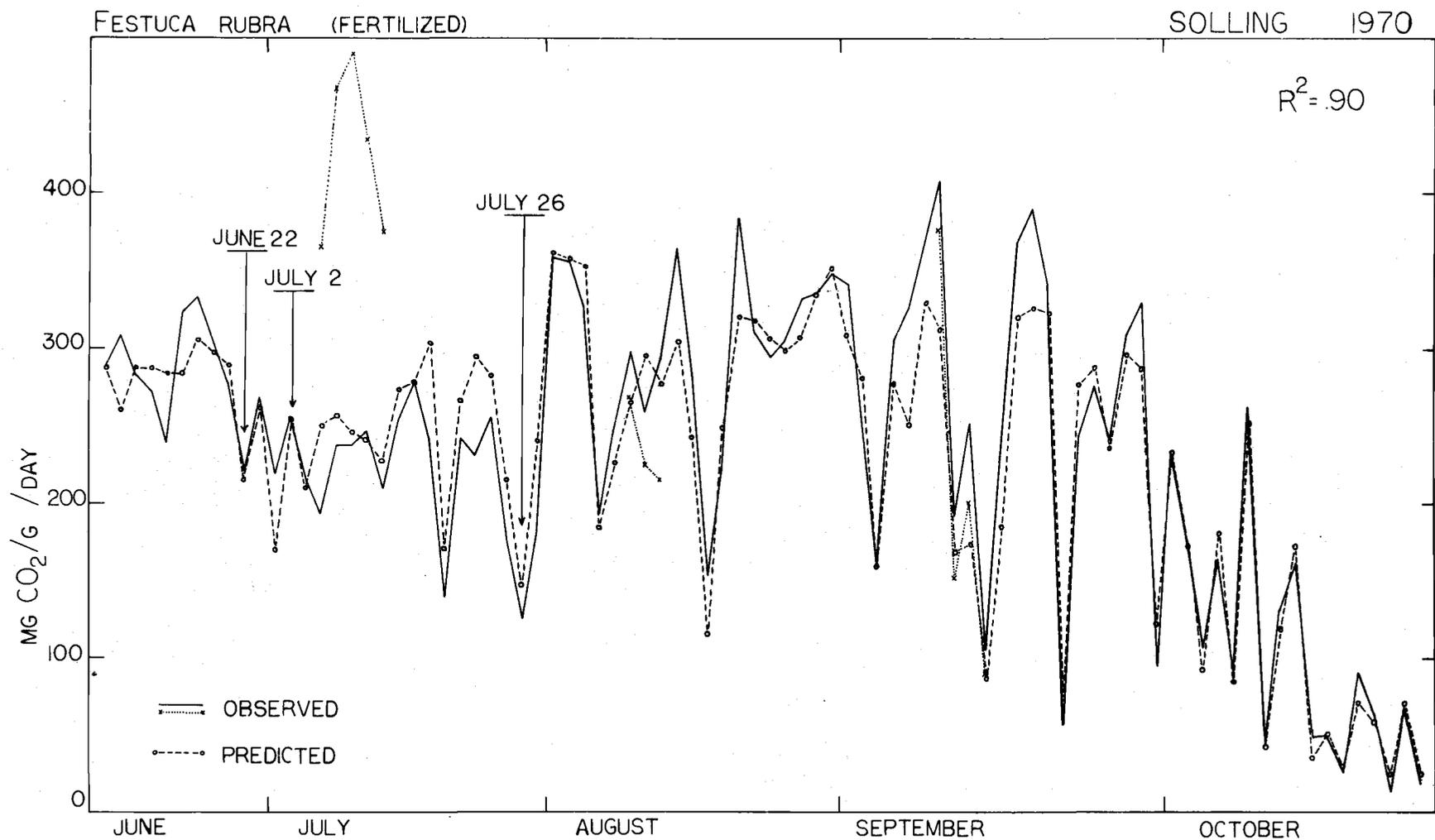


Figure 15. Predicted and observed photosynthetic rates for Festuca (NPK) for the season. The predicted values were obtained from the multiple linear regression equation: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \beta_4 (TEMP) + \beta_5 (TEMP)^2 + \beta_6 (VPD) + \beta_7 (CHL) + \beta_8 (TIME) + \beta_9 (TEMP \times VPD) + \epsilon$.

unusually high rates. The depression could possibly be due to the photoinactivation of the photosynthetic apparatus, as was suggested by Czopek (1967), who found a similar depression in certain meadow plants after the period of maximum insolation. Such depressions have also been found for species of Festuca following periods of high temperatures and light in June and July. These depressions did not occur when temperature and light levels were low during this period (Kelly et al., 1969).

Regression Fit for Festuca (NPK) Based on Radiation, Temperature, Vapor Pressure Deficit, Chlorophyll and Time

Various regression equations, including a variety of parameters, were tested to see which one best fit the daily photosynthetic rate of Festuca (NPK) over the June to October period. The regression model used initially was: $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (TEMP) + \beta_3 (VPD) + \beta_4 (TIME) + \beta_5 (CHLOROPHYLL) + \beta_6 (RAD)^2 + \beta_7 (RAD)^3 + \beta_8 (TEMP \times VPD) + \beta_9 (TEMP)^2 + \epsilon$. The model explains 90% of the variation with the high July photosynthetic rates mentioned in the previous section omitted and 87% with them included (Table 12A and 12B). This is an increase of 5% and 7% respectively over the regression based only on radiation terms. Observed and predicted values for the regression with the high July values omitted are depicted in Figure 15. All of the radiation terms were significant at the 1%

Table 12. Coefficients, t-significance and R^2 values for the seasonal photosynthetic regressions for *Festuca* (NPK) using parameters of radiation, temperature, vapor pressure deficit, chlorophyll and time. Parameters are listed in the order in which they entered the three regression equations (A, B, and C), t-significance is based on the full model.

A) Variable	Coefficient	t-significance ^a	R^2
Constant	-141.0447	----	----
(TEMP)	.8880	----	.60
(TEMP) ²	.1762	----	.65
(RAD)	1.9851	**	.69
(RAD) ²	-.0044	**	.82
(TEMP X VPD)	-.2540	----	.86
(RAD) ³	3.25E-6 ^b	**	.88
(TIME)	.3133	**	.89
(CHL)	5.0454	*	.90
(VPD)	-.6234	----	.90

B) Variable	Coefficient	t-significance	R^2
Constant	-162.8096	----	----
(TEMP)	.6298	----	.59
(RAD)	1.9373	**	.64
(RAD) ²	-.0038	**	.79
(TEMP X VPD)	-.1984	----	.83
(CHL)	6.5275	*	.84
(RAD) ³	2.62E-6	**	.85
(TEMP) ²	.1773	----	.86
(TIME)	.3696	*	.87
(VPD)	-4.2864	----	.87

C) Variable	Coefficient	t-significance	R^2
Constant	-100.6670	----	----
(RAD)	1.5474	**	----
(TEMP)	6.8266	**	----
(CHL)	7.9836	**	----
(RAD) ²	-.0029	**	----
(RAD) ³	1.83E-6	*	----
(TEMP X VPD)	-.2759	**	.85

a ** Significant 1%
 Significant 5%

b Exponential notation, equivalent to $3.25 \cdot 10^{-6}$

level (t-test), while the terms (TIME) and (CHLOROPHYLL) were significant at the 5% level.

Although the expanded regression model has improved the fit of predicted to observed values the deviations are still in the same direction as in the model based entirely on radiation terms. The July period is still overestimated and the high radiation days in late August and September are still being underestimated, although not as much.

The extreme temperature days discussed in the previous section, June 22, July 2 and July 26 have been fitted by the expanded model. However, the low radiation, low temperature day July 1 has now been underestimated. A (TEMP x TIME) interaction term was added to the regression equation with the hope of fitting such days since the temperature response probably varies considerably with time. However, it did not improve the fit and the term was statistically insignificant.

The regression equation $PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (TEMP) + \beta_3 (CHLOROPHYLL) + \beta_4 (RAD)^2 + \beta_5 (RAD)^3 + \beta_6 (TEMP \times VPD) + \epsilon$ gave the best fit with a minimum number of terms. All terms were significant at the 1% level except $(RAD)^3$ which was significant at the 5% level (t-test). This equation explained 85% of the variation (high July values included) (Table 12C). When the (TEMP) term was dropped and replaced with a (TIME) term the R^2 dropped to .82, the

latter equation being identical to the one used for Festuca (0) which explained 91% of the variation. The coefficient for the (TIME) term was positive for Festuca (NPK) in contrast to the highly significant negative (TIME) coefficient for Festuca (0). The (CHLOROPHYLL) coefficient was positive and the (TEMP x VPD) coefficient negative as it was for Festuca (0).

Festuca (NPK) exhibited a much more variable photosynthetic response than Festuca (0) which was expressed by the greater amount of variation explained by the regression equations for Festuca (0). Festuca (0) also had a declining photosynthetic rate throughout the season which was reflected in the negative (TIME) coefficient, while no such trend was apparent for Festuca (NPK). The parameters (TEMP), (VPD), (TEMP x VPD) and (CHLOROPHYLL) were all significant in some of the regressions that were tested. The (RAD), (RAD)² and (RAD)³ terms were significant in all cases.

Seasonal Differences in Photosynthetic Rate
between Festuca (0) and Festuca (NPK) Based
on Leaf Dry Weight, Area and Chlorophyll

Figure 16 depicts daily photosynthesis (average of 5 days) over the growing season for the three reference bases. Festuca (0) and Festuca (NPK) have similar photosynthetic rates when calculated on the basis of chlorophyll, the maximum average over 5 days being nearly 70 mg CO₂/mg chlorophyll/day with both showing a gradual

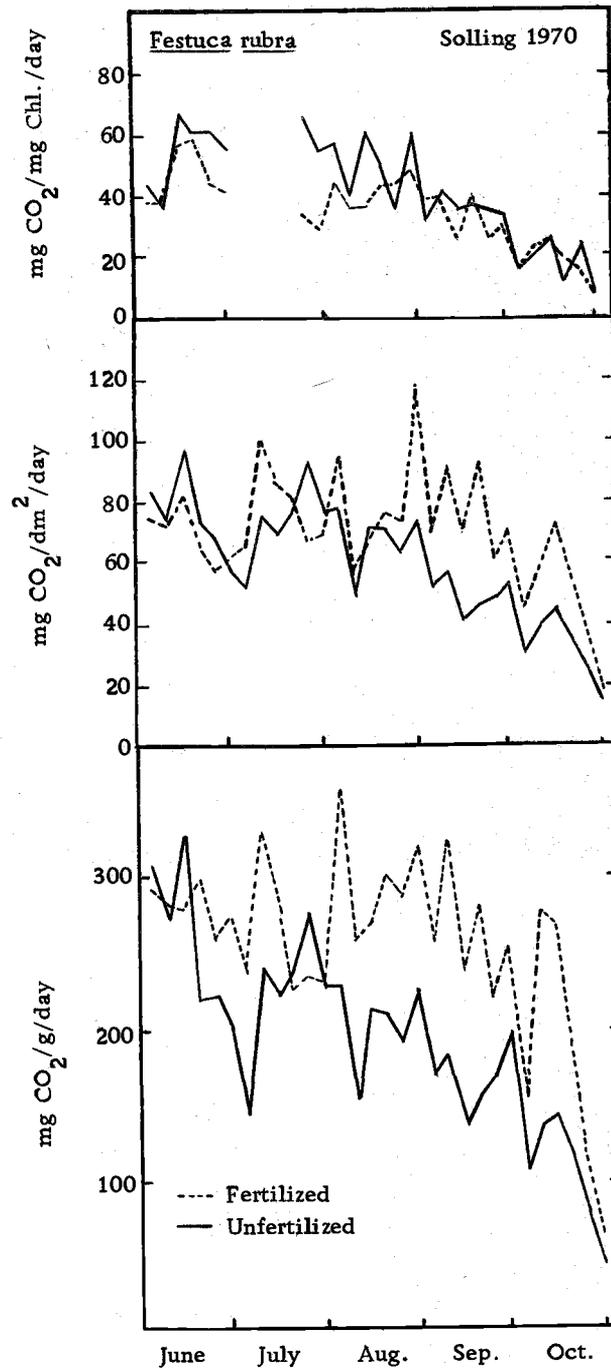


Figure 16. Seasonal changes in daily net photosynthesis for Festuca (NPK) and Festuca (0). Photosynthetic rate is expressed on a leaf dry weight, surface area and chlorophyll basis. Each point represents an average of five days.

decline in the rate from August until October. On a leaf surface area basis the rates between the fertilized and unfertilized Festuca were similar until August when the unfertilized grass dropped off markedly, while the fertilized grass retained a high photosynthetic rate until October. A similar response is found on a dry weight basis, although the greater photosynthetic rate for Festuca (NPK) is even more pronounced than on an area basis. The unfertilized Festuca shows a continual decline in daily photosynthesis while the fertilized Festuca retains a high rate until light and temperature became limiting toward the latter part of the season. Osman and Milthorpe (1971) working with wheat also found that high nutrient plants maintained high photosynthetic rates for longer periods than low nutrient plants.

The maximum daily photosynthesis averaged over five days was $118 \text{ mg CO}_2/\text{dm}^2/\text{day}$ and $360 \text{ mg CO}_2/\text{g dry weight}/\text{day}$ for Festuca (NPK). The rate based on dry weight is above that reported by Stocker (1967) who, using cut leaf samples, found a maximum daily photosynthetic rate of $213 \text{ mg CO}_2/\text{g dry weight}/\text{day}$ for Festuca rubra. On an area basis he found photosynthetic rates similar to those reported here ($118 \text{ mg CO}_2/\text{dm}^2/\text{day}$) although he noted that the area determination was probably inexact. For Festuca (0) maximum daily photosynthetic rates were somewhat lower ($330 \text{ mg CO}_2/\text{g dry weight}/\text{day}$ and $103 \text{ mg CO}_2/\text{dm}^2/\text{day}$).

CO₂ Fixed by Festuca (NPK) and Festuca (0)
from June until October

The highest monthly CO₂ fixation for Festuca (NPK) was in August (9, 212 mg CO₂/g dry weight/month) while for Festuca (0) the maximum was in June with 7, 784 mg CO₂/g dry weight/month (Table 13). On an area basis the maximum for Festuca (NPK) was also in August with 25.8 mg CO₂/cm²/month, while for Festuca (0) it was in July with 22.9 mg CO₂/cm²/month. On an area basis Festuca (0) actually had greater photosynthetic production than Festuca (NPK) in June.

Expressed on a percentage basis for photosynthetic rates based on leaf weight, Festuca (0) fixed 92% as much CO₂ as Festuca (NPK) in June. This dropped off gradually until in October it only fixed 59% as much. On an area basis the decrease was not quite as large with the photosynthetic rate of Festuca (0) being 109% of the Festuca (NPK) rate in June and 66% in October. For the entire measuring period from June until October Festuca (0) fixed 76% as much CO₂ as Festuca (NPK) on a dry weight basis and 84% on a leaf surface area basis.

Table 13. Comparison of monthly solar radiation and monthly net photosynthesis of Festuca (NPK) and Festuca (0) based on leaf dry weight and leaf surface area.

	June	July	Aug.	Sept.	Oct.	Total
Radiation per month cal/cm ²	14,789	10,962	9,838	6,838	3,291	----
Net Photosynthesis <u>Festuca</u> (NPK) mg CO ₂ /g/month	8,424	7,886	9,212	7,901	5,412	38,835
Net Photosynthesis <u>Festuca</u> (0) mg CO ₂ /g/month	7,784	6,982	6,298	5,083	3,174	29,321
Photosynthesis <u>Festuca</u> (0) as % of <u>Festuca</u> (NPK) on dry weight basis	92%	89%	68%	64%	59%	76%

Net Photosynthesis <u>Festuca</u> (NPK) mg CO ₂ /cm ² /month	20.7	24.3	25.8	23.0	14.6	108.4
Net Photosynthesis <u>Festuca</u> (0) mg CO ₂ /cm ² /month	22.7	22.9	21.1	14.8	9.7	91.2
Photosynthesis <u>Festuca</u> (0) as % of <u>Festuca</u> (NPK) on area basis	109%	94%	82%	64%	66%	84%

Photosynthetic Efficiency on a Monthly Basis
for Festuca (0) and Festuca (NPK)

Another approach in comparing the amount of CO₂ fixed is on an energy basis whereby the total solar radiation is considered. Pütter (1914) was one of the first to use this approach in analyzing the efficiency of various cereals. The photosynthetic efficiency was computed as being the amount of chemical energy (calories) produced by a cm² surface area of plant divided by the amount of photosynthetic active radiation (PhAR) received per cm². One mg CO₂ was computed as yielding .682 mg hexose which has the energy equivalent of 2.55 cal. Photosynthetic radiation was computed as being 45% of total solar radiation. On this basis the efficiency (on a monthly basis) of Festuca (NPK) had a minimum value of .79% in June which increased to 2.5% in October (Table 14). For Festuca (0) the June value was .87% with an increase to 1.67% in October. Thus the efficiency of the fertilized grass was much higher toward the latter part of the growing season.

Several possible errors should be considered when making these computations. One large source of error in relating daily photosynthesis to daily incoming radiation is that two days can have the same radiation total yet have different distributions. With other factors being the same, the light on one day could be evenly

Table 14. Computed photosynthetic efficiency of Festuca (NPK) and Festuca (0).

	June	July	Aug.	Sept.	Oct.
Radiation/month (cal/cm ² /month)	14,789	10,962	9,838	6,838	3,291
45% of total radiation (cal/cm ² /month)	6,655	4,933	4,427	3,077	1,481
Photosynthesis <u>Festuca</u> (NPK) (mg CO ₂ /cm ² /month)	20.7	24.3	25.8	23.0	14.6
(Calories/cm ² /month)	52,785	61,965	65.79	58.65	37.23
Efficiency	.79%	1.26%	1.49%	1.91%	2.51%
Photosynthesis <u>Festuca</u> (0) (mg CO ₂ /cm ² /month)	22.7	22.9	21.1	14.8	9.7
(Calories/cm ² /month)	57.9	58.4	53.8	37.7	24.7
Efficiency	.87%	1.18%	1.22%	1.23%	1.67%

distributed at a level just equaling the radiation saturation level for photosynthesis while on another day the radiation could remain at a very low level with a short period of very intense radiation considerably above the light saturation level. The day with the even distribution of light would probably have the greater photosynthetic production.

This is part of the explanation for the different efficiencies computed for each month based on leaves optimally exposed to sunlight. In June and July much of the incoming radiation was above the light saturation level for Festuca rubra and thus was not used fully, yet it was calculated into the efficiency term. This is, of course, not true for a plant community with a high leaf area index, which might never reach light saturation.

The distribution of photosynthetic active radiation also changes during the year and with the cloud cover. The active portion is approximately 38% of total radiation on clear days and 58% on cloudy days (Czopek, 1967). Since the latter part of the year had a greater percentage of cloudy days the effect would be to decrease the apparent efficiency of the tabulated values which were computed on the assumption that photosynthetic active radiation (PhAR) was 45% of total radiation.

It should also be noted that these efficiency computations are on a monthly basis. For shorter time periods the efficiency can be

substantially higher or lower. Nevertheless the efficiency term can be used as an index of the activity of the photosynthetic apparatus where the same species is subjected to the same environmental conditions.

Analysis of Specific Factors Affecting the Photosynthetic Rate of *Festuca rubra*

Although the specific environmental factors have been considered in the general regression equations, there is a need to consider the relative importance of each one in specific situations.

Photosynthetic Response to Light

Photosynthetic rates were related to radiation using computed hourly means rather than the individual measurements which were made at six minute intervals. With individual measurements one is faced with the difficulty of relating photosynthetic rates which are recorded with a time lag, which is dependent on the volume and flow rate of the system, to light measurements which are instantaneous. Using hourly means also has its drawbacks since fluctuations in the light intensity are not taken into account. However, due to the voluminous amount of data and since a comparison between a regression fitted to the six-minute measurements showed only slight deviations from the hourly means (Appendix, Figure 27), the hourly means

were used.

Hourly means of photosynthetic rates and concurrent light data (klx) were selected over weekly periods so that the entire range of light intensities was represented (45 to 80 individual hourly means). The regression equation: $PS_n = \beta_0 + B_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \epsilon$ was used to give the maximum flexibility in fitting the light curve.

The photosynthetic response to light for various times of the year for Festuca (0) and Festuca (NPK) is depicted in Figure 17. The R^2 values for the regressions depicted ranged from .86 to .95 for Festuca (0) and .85 to .94 for Festuca (NPK).

It was initially hoped that the light response curve of photosynthesis could be obtained by relating photosynthesis to light under similar temperature and moisture conditions. However, it was only seldom that similar conditions occurred. Toward the end of the growing season it was often difficult finding sufficient data when light levels were above the saturation level. Consequently, the photosynthetic response to light in October represents photosynthetic rates measured at 6 minute intervals on one day, whereas the other curves were all obtained from hourly means over a 7 day period.

The dip in the curve at higher light intensities is due to the slightly reduced photosynthetic rate found at the higher light intensities which is often associated with high temperature and VPD levels.

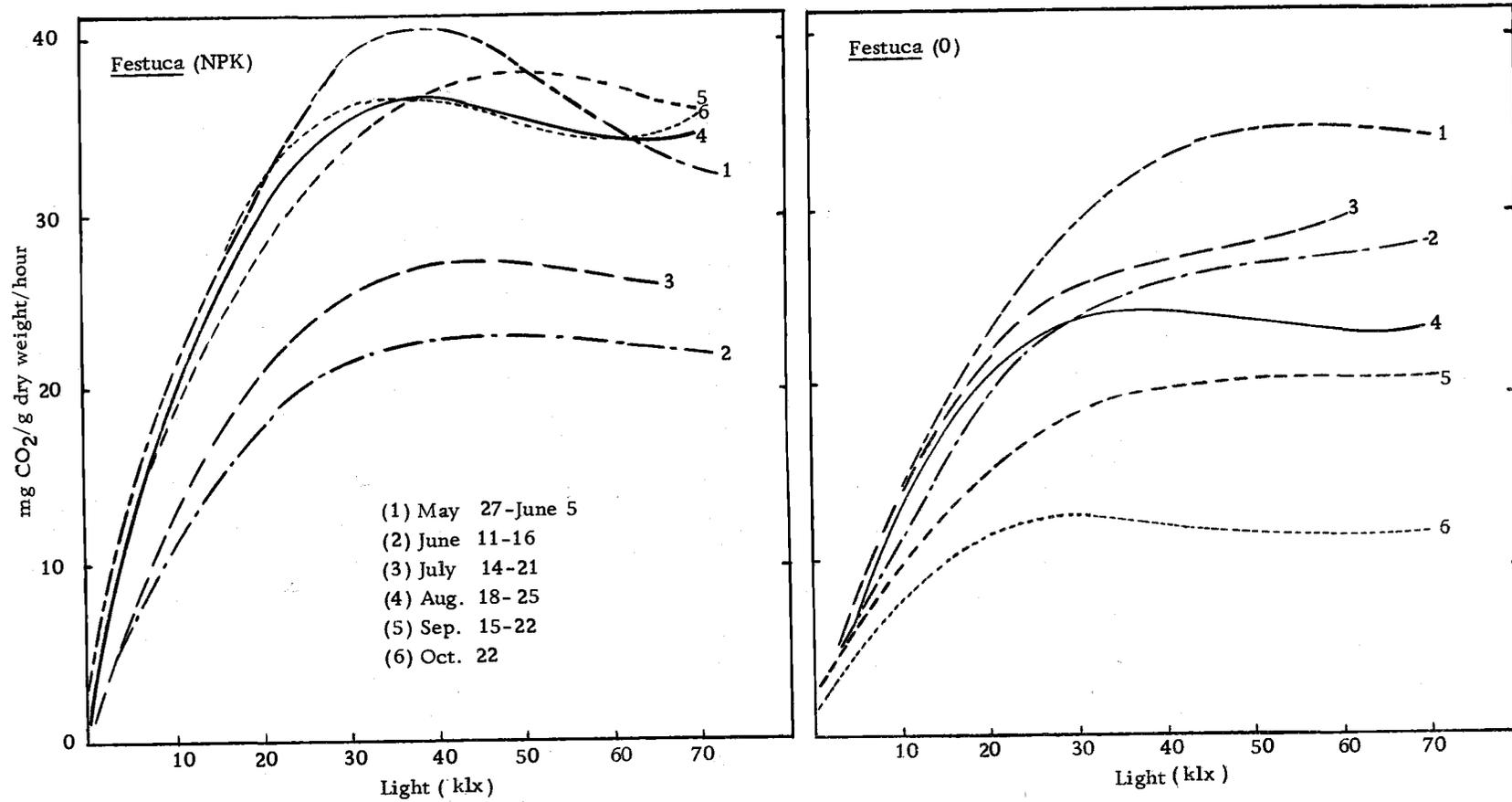


Figure 17. Seasonal changes in the photosynthetic response to light for Festuca (NPK) and Festuca (0). Each curve represents a regression fit to 45 to 80 hourly means.

A comparison of photosynthetic rates in the morning (until noon) and in the afternoon over a one week period in early September showed that the afternoon photosynthetic rates were approximately 10% lower than the morning rates (Appendix, Figure 28).

For Festuca (0) the photosynthetic rate at light saturation was the highest in May with a gradual decline until October. Light saturation was reached at approximately 30 klx for all samples except for the May sample which did not reach light saturation until light levels were above 40 klx. From May until August the decline in the photosynthetic rate was expressed by reduced rates above light saturation. Reduced rates above light saturation have been attributed to reduced levels of carboxylating enzymes and to increased CO₂ diffusion resistance (Wareing, Khalifa and Treharne, 1968; Björkman, 1968; and Holmgren, 1968). The September and October curves show reduced rates in the light limiting (initial slope) region as well, an indication that the photochemical reactions were also reduced, possibly due to aging and/or nutrient deficiency.

It should be noted that the October 22 curve depicts a day when air temperatures were seldom above 10° C in the cuvette, which is partly an explanation for the low light saturated photosynthetic rate found for Festuca (0) although no such effect was noted for Festuca (NPK). Photosynthetic rates measured on another sample of Festuca (0) on October 18, when temperatures were near 15° C were found to

be similar to the rates measured in September. The photosynthetic rate of Festuca (NPK) on October 18 was only slightly higher (41 mg CO₂/g dry weight/hour, average over a one hour period) than the rate recorded on October 22.

Festuca (NPK) had high photosynthetic rates in May which dropped considerably in June and July. During the June and July period the photosynthetic rates of Festuca (NPK) were similar to the rates of Festuca (0). Reduction in photosynthetic rates during the June-July period was in the light limiting as well as in the light saturated rate. The decrease in the photosynthetic rate for the light limiting (photochemical) portion of the light curve can perhaps be explained by reduced chlorophyll levels, although it has been suggested (Satoh, 1970) that bleaching of chlorophyll is a secondary response occurring after photosynthetic activity has been reduced.

Photosynthetic rates for Festuca (NPK) during August, September and October were nearly as high as in May. Light saturation was attained between 30 and 40 klx for Festuca (NPK). The slope of the line indicating the light limiting portion of the light curve was steeper for Festuca (NPK) than for Festuca (0) except during the June-July period.

The Effect of Temperature and Vapor Pressure Deficit

Field Measurements. The effects of temperature and VPD were

closely related since VPD is based on leaf temperature and water vapor content of ambient air. For the majority of the days analyzed there was a direct correlation between them, although occasionally there was a lag in the VPD increase which was due to condensed water in the tubing (Figure 18). Such patterns were rare however, and usually occurred when light and temperature were at low levels.

For a five day period in June photosynthetic rates were plotted against light, temperature and VPD. From these plots, photosynthetic rates were chosen when light was considered above saturation (30 klx) and related to the temperature and VPD values occurring for that photosynthetic rate. Each point plotted in Figure 19 represents a uniform photosynthetic rate over a 15 to 30 minute time span. The photosynthetic rate of Festuca (NPK) shows a rapid decline as air temperature increases from 20° C to 32° C. A similar decline is shown when photosynthetic rates are plotted against VPD levels. One sample at 30° C had a relatively low VPD value of 9 mg H₂O/liter, yet maintained a high photosynthetic rate which was identical to the rate at 22° C, perhaps an indication that Festuca (NPK) is more sensitive to moisture levels than to temperature. However, the high rate was maintained for only a short time (15 minutes). It is doubtful whether the high photosynthetic rate could have been maintained for longer periods.

The decline in the photosynthetic rate with increasing

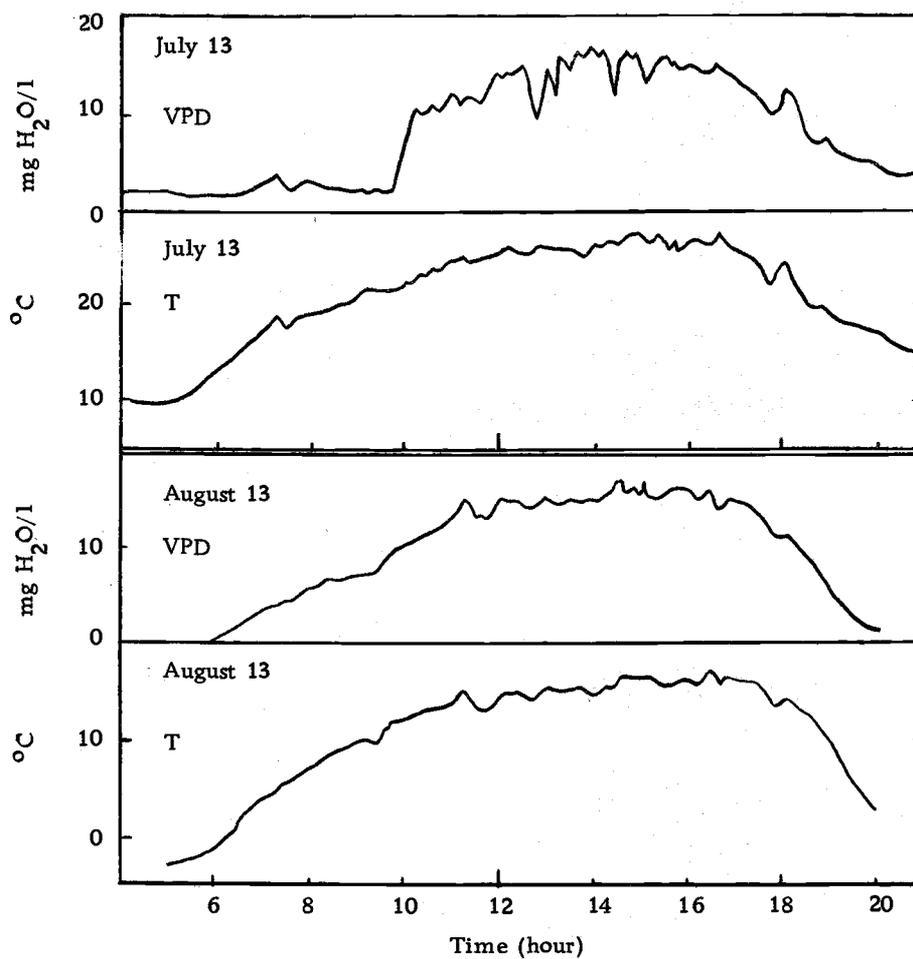


Figure 18. Changes in temperature (T) and vapor pressure deficit (VPD).

temperature and VPD is not as steep for Festuca (0) as for Festuca (NPK). Photosynthetic rates are probably limited by other factors such as nutrient supply for Festuca (0), so that the response to temperature and VPD is not fully expressed (El-Sharkawy and Hesketh, 1964).

A similar comparison between photosynthetic rates and temperature and VPD was made for a one week period in July. Hourly means of temperature and VPD, when light was considered above saturation (30 klx) were plotted against photosynthetic rates (Figure 20). The slopes of the individual sample plots indicate that Festuca (NPK) (sampled 3 weeks after cutting) was the most sensitive to changing temperature and VPD, while Festuca (0) was the least sensitive. The Festuca (NPK) sample which had not been cut showed a slightly steeper decline in photosynthetic rate with increasing temperature and VPD than Festuca (0).

In order to get a combination of environmental values not normally encountered, the temperature of the cuvette was reduced to 12.5° C, causing a corresponding decrease in VPD to 1.2 mg H₂O/liter. The photosynthetic rate of Festuca (NPK) (3 weeks after cutting) showed a drop of 12% from the rate at 19° C which also had higher VPD values (5-7 mg H₂O/l).

Plant response to atmospheric moisture would no doubt be considerably greater if the plants were not able to recover to low

water stress during the night. Sample measurements of plant moisture stress made on herbaceous plants at the end of the dry period in late August showed minimum stress at night of less than .5 atmospheres with maximum daytime stress of 9.5 atmospheres.

Photosynthetic rates (hourly means with light above saturation) were plotted against temperature and VPD for a two week period from August 25 until September 8 for Festuca (NPK) and Festuca (0) (Figure 21). There was considerable variation in the photosynthetic rates at specific temperature and VPD levels. Maximum photosynthetic rates were attained between 18° and 22° C for both Festuca (0) and Festuca (NPK). For Festuca (NPK) photosynthetic rates declined rapidly at temperatures above 24° C while no such pronounced decline was found for Festuca (0). The decline in photosynthetic rate with temperature was less pronounced toward lower temperatures. Similarly the response to VPD indicates a decline in photosynthetic rates with increasing VPD for Festuca (NPK) but not for Festuca (0).

Highest photosynthetic rates were found in the spring and fall for Festuca (NPK) when temperatures were generally moderate. High temperatures with their associated high VPD apparently have a greater effect in reducing photosynthetic rates than low temperatures for Festuca rubra in the Solling area. Woledge and Jewiss (1969) working with tall fescue (Festuca arundinaceae) found that optimum temperatures for photosynthesis for that species were

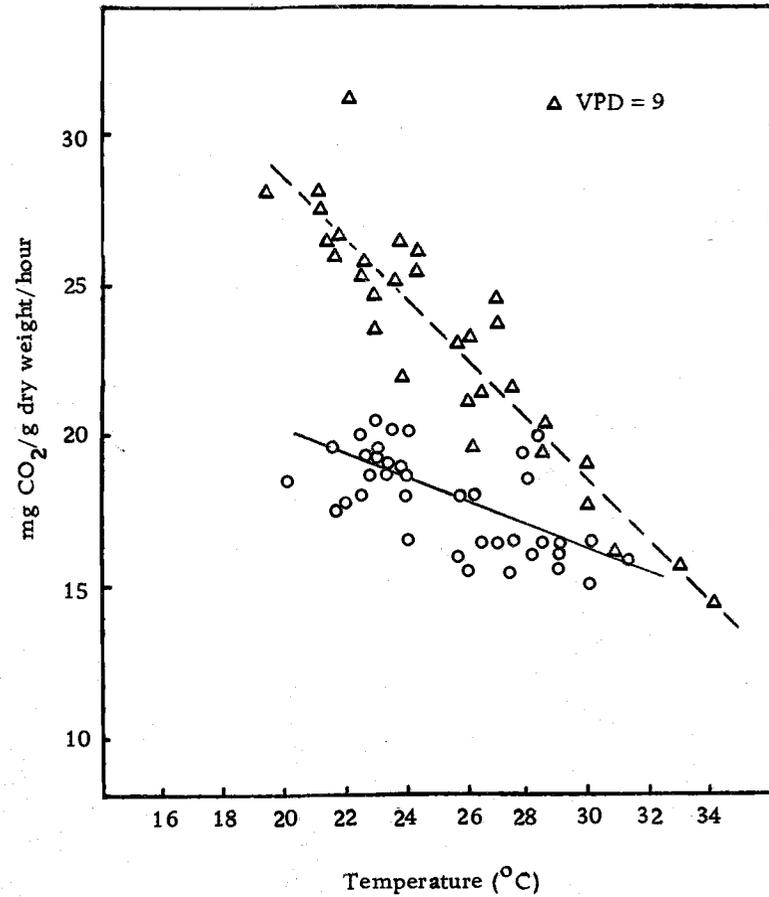
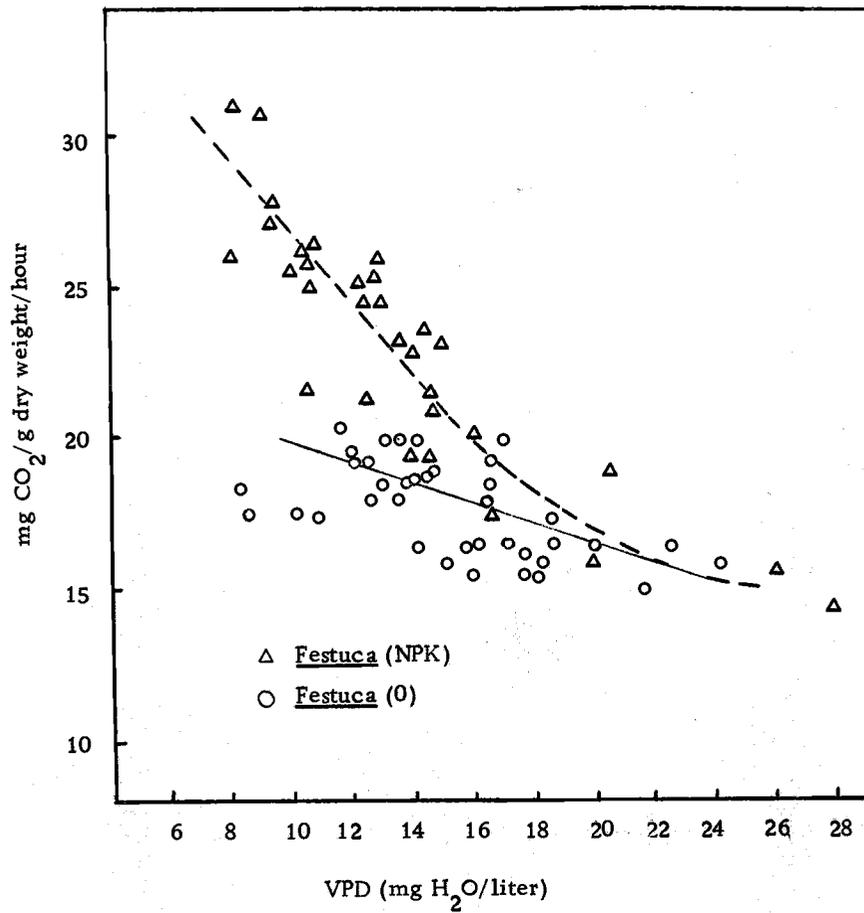


Figure 19. Photosynthetic response to temperature and vapor pressure deficit for Festuca (NPK) and Festuca (0) for the period June 17 to 22.

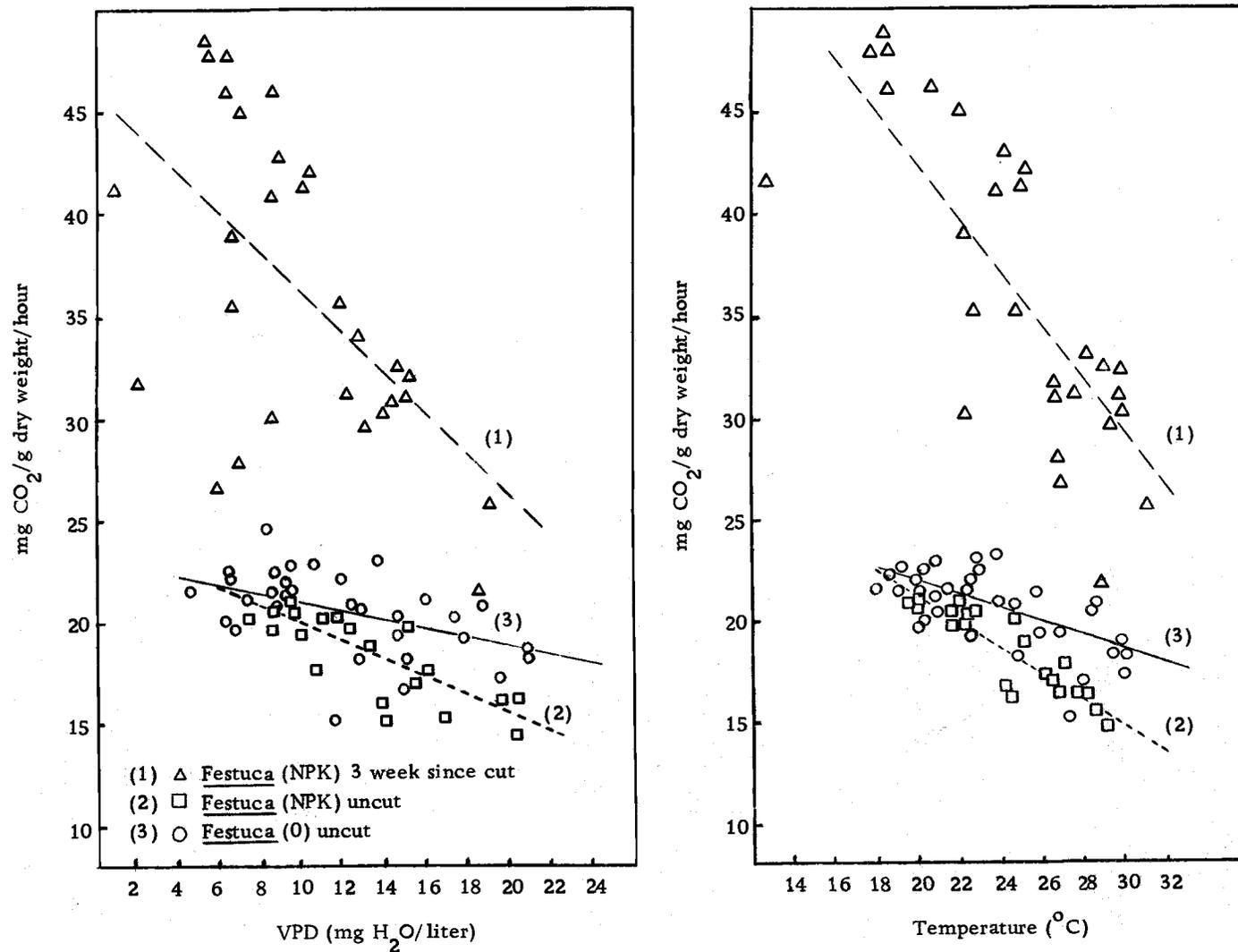


Figure 20. Photosynthetic response to temperature and vapor pressure deficit for Festuca (NPK) and Festuca (0) for the period July 8 to 13.

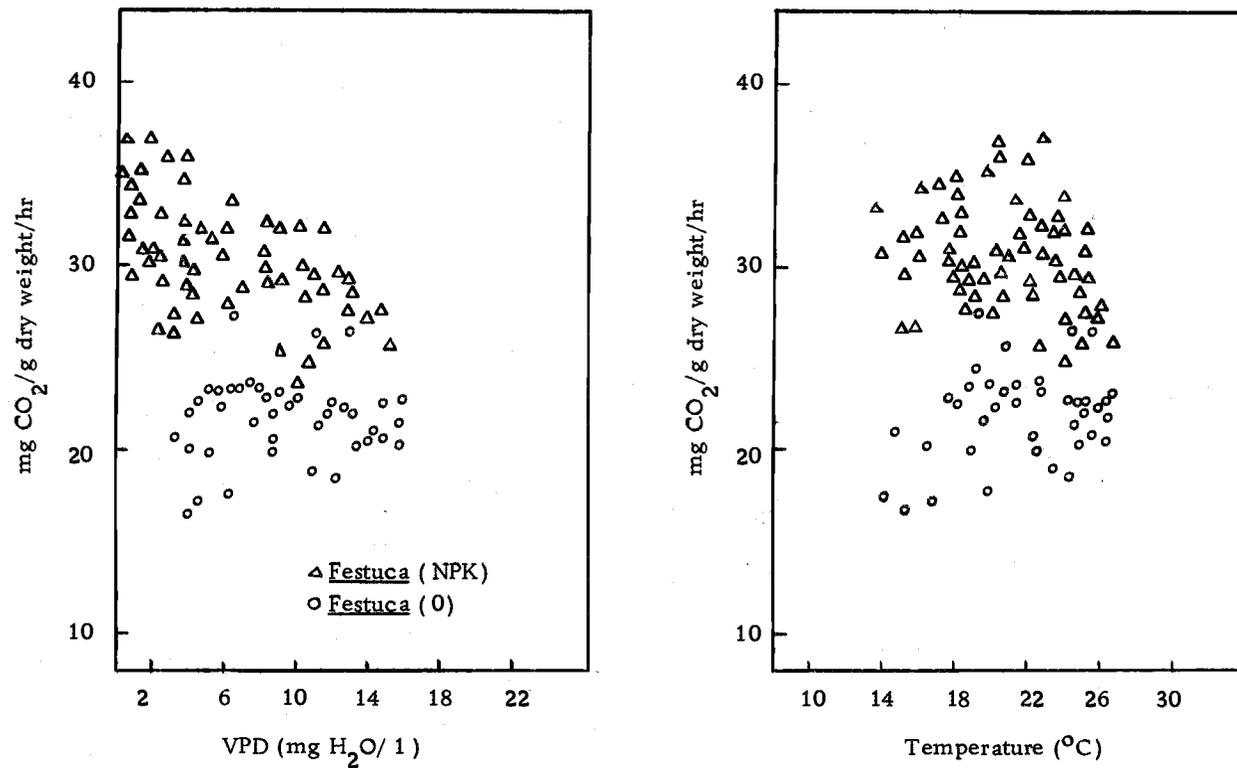


Figure 21. Photosynthetic response to temperature and vapor pressure deficit for Festuca (NPK) and Festuca (0) for the period August 25 to September 8.

between 15° and 20° C with rates nearly as high (10 to 15% lower) found at 10° C. That is the same range of temperatures for which maximum photosynthetic rates were found for Festuca rubra, and the temperature range most common in the Solling during the growing season.

The effect of a light frost on the night of September 23-24 was expressed by reduced photosynthetic rates on September 24 with the grass showing a high sensitivity to changing VPD (Figure 22). This was particularly true for the fertilized Festuca and is the reason for the afternoon depression found on September 24 which was mentioned under the heading "Daily Photosynthetic Patterns on Clear Days." The reduced rates were only expressed for three days following the frost, showing complete recovery on September 28.

Laboratory Measurements. Laboratory experiments on Festuca (NPK) and Festuca (0) where photosynthetic rate was measured at 48 klx over a range of temperatures from 4° to 24° C (28° C in two cases) indicate that there is some adaptation to lower temperatures (Figure 23). In September the optimum temperature was between 16° and 20° C for Festuca (NPK) with a photosynthetic rate of 38 mg CO₂/g dry weight/hour at 8° C. From the laboratory experiments the adaptation does not appear to be ideal (Billings et al., 1971), since the photosynthetic rate dropped considerably with the drop in temperature optimum. However, the temperature adaptation is no

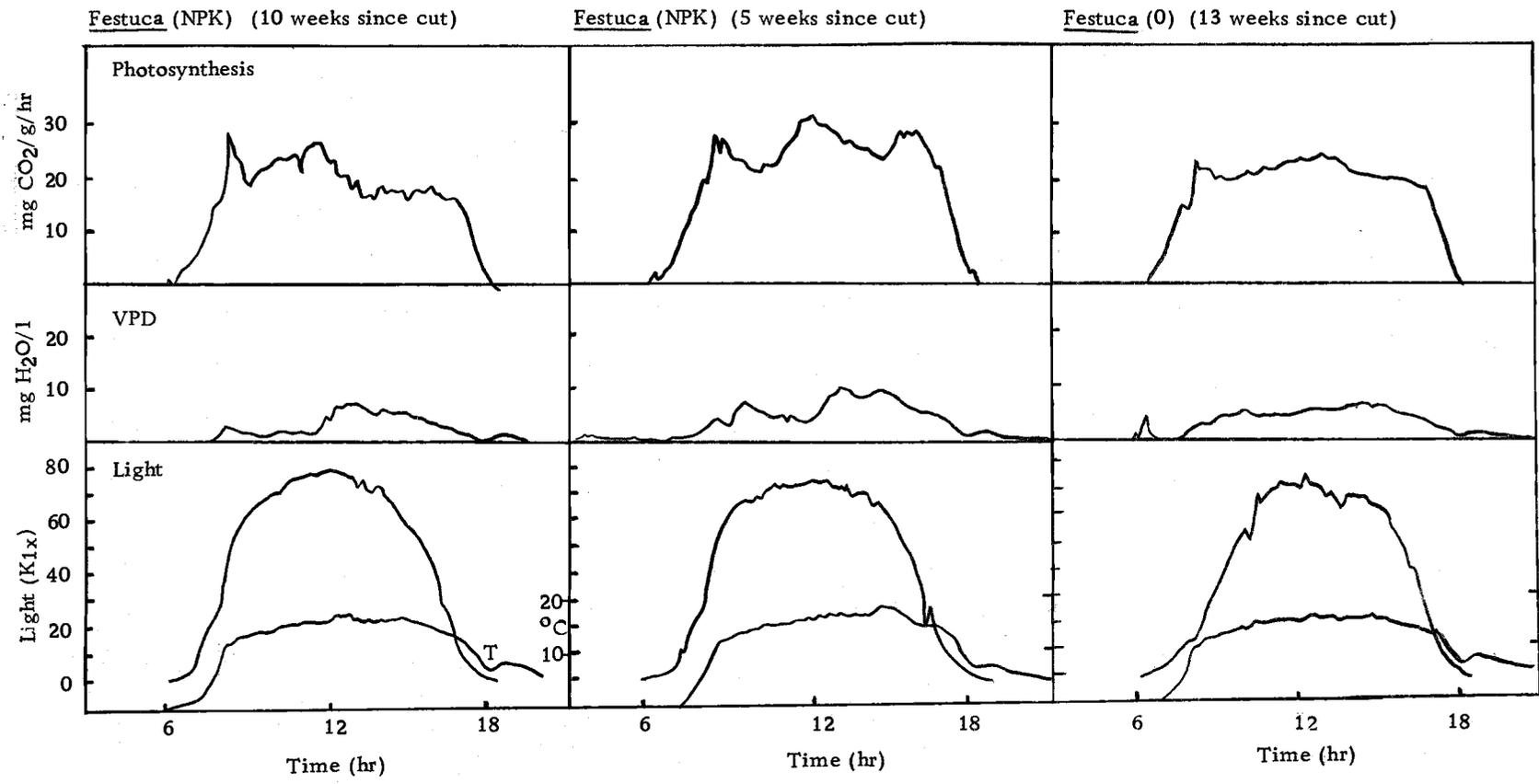


Figure 22. Photosynthetic response of *Festuca* (NPK) (5- and 10 weeks since cut) and *Festuca* (0) 13 weeks since cut) on September 24, following a light frost. Vapor pressure deficit (VPD), air temperature (T) and light are also plotted.

doubt confounded by the effects of aging and changing photoperiod as well. For Festuca (0) the maximum photosynthetic rate in September was 30 mg CO₂/g dry weight/hour at a temperature between 20° and 24° C. This declined to a maximum of 11 mg CO₂/g dry weight/hour between 8° and 12° C in November.

Such a shift of temperature of maximum photosynthesis was also indicated by measurements made in the field, although the photosynthetic rates of Festuca (NPK) were considerably greater than those measured in the laboratory. Photosynthetic rates of Festuca (NPK) measured on October 22, when temperatures seldom reached 10° C, were higher (39.9 mg CO₂/g dry weight/hour) than many rates recorded during the summer and considerably higher than the laboratory rates, which were determined using cut leaves. For Festuca (0) on the other hand the photosynthetic rates measured in the laboratory were similar to the rates measured in the field.

It has been suggested that the photosynthetic rates of cut samples, as those measured in the laboratory, can be considerably below those found on entire, attached leaves. Eagles and Treharne (1969) found photosynthetic rates of cut Dactylis glomerata to be 60% of the rate of entire, attached leaves. This could be due to increased respiration of the cut segments (Roberts, 1951) which was indicated by the higher respiratory rates found on cut samples measured in the laboratory (Appendix, Table 17). It should be noted that in some

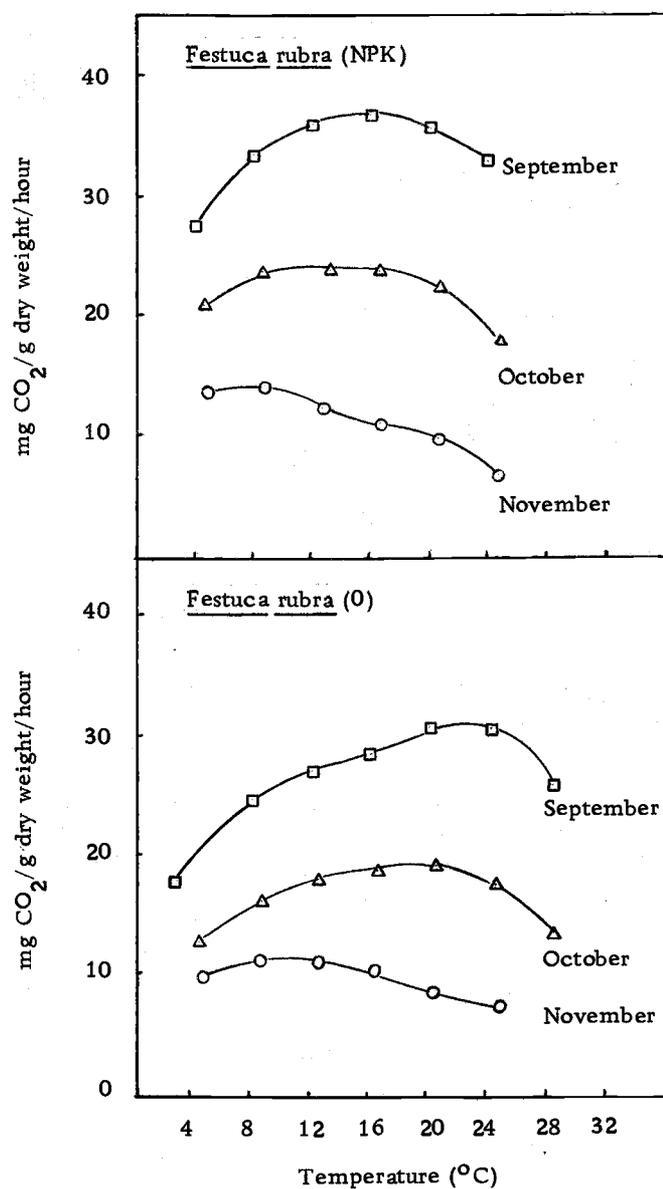


Figure 23. Changes in the photosynthetic rates of *Festuca rubra* (NPK) and *Festuca rubra* (0) with temperature from September until November, as measured on cut samples under laboratory conditions at 48 klx.

cases no effect of cutting on photosynthetic rates has been found (Wilson et al., 1969), while others have found an increase in photosynthetic rates due to cutting injury (Lubimenko and Stscheglova, 1932).

The Effect of Time since Cutting

The effects of cutting on photosynthesis were very difficult to distinguish from the influence of the environmental factors. As the grass is cut one deals with different age material as well as exposing previously shaded material to a higher light intensity environment. Pearce et al. (1965) working with orchard grass found that the efficiency of leaves remaining after cutting was lower and that they did not respond to high light intensities immediately after cutting. They further suggest that the length of the lag period (often 8 to 10 days) may depend on the plant's carbohydrate reserves. In these experiments it was impossible to measure shortly cut grass immediately (up to 21 days) after cutting since the leaves could not be sealed into the cuvette.

Comparisons of daily photosynthesis (sample of 3, 4 or 5 individual days) for Festuca rubra (NPK) at different times since cutting of the meadow are presented in Table 15. For the July 7-14 period, the 3 weeks-since-cutting grass assimilated nearly twice as much CO₂ as the uncut grass. For the August 11-18 period the "younger"

Table 15. Daily photosynthesis for Festuca (NPK) measured at different times since cutting of the meadow. Percentage photosynthetic rates are also given.

Weeks since cutting and % rate	Date measured	Daily photosynthetic rate mg CO ₂ /g/day				
		Day 1	Day 2	Day 3	Day 4	Day 5
3 uncut uncut/3 (%)	July 7-14	365.08	467.74	491.51	375.48	-----
	"	192.22	236.57	238.09	220.52	-----
	"	53%	51%	48%	59%	-----
5 8 8/5 (%)	Aug. 11-18	312.53	257.62	293.61	-----	-----
	"	264.25	225.46	215.76	-----	-----
	"	85%	88%	73%	-----	-----
3 8 3/8 (%)	Sept. 8-15	377.02	151.59	201.30	90.00	-----
	"	409.84	191.10	252.72	103.66	-----
	"	92%	79%	80%	87%	-----
5 10 10/5 (%)	Sept. 22-29	262.92	276.32	238.05	309.49	330.30
	"	210.44	259.47	255.19	288.36	315.89
	"	80%	94%	107%	93%	96%

grass (5 weeks-since-cutting) also had the higher assimilation rate. However, for the September 8-15 period the "older" grass (8 weeks-since-cutting) had the higher rates. This response can perhaps be explained by the action of the environmental factors. Shortly after the cutting of the grass on June 22 considerable amounts of precipitation fell and for a one week period in early July temperatures were quite cool (Figure 1). Thus the grass was not exposed to a high temperature, high light environment immediately after cutting. The measurements listed in Table 15 were made immediately following this cool, wet period. The 3 weeks-since-cut sample measured during the September 8-15 period was cut on August 26 after which followed a period of warm temperatures and high light intensities with very little precipitation (9 mm as opposed to over 100 mm following the cutting in June). Perhaps this had an adverse effect on the 3 weeks-since-cutting grass, resulting in higher rates for the older grass.

A comparison between grass 5 and 10 weeks-since-cutting from September 22 to 29, points out the difficulties of making such comparisons. On four out of the five days measured the 5 weeks-since-cutting grass had slightly higher photosynthetic rates than the 10 week grass; however, on one day the rate for the 10 week grass was 7% higher than for the 5 week grass. That was on a day of relatively low light intensity ($149.6 \text{ cal/cm}^2/\text{day}$) where the light

was usually below the light saturation level. Apparently the photosynthetic rate for the 5 and 10 week grass was similar for the light limiting portion of the light response curve with a slightly higher photosynthetic rate at light saturation for the 5 week grass.

Further comparisons between the photosynthetic rates of grass of different times since cutting during October were limited by the low light intensities. Full photosynthetic potential of the leaves at the higher light intensities could never be expressed. However, in late October brief periods of sunlight allowed a comparison of photosynthetic rates to be made between grass cut 9 weeks previously and the same grass with the tips removed, leaving approximately 15 cm of grass. The photosynthetic rates of this more juvenile grass were approximately 20% greater than that of the 9 week grass without the tips removed. It should be noted that this occurred despite the fact that the 9 week grass (uncut) had a considerably higher chlorophyll content (Figure 24). This points out the difficulties in separating the effects of aging from the effects of chlorophyll concentration as suggested by Heath (1969).

The Effect of Chlorophyll Content

Various authors have attempted to relate the photosynthetic activity, as well as the growth of plants, to the chlorophyll content of the leaf or plant community (Pilát, 1967; Aruga and Monsi, 1963;

Medina and Lieth, 1964; Brougham, 1960; and others). In analyzing the effects of nitrogen nutrition on photosynthetic rates of sugar beet, Nevins and Loomis (1970) found a positive correlation between dim-light photosynthesis and chlorophyll content. However, above a level of 4 mg chlorophyll per dm^2 foliage it was not considered limiting. Brix (1971) working with Douglas-fir found a slightly steeper photosynthetic curve in response to light on fertilized shoots which he suggested might be due to chlorophyll content. Anderson (1967) found that the normal chlorophyll content of leaves is adequate to absorb the incident light under most natural conditions. She further suggested that sun leaves with more than 4 mg chlorophyll per dm^2 are rarely exposed to sufficient light energy to saturate all of the reaction centers. On the other hand Rabinowitch (1951) suggested that the "Photocatalyst" chlorophyll can "impose ceilings" on the photosynthetic rate.

Šesták (1966) using dry weight increase as a measure of photosynthetic activity found a linear relationship between chlorophyll content and photosynthesis, but that this relationship was seldom uniform. The variations probably were due to changing radiation levels as well as to changes occurring with leaf aging. Due to some of this large variability he found the relationship became sigmoidal. Keller and Koch (1962) working with poplar found close correlation between the nitrogen content of foliage and the chlorophyll content ($r = .89$) as well as some correlation between nitrogen content and

photosynthesis.

All of these papers seem to suggest that amounts of chlorophyll can give some indication of the photosynthetic potential of plants, especially when working with plants deficient in their nutrient supply or under extreme light conditions. No doubt the influence of nutrient deficiency also influences the activity and amount of various enzymes involved in the photosynthetic process as well.

The chlorophyll levels of Festuca (NPK) and Festuca (0) fluctuated greatly during the growing season. The level was generally higher for the fertilized grass, both on a dry weight and leaf area basis (Figure 24). The greater variation in chlorophyll content on a leaf area basis is no doubt partially due to the greater error associated with the leaf area measurements. The trend in both the fertilized and unfertilized grass during the year was similar.

On a dry weight basis the chlorophyll content reached two peaks, one at the beginning of the year and a second in early October. This was true for both fertilized and unfertilized Festuca. When based on leaf area, the fertilized Festuca had a high level of chlorophyll in late July as well.

The age of the plant material undoubtedly has an effect on the chlorophyll content as suggested by Šesták (1966). The numbers in Figure 24 refer to the weeks since the meadow was cut and it can be seen that no clear relationship between the age of the grass (time

since it was cut) and chlorophyll level was found in the field. This probably was due to the widely different environmental conditions found in the field prior to sampling.

High light and temperature levels were generally associated with low chlorophyll levels. Such conditions occurred in mid-late June, and early and late August. It should be noted that the chlorophyll levels found in Festuca rubra, on a leaf area basis might be considered below optimum levels as suggested by Nevins and Loomis (1970). Maximum chlorophyll levels were seldom above 3 mg chlorophyll per dm^2 . The roll-leaf, as found in Festuca rubra presents an unusual structure since only half of the cylindrical leaf area is exposed directly to insolation.

The fact that chlorophyll might be partially responsible for limiting the photosynthetic rate is shown in Figure 24. In addition to leaf chlorophyll content, the maximum photosynthetic rates found for a six minute period over a weekly interval are also plotted. The apparent correlation between chlorophyll content and maximum photosynthesis is quite evident, although high chlorophyll levels do not always correspond to the highest photosynthetic levels. This is partially again due to the varying environmental conditions prevailing during each measuring period, and possibly due to the changing levels of enzymes active in the photosynthetic process. Unfortunately the levels of such enzymes as carboxydismutase were not measured.

Two regressions relating the percent of maximum photosynthesis observed to percent of maximum chlorophyll for Festuca (0) and Festuca (NPK) give an R^2 value of .38, which, although quite low, is nevertheless significant at the 1% level based on an F-test (Appendix, Figure 30). The significant correlation between photosynthetic rate and chlorophyll level of course does not necessarily imply a causal relationship.

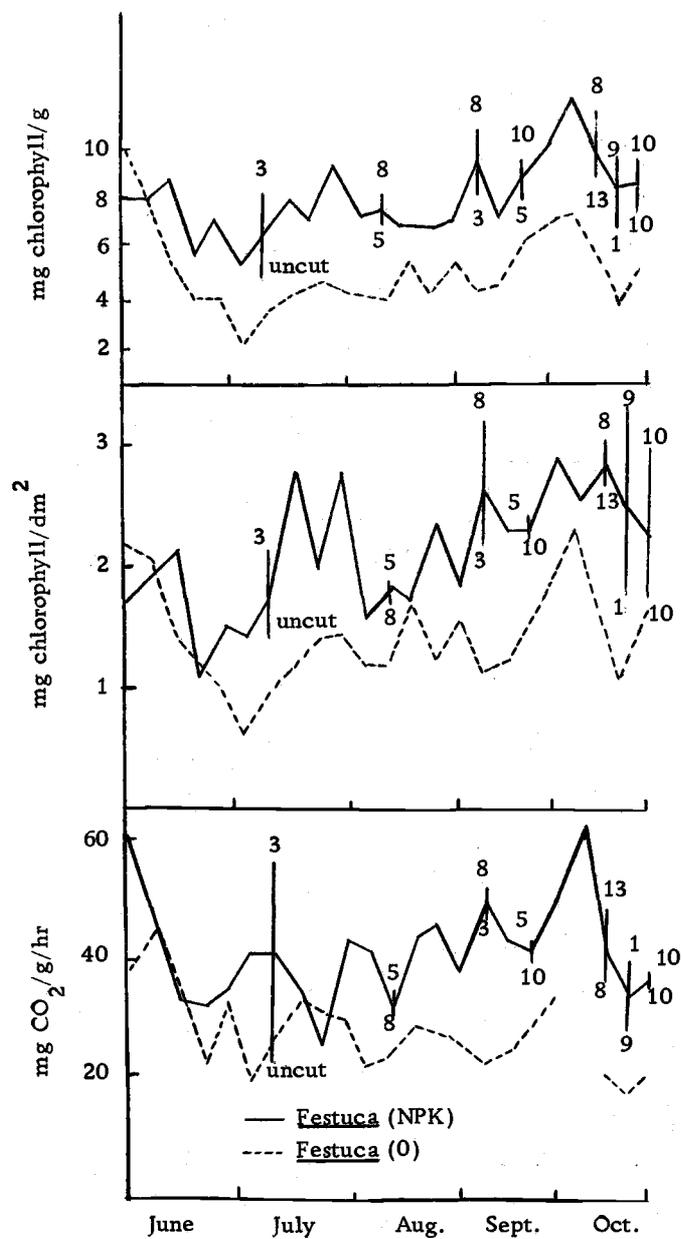


Figure 24. Seasonal changes in leaf chlorophyll content and maximum photosynthetic rate for *Festuca* (NPK) and *Festuca* (0). The numbers denote weeks since that portion of the meadow was mown (cutting).

FINAL CONSIDERATIONS AND CONCLUSIONS

The objectives of this study were to identify special characteristics of the meadow production process in northern Germany and to offer suggestions for future studies. Final considerations will be made on an environmental and a methodological basis.

Environmental Considerations

The seasonal change in the photosynthetic rates of Festuca rubra can perhaps be best discussed on the basis of the minimum number of factors which need to be considered in determining its photosynthetic rate. This minimum number of factors, as suggested by Cleary (1971), are the moisture effect, the temperature effect, the light effect, the nutrition effect and the preconditioning effect. Let us look at each of these and see what impact each might have on the photosynthetic rates of Festuca rubra in the Solling area.

The seasonal photosynthetic regression equations based on radiation for the three reference bases indicated that 87% to 88% of the variation in photosynthetic rates for Festuca (0) and 75% to 87% of the variation for Festuca (NPK) could be accounted for. The addition of the parameters temperature, vapor pressure deficit, chlorophyll and time explained a further 5% of the variation when photosynthetic rates were based on dry weight.

In order to avoid variation due to different chlorophyll content and leaf age, regressions relating photosynthetic rates to radiation (as in Figure 17) were run for 11 one week periods and representing 50 to 80 hourly means. For Festuca (0) 79% to 95% of the variation was explained by the regression based solely on radiation. An expanded regression having the additional terms: (TEMP), (TEMP)², (VPD), and (VPD)²; seldom improved the regression fit by more than 4% and in only 5 cases were any of these terms significant.

For Festuca (NPK) the radiation regression explained from 85% to 97% of the variation with usually less than a 5% increase in the variation explained due to the temperature and vapor pressure deficit terms. The temperature and VPD terms were significant in only 15 out of a possible 56 times.

For the growing season in 1970 soil moisture could not be considered as a limiting factor due to the uniform distribution of precipitation throughout the measuring period. However, low atmospheric humidity could be considered as limiting photosynthesis occasionally. This was generally in conjunction with high temperatures except for the sensitive plant response to increasing vapor pressure deficit for a three day period following a light frost in September. VPD was only significant twice in explaining the photosynthetic rates for Festuca (0) and five times for Festuca (NPK).

Temperature as a limiting factor in the Solling during the

growing season for Festuca rubra was more important in terms of high rather than low ranges. When temperatures could be considered suboptimal the radiation levels were usually so low that they constituted the primary limiting factor. During the growing season low temperatures were seldom found to limit photosynthesis, while high temperatures (above 24° C) caused marked reduction in the photosynthetic rate, with Festuca (NPK) expressing the greater sensitivity to increasing temperatures. There was considerable variation in the photosynthetic response to temperature much of which was probably due to the length of time for exposure to a given temperature (Figure 21). Thus, time of exposure should always be specified when depicting photosynthetic response to temperature (Heath, 1969).

Field measurements made in October indicated that Festuca (NPK) had higher photosynthetic rates in late October at 10° C than on many days in midsummer when temperatures were near 20° C which could be considered the optimum temperature. The less sensitive photosynthetic response of Festuca (0) to high temperatures was probably due to other factors, such as nutrient deficiency, limiting the photosynthetic rate. This could have been due to lower enzyme levels such as carboxydismutase as suggested by Medina (1970) or by higher total diffusion resistance of carbon dioxide. Leaf resistance as calculated from the transpiration rates generally ranged from 30 to 50 sec/dm for Festuca (NPK) and seldom below 50 and

often above 100 sec/dm for Festuca (0) (Appendix, Figure 31). Peaslee and Moss (1968) showed reduced stomatal aperture in K deficient leaves of maize which they suggested might be due to the loss of potassium ions to the mesophyll by the guard cells resulting in less ability in the opening of the stomata. Shimshi (1967) found that nitrogen deficiency reduced stomatal aperture which he suggested might be mediated through the chlorophyll content.

The effects of the improved nutrition for the fertilized Festuca was expressed by a continuing high rate of photosynthesis throughout the growing season while the unfertilized Festuca (0) had a continual declining photosynthetic rate (Table 13). This could also have been due to the more rapid aging by the unfertilized Festuca. Over the entire growing season Festuca (0) fixed 76% as much CO₂ as Festuca (NPK) on a dry weight basis while on an area basis it was 84%. The lower rates of the unfertilized grass were also expressed in a comparison of the photosynthetic efficiencies of the two treatments (Table 14).

Looking at the total aboveground biomass production (all species on the meadow) (Figure 25) one finds that the fertilized plot (NPK) produced approximately 2.5 times as much aboveground biomass as the unfertilized plot. Furthermore one finds that the aboveground biomass continued to increase on the fertilized plots until October while for the unfertilized plot there was little increase from August

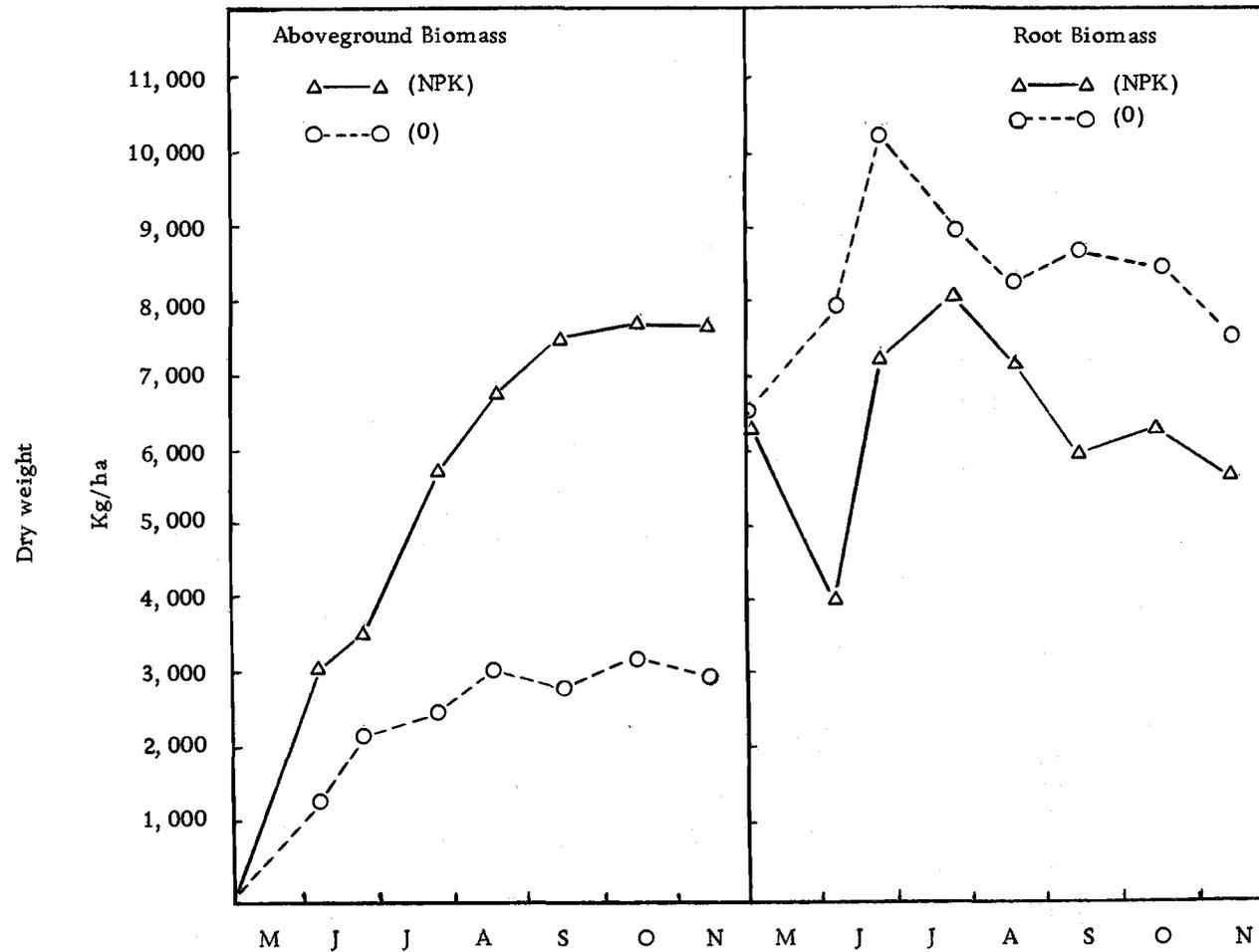


Figure 25. Changes in the aboveground and root biomass on the fertilized and unfertilized plot during the growing season in 1970. (Data from Speidel, personal communication)

on. If one can assume from these results a similar response for Festuca rubra, then this is similar to the findings on the seasonal changes in the photosynthetic rate which showed a seasonal decline for Festuca (0) but not for Festuca (NPK).

Root biomass, although the same for both the fertilized and unfertilized plot at the beginning of the growing season was approximately 30% greater on the unfertilized plot throughout the majority of the growing season, an indication that more of the photosynthate is distributed into the roots for the unfertilized plants, probably including Festuca rubra.

The productivity of a given site is usually a function of both the photosynthetic rate of the species in the community under specified environmental conditions and the leaf area of that community. The ability to produce a high leaf area rapidly in the spring as conditions become favorable is to a large extent a function of the carbohydrate reserves of the plant found in the roots (Speidel and Weiss, 1972). If the results in Figure 25 can be considered as applying to Festuca rubra one can see that for Festuca (0) much of the photosynthate is expressed by increased root biomass rather than increased aboveground biomass.

Another result of the fertilization treatment was the increased level of chlorophyll found on the fertilized plots. Although there was significant correlation between chlorophyll content and photosynthetic

rates it is doubtful whether chlorophyll levels were limiting in any but the lowest concentrations (Bouma, 1970). Changing enzyme levels as well as the aging effect complicate the determination of the true effect of chlorophyll concentrations. The highest chlorophyll concentrations were found at the beginning and toward the end of the growing season when temperatures and light levels were low.

The effect of preconditioning on photosynthetic rates were expressed during the growing season by reduced photosynthetic rates following the period of high temperatures and high light in June and by the slightly reduced photosynthetic rates following a light frost in late September.

The preconditioning effects were also closely related to the time since the meadow was mowed (age). For example, the newly cut grass in July which was exposed to two weeks of low temperatures and low light following cutting had extremely high photosynthetic rates when measured three weeks after cutting when conditions became more favorable. A period of cool temperatures and low light might be favorable to a newly cut meadow community where the lower leaves are suddenly exposed. In contrast, a community with a high leaf area would probably be favored more by a high light environment. This makes it difficult to say by which amount the photosynthetic rate was reduced by the environmental factors.

Furthermore, a meadow cut short has a very low photosynthetic

area, thus needing a considerable mobilization of reserves to build up the leaf area. Brougham (1956) found that a pasture cut to 5 inches produced 20% more herbage than the same pasture when cut to one inch. This was primarily due to the fact that it took only 4 days for the 5 inch cut pasture to reach 100% light interception while it took 24 days for the one inch cut pasture to reach 100% light interception.

The high photosynthetic rate of the one three-week-after-cutting sample can perhaps be partially explained by the findings of Wareing, Khalifa and Treharne (1968). They suggest that partial defoliation reduces competition between leaves for cytokinins from the roots. The increased amounts of cytokinins available after cutting are thought to stimulate enzyme synthesis, resulting in higher photosynthetic rates.

In conclusion one can say that the photosynthetic rates of Festuca rubra in the Solling area during the growing season are determined primarily by the radiation levels with moisture and temperature playing a minor role. Fertilization apparently affects the redistribution of photosynthate so that more is channelled into aboveground production and it also allows Festuca rubra to maintain a high photosynthetic rate throughout the growing season.

Methodological Considerations

Although the gas exchange measuring system functioned well throughout the course of the study, several difficulties arose due to the structure of the grass. The cuvette used was originally designed for the measurement of gas exchange in plants with a single stem. It was often quite difficult to seal sufficient amounts of grass into the cuvette and to assure no leaks in the system. Furthermore, since the cuvette had to be tilted it was impossible to measure the grass shortly after cutting since it was of insufficient size to reach into the cuvette.

A smaller cuvette could have overcome some of these problems. A "dome" or "surface" cuvette which is simply placed over a segment of meadow would have been a useful addition in determining the gas exchange of the meadow community. Although small plants which could not be sealed into a cuvette could be measured in such a system, some of the difficulties with soil respiration would have to be overcome.

A supplementary light source would have been particularly valuable in the Solling area where light intensities are often well below the light saturation level. Furthermore the fluctuating light levels so common in the Solling made it difficult to measure temperature responses at uniform light intensities on many occasions.

The desirability of making more replicate measurements was well brought out in this study due to the many variables which were included. In addition to the ever changing environmental factors there were two levels of fertilization, seasonal changes and effects due to "time since mowing." The mowing effect proved to be insignificant, except in one instance, when perhaps with more continuous measurements more insight could have been gained into how mowing influences photosynthetic rates.

One must emphasize the need for making replicate measurements since one is constantly faced with changing environmental factors in such field studies. This was particularly true for the conditions encountered in the Solling area.

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APPENDIX

Computation of Net Assimilation Rate

$$NAr = \frac{10^3 \text{ MWt (mg CO}_2\text{)} \cdot S \frac{\text{(ppm CO}_2\text{)}}{\text{(mm)}} \cdot \Delta \text{CO}_2 \text{ (mm)} \cdot \frac{1}{10^6}}$$

$$\frac{273 \text{ (}^\circ\text{K)}}{760 \text{ (mm Hg)}} \cdot \frac{P \text{ (mm Hg)}}{T \text{ (}^\circ\text{K)}} \cdot FR \frac{\text{(l)}}{\text{(hour)}} \cdot \frac{1}{\text{(DWt) (g)}}$$

$$NAr = 0.426 \cdot 10^{-3} \frac{P \cdot \text{CO}_2 \cdot FR}{T \cdot \text{DWt}} \quad \left[\frac{\text{mg CO}_2}{\text{g hour}} \right]$$

NAr = Net Assimilation rate

MWt = Molecular weight of CO₂ (44)

MV = Mole volume of CO₂ at STP (22.4)

S = Sensitivity of the infra-red gas analyzer (in this case
75 ppm CO₂/125 mm (chart width) = .6 ppm CO₂/mm)

P = Ambient air pressure at time of measurement

T = Air temperature of gas analyzer at time of measurement

FR = Flow rate of the air through the gas analyzer

DWt = Dry weight of plant specimen (also leaf area or chlorophyll)

ΔCO₂ = CO₂ difference between measuring and comparison air in
mm scale on chart recorder

10³ = Correction for mg

10⁶ = Correction for ppm

Computation of Transpiration Rate

$$Ts = \Delta H_2O \left[\frac{\text{mg H}_2\text{O}}{1} \right] \cdot FR \left(\frac{1}{\text{hr}} \right) \cdot \frac{1}{\text{DWt (g)}} = \left[\frac{\text{mg H}_2\text{O}}{\text{g hr}} \right]$$

Ts = Transpiration rate

ΔH₂O = Difference between outgoing and by-pass humidity

FR = Flow rate

DWt = Dry weight of plant specimen (also leaf surface area)

Computation of Total Water Diffusion Resistance

$$R = \text{VPD} \left[\frac{\text{mg H}_2\text{O}}{\text{dm}^3} \right] \cdot \frac{1}{T_s} \left[\frac{\text{dm}^2 \text{ hr} \left(3,600 \frac{\text{sec}}{\text{hr}} \right)}{\text{mg H}_2\text{O}} \right]$$

$$R = \text{VPD} \cdot \frac{1}{T_s} \left[\frac{\text{sec}}{\text{dm}} \right]$$

R = Total resistance to water vapor diffusion

VPD = Vapor pressure deficit between leaf and air

T_s = Transpiration rate

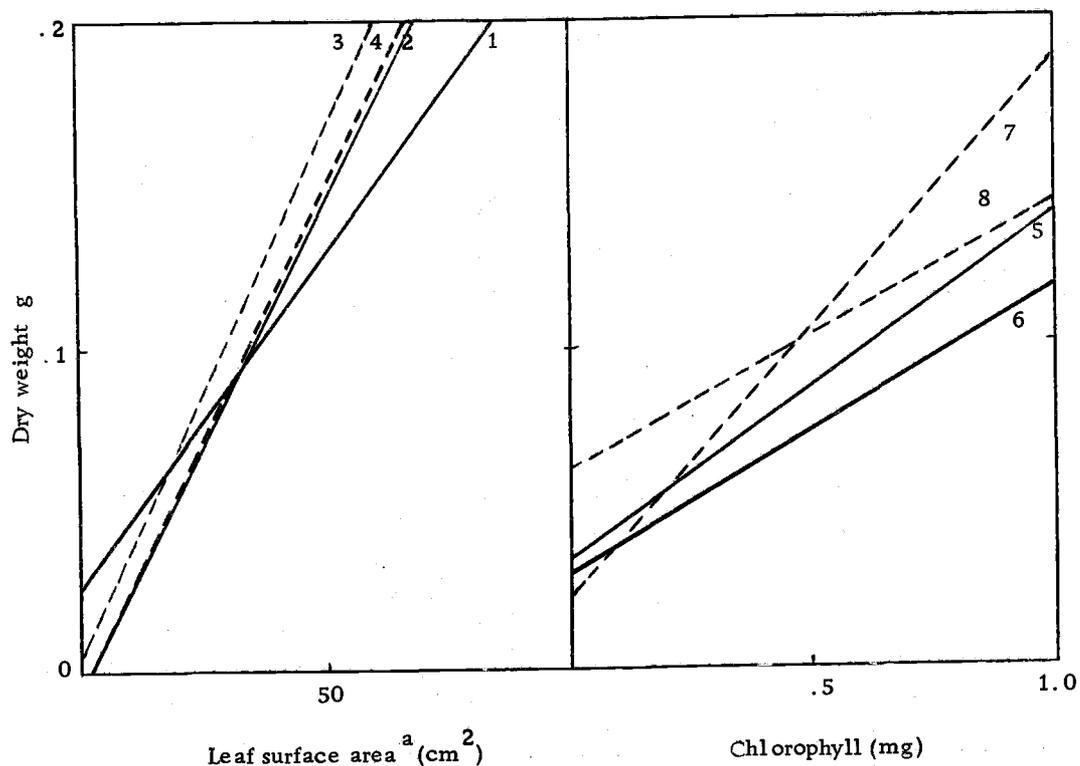


Figure 26. Relationship between leaf dry weight (g), surface area (cm^2) and chlorophyll content (mg), for *Festuca rubra* leaves from fertilized and unfertilized plots. Leaf dry weight = $\beta_0 + \beta_1 + \epsilon$ (leaf area or mg chlorophyll). Numbers refer to Table 16.

^aOutside surface of rolled leaf

Table 16. Coefficients, F-significance and R^2 values for the regression equations relating leaf dry weights to leaf area and mg chlorophyll. Numbers refer to plot in Figure 26.

No.	Regr.	Fert.	Time	β_0	β_1	R^2	F ^a
1	dwt/area	NPK	May-Aug	.0279	.0020	.72	**
2	"	NPK	Aug-Nov	-.0040	.0030	.80	**
3	"	(0)	May-Aug	-.0043	.0034	.95	**
4	"	(0)	Aug-Nov	.0035	.0030	.93	**
5	dwt/chlorophyll	NPK	May-Aug	.3414	.1055	.62	**
6	"	NPK	Aug-Nov	.3170	.0846	.71	**
7	"	(0)	May-Aug	.0231	.1651	.39	*
8	"	(0)	Aug-Nov	.0609	.0798	.29	-

^aF-test: ** significant 1%
* significant 5%

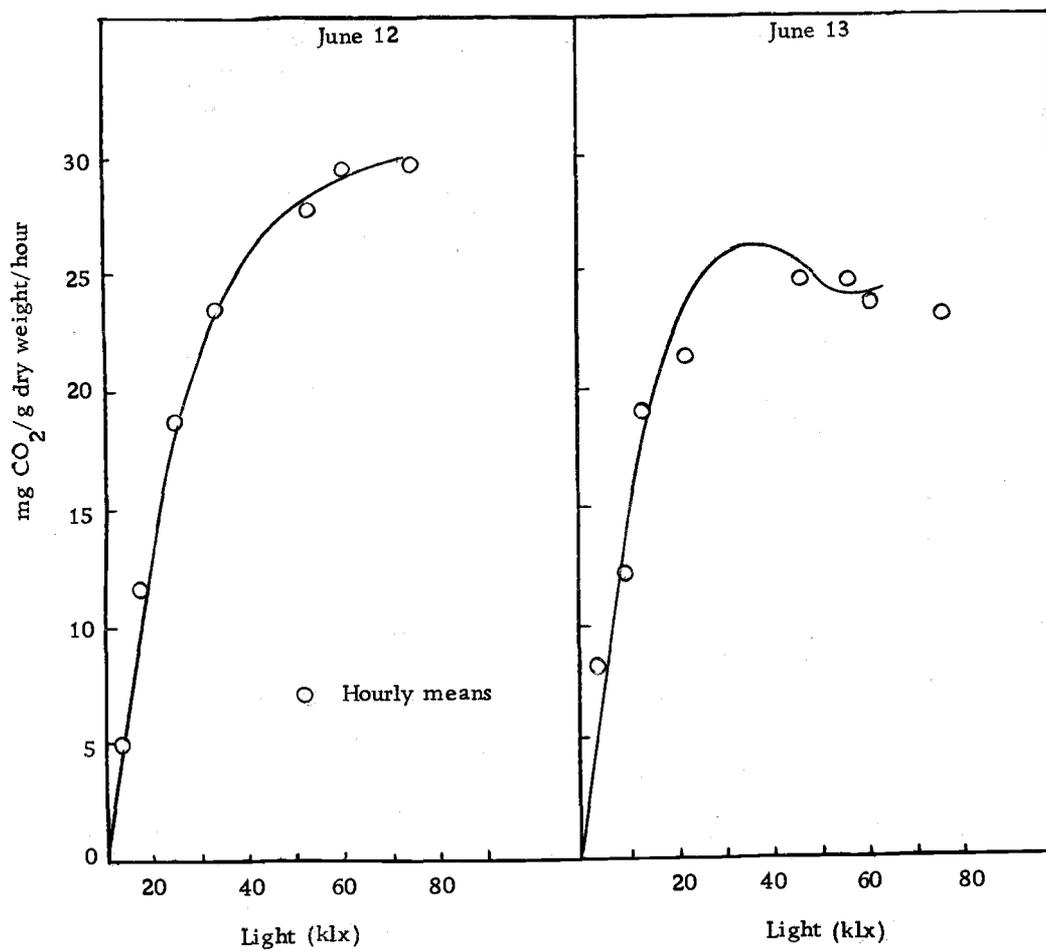


Figure 27. Comparison of regression fitted to 6-minute values and the respective hourly means for two days in June. Regression model used was:

$$PS_n = \beta_0 + \beta_1 (RAD) + \beta_2 (RAD)^2 + \beta_3 (RAD)^3 + \epsilon.$$

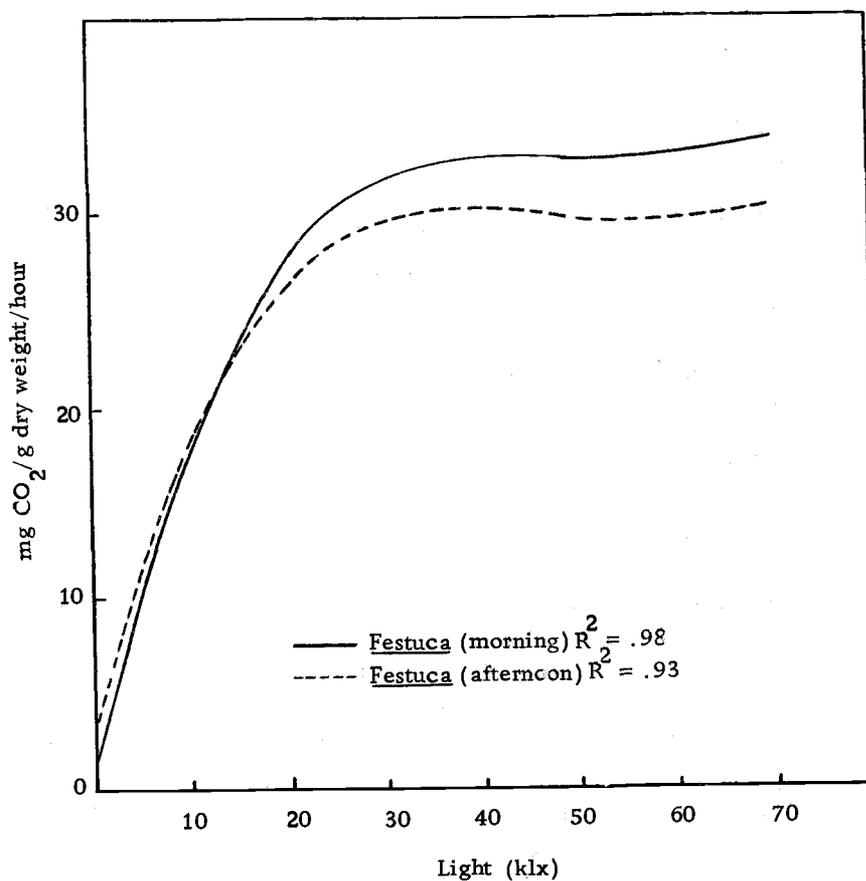


Figure 28. Comparison of photosynthetic response to light for *Festuca rubra* (NPK) based on hourly mean rates in the morning (until 12:00) (solid line) and in the afternoon (broken line). The data covers hourly means in a one-week period from September 1 to 8. Fitted model: $P_s = \beta_0 + \beta_1 (\text{RAD}) + \beta_2 (\text{RAD})^2 + \beta_3 (\text{RAD})^3 + \epsilon$.

Confidence interval at light = 70 klx (Above)

	95%	99%
<i>Festuca</i> (am)	29.8--37.40	28.47--38.71
<i>Festuca</i> (pm)	24.92--35.73	23.04--37.61

Respiration of *Festuca rubra*

Large fluctuations in the ambient CO₂ concentration during the night hours, which were most probably due to soil respiration, often prevented the reliable measurement of plant respiration. This was particularly true on calm evenings following rain. Consequently portions of the meadow were dug up and potted and brought to the laboratory where respiration was measured on cut leaf segments. Respiration was measured at 5° C intervals from 5° to 20° C, and it was hoped that from these measurements the field respiration could be computed for the missing days based on the temperature data, similar to the approach used by Czopek and Starzecki (1967) and Czopek (1969).

The respiration rate for the unfertilized *Festuca* was noticeably less than that of the fertilized *Festuca* at all temperatures (Figure 29). Maximum respiration rates occurred in September for *Festuca* (NPK) and in October for *Festuca* (0). Higher rates probably also occur in the early growing season as was indicated by some field measurements. Similar increased respiration rates in early fall were found by Czopek (1969) for *Dactylis glomerata* and *Rumex acetosella*.

From the laboratory measurements, respiration rates were calculated for 44 days where field respiration data were available and a regression tested relating field respiration to temperature, (temperature)², previous day photosynthesis and laboratory computed

respiration. The regression had an R^2 of .34 with previous day photosynthesis being the only significant term (5% based on a t-test). Except for the July period respiration rates predicted from the laboratory studies were considerably greater than those found in the field. Consequently the computed respiration rates were not used for filling in the missing respiration data.

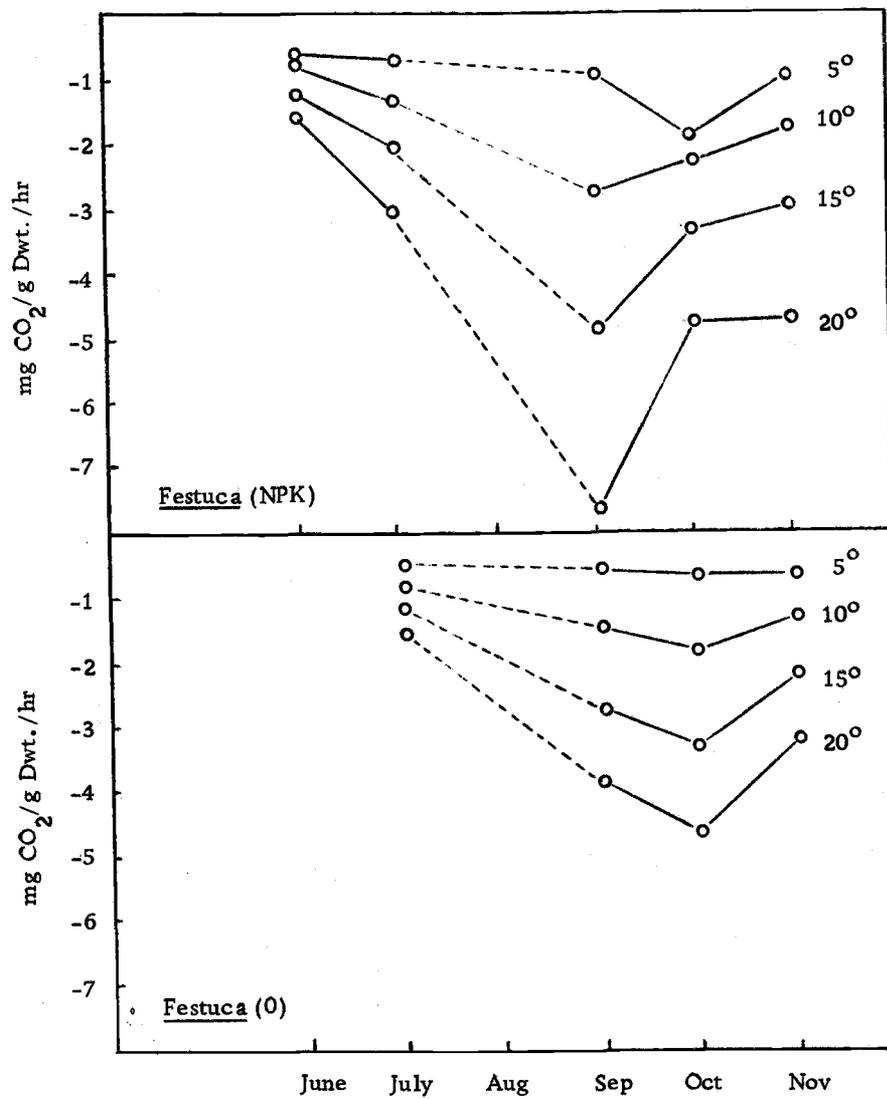


Figure 29. Changes in leaf respiration rates of *Festuca rubra* fertilized (NPK) and unfertilized (0) with temperature during various months of the year. Rates measured in the laboratory.

Table 17. Daily respiration rates of *Festuca* (NPK) computed from laboratory data and as measured in the field. Previous day photosynthesis and night temperature are also listed.

	Field determined respiration mg CO ₂ /g/day	Respiration calculated from laboratory data mg CO ₂ /g/day	Previous day photosynthesis mg CO ₂ /g/day	Temperature °C
JULY	18.60	13.05	217.88	11.3
	11.64	10.80	256.53	9.0
	6.09	9.60	216.74	9.0
	45.91	18.45	467.74	15.2
	5.97	18.00	236.57	16.4
	11.94	11.20	249.26	12.5
	12.81	10.00	188.20	9.6
	13.19	11.48	209.74	10.4
	12.11	10.20	216.30	9.2
	17.38	13.95	242.28	12.3
	8.79	8.80	138.02	8.1
	4.32	10.00	176.61	9.7
	8.42	18.45	183.36	15.3
AUGUST	16.42	32.40	407.78	15.7
	15.15	33.75	359.73	16.0
	14.07	37.35	357.51	17.2
	11.20	27.83	254.22	13.8
	10.00	28.50	225.46	14.0
	10.72	29.45	257.62	14.3
	4.88	13.50	215.76	8.3
	3.79	13.95	293.61	8.6
	7.20	25.52	151.22	11.6
	7.25	22.95	225.67	12.6
	21.13	52.00	348.33	14.8
SEPTEMBER	9.25	28.50	341.79	10.7
	5.51	36.00	253.68	12.3
	8.95	43.20	157.55	12.2
	7.98	31.50	303.82	11.1
	7.46	32.45	370.14	10.6
	17.99	50.05	346.30	14.3
	23.72	59.23	377.02	15.6
	20.92	61.60	409.84	16.6
	17.40	33.55	151.59	10.9
	12.10	37.62	191.10	11.7
	7.30	21.00	201.30	8.6
	9.28	24.00	252.72	9.4
	19.80	49.80	90.00	13.3
	13.06	54.60	103.66	14.2
	5.10	30.00	88.03	9.6
	11.22	22.20	238.05	8.1
	14.59	27.00	255.19	9.0
	7.18	18.38	309.49	7.8
11.62	28.20	288.36	9.2	
8.65	10.45	330.30	5.2	

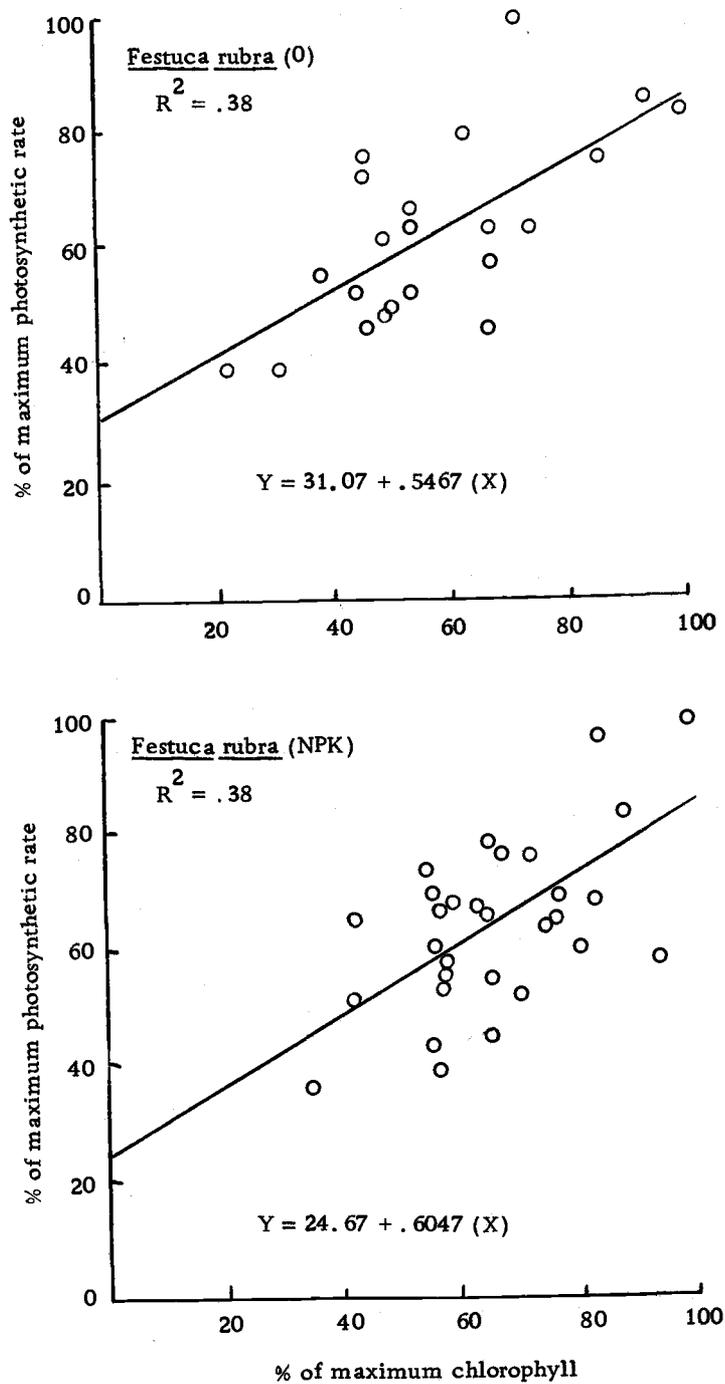


Figure 30. The relation between % of maximum photosynthetic rate to % of maximum chlorophyll content (mg Chl/g dry weight) for Festuca (0) and Festuca (NPK).

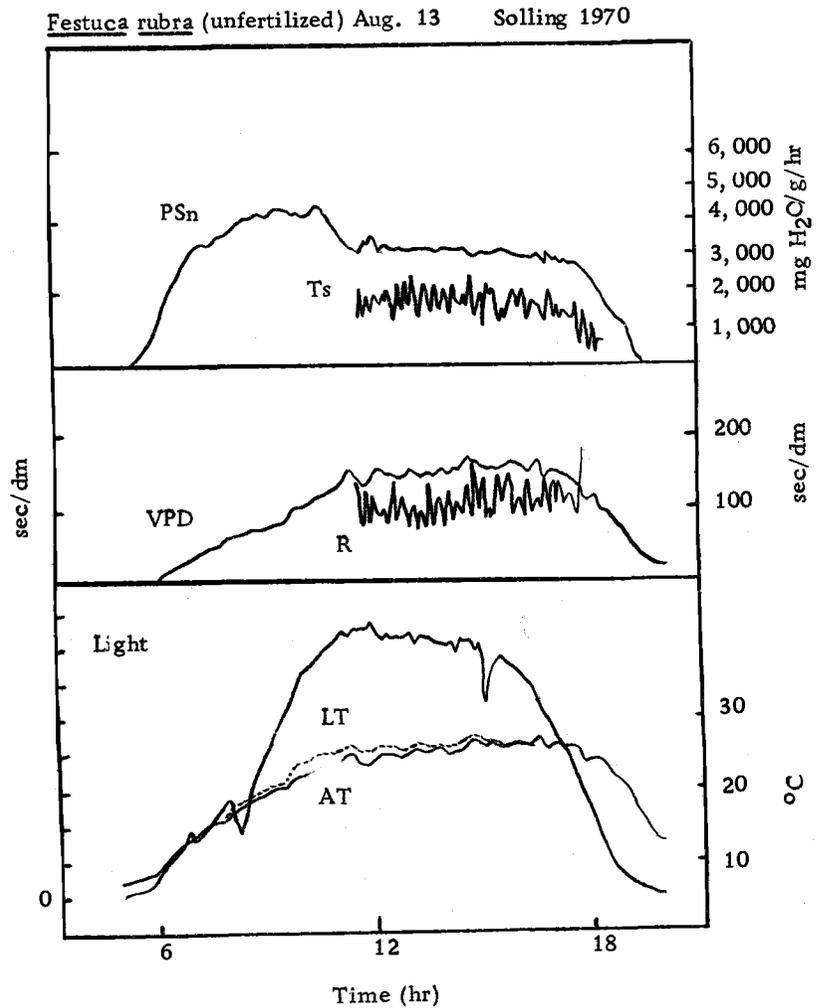
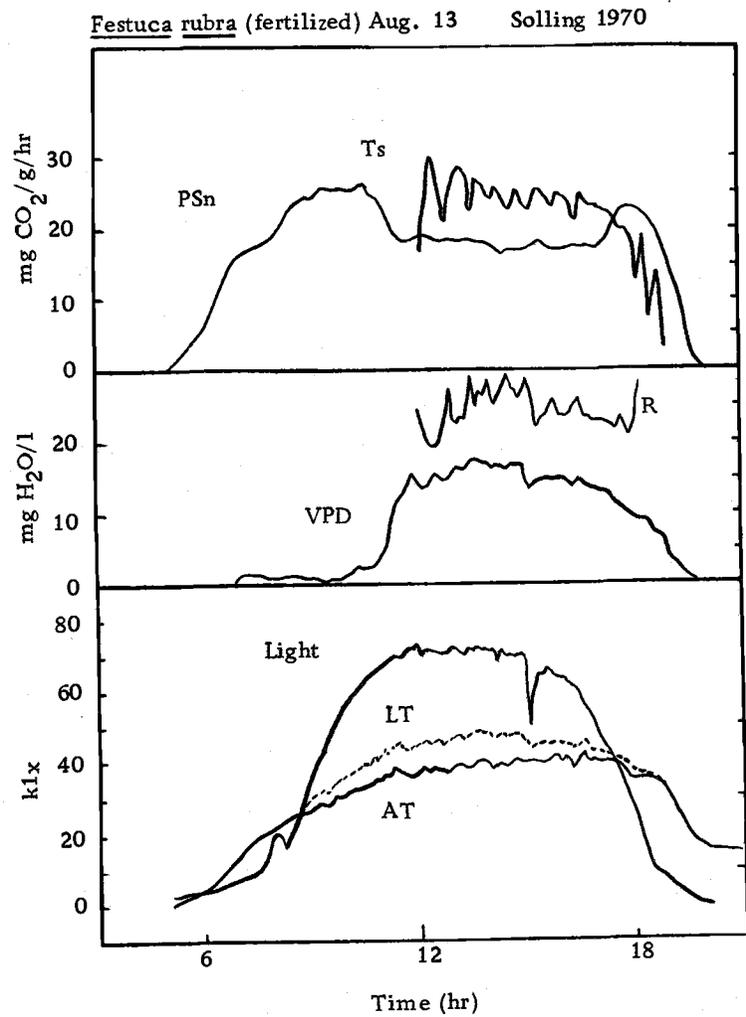


Figure 31. Daily pattern of CO₂ and H₂O gas exchange of Festuca (NPK) and Festuca (0) on August 13, 1970. Depicted are photosynthesis (PSn) mg CO₂/g/hr, Transpiration (Ts) mg H₂O/g/hr, total diffusion resistance (R) sec/dm, Vapor pressure deficit (VPD) mg H₂O/l, light (klx), leaf (LT) and air temperature (AT) °C. Note the different scales for (R).