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RESEARCH MEMORANDUM

RM 72-22

THE EFFECTS OF ENVIRONMENTAL FACTORS
ON RATES OF PRIMARY PRODUCTION OF
TWO DESERT GRASS SPECIES

Gary L. Cunningham
&
Fred R. Balding

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ON RATES OF PRIMARY PRODUCTION OF
TWO DESERT GRASS SPECIES

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Fred R. Balding

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Las Cruces, New Mexico

APRIL 1972

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ABSTRACT

Two models were developed to predict net CO$_2$ exchange for desert grass species, using as the driving variables irradiance, air temperature and soil water potential. One model ("PSYN") assumes that one of the three driving variables will be rate-limiting to net CO$_2$ exchange; the second model ("GAS") does not make this assumption. Input and validation data for both models were obtained with a differential infrared gas analysis system using potted plants of *Tridens pulchellus* and *Panicum obtusum* in a controlled environment chamber. The rationale and flow diagrams for the models are presented.

When tested, the models gave reasonably accurate estimates of actual rates of net CO$_2$ exchange observed in the laboratory.
INTRODUCTION

This report is a statement of progress to date in developing predictive models of net CO₂ exchange for desert grass species. Work has proceeded thus far on two species: *Tridens pulchellus* and *Panicum obtusum*. It is felt, however, that the experimental and modelling approaches used will be applicable to other species.

The general philosophy of the approach adopted has been to develop models with acceptable predictive capabilities while limiting the driving variables to as few, easily obtained, environmental measures as possible. This approach should make the net CO₂ exchange models into more flexible building blocks in the construction of ecosystem models and submodels. The driving variables which have been considered essential are irradiance, air temperature and soil water potential. Others may be necessary but these should constitute a minimum set.

Two different modelling approaches have been used. One approach assumes that one of the three driving variables will be rate-limiting to net CO₂ exchange. The second approach does not make this assumption. The net CO₂ exchange data needed for both models is essentially the same. For each species of grass, the model requires information on the temperature response of net CO₂ exchange at maximum irradiance levels and optimum soil water potential (-0.3 bar). The response of net CO₂ exchange to irradiance at optimum temperature and soil water potential, and the response to varying soil water potential at optimum temperature and maximum irradiance, are also required.

Before presenting the models and evaluating their predictive capabilities, a description is given of the methods used to measure these responses of net CO₂ exchange to the driving variables.

METHODS

Laboratory measurements of net CO₂ exchange rates were made (DSCODE A3UCG01) to obtain the input and validation data for the models. Plants of *Tridens pulchellus* were grown from seed collected in the area of the Jornada Validation Site (Whitford and Ludwig, 1971). Plants were established in 27 cm x 17 cm x 12 cm pots containing soil from areas on the validation site dominated by *Tridens*. The pots were thinned to from 2 to 5 individuals per pot. It was felt this would give a root-to-soil volume ratio comparable to that found in the field. Single clumps of *Panicum obtusum* were transplanted from the playa on the Jornada site to the same type pots used for the *Tridens*. Clumps selected were small enough that most of the roots and adjacent soil could be transferred to the pots. Any additional soil needed to fill the pots was taken from the area immediately around the transplanted clump.

After plants of both species were established in the pots they were placed in a controlled environment chamber (Environator, model HL 3458) for premeasurement acclimation. Both species were acclimated to environmental conditions selected to simulate as closely as possible the environment of the Jornada site during mid-August, the usual time of maximum growth for both species in southern New Mexico (Whitford and Ludwig, 1971). The acclimation conditions were: day temperature 32°C; night temperature 16°C; relative humidity approximately 25%; photoperiod 12 hours; irradiance 53 watts m⁻² in the wavelengths from 400 to 700 nm. Irradiance values given both here and following were measured with a spectroradiometer (ISCO, model SR). Soil water potential varied during the acclimation period from -0.3 to approximately -50 bars. This variation was obtained with a 2- to 3-day watering schedule. Soil water potentials between 0.0 and -40 bars were measured with a thermocouple psychrometer (Wescor, model PT51-10). Soil water potentials below -50 bars were measured with gypsum resistance blocks (Balding and Cunningham, 1972). Plants were maintained under the above acclimation conditions for at least 2 weeks prior to measurements of net CO₂ exchange rates. Under these conditions plants of both species exhibited growth forms similar to plants growing on the validation site in mid-August.
The day prior to measurement of CO₂ exchange, three pots of the species to be measured were watered to bring the soil water potential to the -0.3 bar level. The soil surface of each pot was sealed with a mixture of petroleum jelly and paraffin (2:3 by volume). This prevented both evaporation from the soil and CO₂ exchange between the soil and the measuring air stream.

For measurement of net CO₂ exchange rates the three replicate pots were each sealed in a 30.5 cm x 22.9 cm x 33.0 cm plexiglass cuvette. Each of the cuvettes was equipped with a fan to provide internal air circulation. The three cuvettes were placed in a controlled environment chamber which was used to provide various combinations of irradiance and temperature within the cuvettes. Air temperatures within the cuvettes were monitored with shielded copper-constantin thermocouples connected to a recorder (Leeds and Northrup Speedomax W).

Net CO₂ exchange rates were measured with the differential infrared gas analysis system shown in Figure 1. Air was pulled into the laboratory from outside and passed through a water vapor trap. The water vapor trap consisted of copper coils and glass collecting vials immersed in 30 gallons of water refrigerated to 4°C. The air then passed through a 2-gallon plastic reservoir which dampened ambient CO₂ concentration and air pressure fluctuations in the system. Air flow from the reservoir was passed to the three cuvettes and the reference cell of the infrared gas analyzer (IRGA; Beckman model 215A). Flow rates to the cuvettes and the IRGA were controlled by 4 flowmeters (Brooks Sho-Rate type 1355-0I1AAA). Air passing through the cuvettes was either exhausted or, in the case of the cuvette being measured, diverted by the switching system through a vapor trap to the sample cell of the IRGA.

The rates of net CO₂ exchange at several temperatures were measured at the maximum level of irradiance obtainable in the controlled environment chamber (53 watts m⁻² from 400 to 700 nm). The rates were then measured at 5 levels of irradiance at the optimum temperature observed for the maximum irradiance level. All values of the net CO₂ exchange used were the means of the three replicate pots. The data obtained by the above method were used to construct the irradiance and temperature response tables used in the models.

Rates of net CO₂ exchange were also measured at various combinations of irradiance and temperature to obtain validation data for the models.

Net CO₂ exchange measurements were never made on any one pot for more than 12 hours. At the conclusion of the set of measurements the above-ground portions of the grasses were harvested and the dry weight of the green portions obtained.

MODELS

One of the two models, which we have named PSYN, assumes that the level of one of the three environmental factors used as driving variables will be rate-limiting to net CO₂ exchange. A flow diagram of the computer program for this model appears in Figure 2. In this model the response of net CO₂ exchange to temperature at maximum irradiance and optimum soil water potential is entered as a two-dimensional table. The computer program then interpolates linearly between values in the table to arrive at a maximum possible rate of net CO₂ exchange for a given air temperature value. The response of net CO₂ exchange to irradiance at the optimum air temperature and soil water potential and the response to soil water potential at optimum air temperature and maximum irradiance are also entered as two-dimensional tables (Tables 1, 2 and 3). Maximum possible rates for a specified irradiance and soil water potential are found by linear interpolation between values in these tables. The computer program then selects the minimum of the three maximum possible rates for the specified conditions and assigns that as the rate of net CO₂ exchange.
Figure 1. Diagram of differential infrared gas analysis system.
Table 1. Values of net CO₂ exchange rate at various air temperatures for maximum irradiance and optimum soil water potential used in the PSYN model.

<table>
<thead>
<tr>
<th>Temperature °C</th>
<th>5</th>
<th>7</th>
<th>13</th>
<th>20</th>
<th>26</th>
<th>29</th>
<th>33</th>
<th>40</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tridens</td>
<td>3.3</td>
<td>-</td>
<td>5.4</td>
<td>7.1</td>
<td>10.2</td>
<td>-</td>
<td>10.6</td>
<td>10.0</td>
</tr>
<tr>
<td>Panionum</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td>2.3</td>
<td>-</td>
<td>2.9</td>
<td>-</td>
<td>2.0</td>
</tr>
</tbody>
</table>

Table 2. Values of net CO₂ exchange rate at various irradiances for optimum air temperature and soil water potential used in the PSYN model.

<table>
<thead>
<tr>
<th>Irradiance in watts m⁻² (400 - 700 nm)</th>
<th>11</th>
<th>23</th>
<th>27</th>
<th>39</th>
<th>53</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tridens</td>
<td>2.7</td>
<td>5.6</td>
<td>6.5</td>
<td>9.2</td>
<td>10.6</td>
</tr>
<tr>
<td>Panionum</td>
<td>0.04</td>
<td>1.0</td>
<td>1.7</td>
<td>2.7</td>
<td>2.9</td>
</tr>
</tbody>
</table>

Table 3. Values of net CO₂ exchange rate at optimum soil water potential and air temperature and maximum irradiance used in the PSYN model.

<table>
<thead>
<tr>
<th>Soil water potential in bars</th>
<th>-0.3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tridens</td>
<td>10.6</td>
</tr>
<tr>
<td>Panionum</td>
<td>2.9</td>
</tr>
</tbody>
</table>
The other model, which we have named GAS, does not assume that one of the driving variables will be rate-limiting to net CO₂ exchange. A flow diagram of the computer program for this model appears in Figure 3. In this model the responses of net CO₂ exchange to air temperature, irradiance, and soil water potential at optimum or maximum values of the other two variables, are entered as coefficients ranging from 0 to 1.0 rather than as actual values of net CO₂ exchange (Tables 4, 5 and 6). The linear interpolation subroutine is used to calculate the three coefficients which are then multiplied by the maximum rate of net CO₂ exchange for the species. This value is the predicted rate of net CO₂ exchange for the specified environmental conditions. The coefficients for the tables were obtained by calculating the percent of the maximum rate at each of the values for the driving variables.

Figure 3. Flow diagram of computer program for GAS model, which does not assume a limiting factor.
### Table 4. Temperature coefficients used in the GAS model.

<table>
<thead>
<tr>
<th>Temperature °C</th>
<th>5</th>
<th>7</th>
<th>13</th>
<th>20</th>
<th>26</th>
<th>29</th>
<th>33</th>
<th>40</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tridens</strong></td>
<td>0.3</td>
<td>-</td>
<td>0.51</td>
<td>0.68</td>
<td>0.96</td>
<td>-</td>
<td>1.0</td>
<td>0.94</td>
</tr>
<tr>
<td><strong>Panicum</strong></td>
<td>-</td>
<td>0</td>
<td>-</td>
<td>0.81</td>
<td>-</td>
<td>1.0</td>
<td>-</td>
<td>0.70</td>
</tr>
</tbody>
</table>

### Table 5. Irradiance coefficients used in the GAS model.

<table>
<thead>
<tr>
<th>Irradiance in watts m(^{-2}) (400 - 700 nm)</th>
<th>11</th>
<th>23</th>
<th>27</th>
<th>39</th>
<th>53</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tridens</strong></td>
<td>0.32</td>
<td>0.53</td>
<td>0.61</td>
<td>0.87</td>
<td>1.0</td>
</tr>
<tr>
<td><strong>Panicum</strong></td>
<td>0.02</td>
<td>0.34</td>
<td>0.58</td>
<td>0.95</td>
<td>1.0</td>
</tr>
</tbody>
</table>

### Table 6. Soil water potential coefficients used in the GAS model.

<table>
<thead>
<tr>
<th>Soil water potential in bars</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tridens</strong></td>
</tr>
<tr>
<td><strong>Panicum</strong></td>
</tr>
</tbody>
</table>
**FINDINGS AND DISCUSSION**

The expected response of the net CO₂ exchange rate of *Tridens* to air temperature at five irradiance levels as predicted by the PSYN model are shown in Figure 4, and those predicted by the GAS model are shown in Figure 5. Figures 6 and 7 show the rates predicted for *Pannion* by the PSYN and GAS models respectively.

The general shapes of the predicted response curves are similar in each case. As expected, however, the PSYN models show less sensitivity to changes in irradiance at low temperatures and less sensitivity to temperature changes at low irradiance.

We do not yet have enough data available to effectively predict the response of net CO₂ exchange rates to changes in soil water potential. This will be incorporated into the models as soon as the measurements have been completed.

To test the predictive capabilities of the two models, predictions of net CO₂ exchange rates were made for the conditions of air temperature, irradiance and soil water potential which had been previously measured. Figures 8, 9, 10 and 11 are plots of the observed values of net CO₂ exchange against the expected values for both species predicted by each model. The accuracies of the models in predicting rates of net CO₂ exchange over the ranges of the environmental variables measured were tested by calculating correlation coefficients for the correlation of observed with predicted values (Figs. 8, 9, 10 and 11). All correlation coefficients were significant at the 0.01 level.

The results obtained thus far indicate that over the ranges of irradiance and temperature measured, both modelling strategies provide reasonable estimates of actual rates of net CO₂ exchange observed in the laboratory.
Figure 5. Rates of net CO₂ exchange predicted for *Tridens pulchellus* by the GAS model.
Figure 7. Rates of net CO₂ exchange for *Panicum obtusum* predicted by the GAS model.
Figure 9. Observed plotted against expected values of net CO2 exchange rates predicted by the GAS model for *Tridens pulcher*. $r = 0.96$.

Figure 10. Observed plotted against expected values of net CO2 exchange rates predicted by the PSYN model for *Panicum obtusum*. $r = 0.87$. 
Figure 11. Observed plotted against expected values of net CO$_2$ exchange rates predicted by the GAS model for Panicum obtusum. $r = 0.88$

**EXPECTATIONS**

The next step in our research program is to increase the number of measurements of net CO$_2$ exchange rates at various soil water potentials. This will allow incorporation of soil water potential as one of the driving variables in the models. To get predictions of rates at irradiance levels more comparable to those found in the desert environment, measurements will need to be made under higher irradiance levels. We plan to do this by using sunlight and a system for controlling cuvette temperature out-of-doors. This system is now in the final stages of construction.

After the models have been completed using laboratory data, their predictive value will be tested against net CO$_2$ exchange rate measurements made on the Jornada Validation Site. The models may need to be revised to include phenology and acclimation conditions of the plants. These revisions will not be made, however, until the predictive capabilities of the simpler models have been tested.

At the present time it is impossible to draw any real conclusions from what has been accomplished. It does appear, however, that the approach being used is valid and can provide accurate predictions of net CO$_2$ exchange rates from a minimum of experimental data and using a minimum set of driving variables.
LITERATURE CITATIONS
