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G. L. Cunningham

J. F. Reynolds

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**FINAL REPORT**

**PRIMARY PRODUCTION AND CARBON ALLOCATION  
IN CREOSOTEBUSH: VALIDATION OF THE MODEL**

G. L. Cunningham (Project Leader)  
New Mexico State University

and

J. F. Reynolds  
North Carolina State University

**US/IBP DESERT BIOME  
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Ecology Center, Utah State University, Logan, Utah 84322

### ABSTRACT

Carbon allocation and net carbon gain were selected as means of assessing the role of the environment in determining resource allocation. The model utilizes a systems approach in which movement of assimilate is in response to changes in source-sink strength of leaves, stems, roots and reproductive structures. Model outputs of simulated reproductive and vegetative production are compared with actual production values measured on experimental plots adjacent to the Jornada Validation Site (New Mexico). Most of the model predictions come within 1 SD of the mean field plant response; the timing of phenophases is simulated more accurately.

### INTRODUCTION

*Larrea tridentata* (DC) Cov. (creosotebush) is one of the most widespread and successful species of the warm desert regions of North America. It is the dominant evergreen perennial over most of its range, which in the United States includes the four major warm deserts: the Colorado of California; the Mohave of California, Nevada, Utah and Arizona; the Sonoran of Arizona; and the Chihuahuan of New Mexico, Texas and Arizona. Considerable variation in climate exists among these desert regions. This climatic variation results in distinct floras in these deserts, but *Larrea* has obtained dominance in many portions of each (Benson and Darrow 1944).

The ability of *Larrea* to dominate a wide variety of desert ecosystems has led to a great deal of investigation of its adaptation to desert conditions. Information from these investigations was reviewed and summarized by Barbour et al. (in press), but they did not attempt to integrate the information into a complete functional description of the autecology of the species. We have attempted such an integration by developing a heuristic model of primary production and carbon allocation (Cunningham and Reynolds 1976).

Mooney (1972) effectively pointed out the importance of understanding how plants gain and allocate their resources to evaluating and predicting their success in a given environment. He correctly emphasized that, although quantitative models of carbon gain and allocation would be invaluable to such an understanding, there is not yet sufficient information for the construction of such models. We feel that even though sufficient information is not available to construct models in accurate detail, preliminary attempts can help focus attention on the significant gaps in our knowledge and provide guides for future research. Carbon is a logical choice for investigation since it is so intimately tied to the procurement and allocation of energy, mineral nutrients and water. Also, the allocation of carbon within the plant can be evaluated by measurement of biomass increments, which makes the collection of data and the validation of predictions much simpler. Thus, we selected carbon gain and allocation as a means of assessing the role of the environment in determining resource allocation.

The *Larrea* primary production and carbon allocation model was developed to be a useful tool for examination of the growth patterns of *Larrea* under an array of

environmental conditions, and the structure of the model should be generalizable to other evergreen perennial desert shrubs. It should also help to elucidate the significant gaps in our knowledge of the biology of *Larrea*.

The model utilizes a systems approach in which movement of assimilate within the plant is in response to changes in source-sink strengths of leaves, stems, roots, early reproductive buds, maturing reproductive buds, flowers and fruits. Two distinct compartments are defined per organ or developmental stage to separate assimilate into a pool fraction (labile or translocatable) and a structural fraction (nonlabile). The changes in magnitude (within upper and lower limits) of a pool compartment during the course of a simulation (i.e., growth and development of the plant) are a function of the rates of maintenance respiration and growth as well as a priority scheme governing allocation of assimilates; the increases and decreases in dry weight of a structural compartment are a function of aging and the magnitude of its associated pool (which determines structural growth and physiological death).

In our original description of the model (Cunningham and Reynolds 1976) no attempt at validation using production and allocation data from the field was made. In an earlier study, designed to ascertain the extent of assimilate allocation to reproductive activity in *Larrea* as a function of season and availability of soil moisture (Cunningham et al. 1974), data on production and allocation were collected. The present report describes our attempts to use these data for validation and refinement of the model.

### METHODS

Data on reproductive and above-ground vegetative production of *Larrea* were collected during 1973 and 1974 on 16 study plots located adjacent to the Jornada Validation Site in south-central New Mexico. Fifteen of the plots were provided additional soil moisture during one or more 3-mo periods during 1973. A control plot received no soil moisture augmentation. A description of the study site, the experimental design, methods of soil moisture augmentation, methods of production data collection and analysis and techniques used for collection of environmental data have been detailed in an earlier report (Cunningham et al. 1974).

The model was used to simulate reproductive and above-ground vegetative production of a 600-g *Larrea* on each of the study plots for the period from February 15,

1973 (day 0), to November 15, 1974 (day 686). The outputs from these simulations are compared with the actual production values measured on the experimental plots. So that simulated values for the standard-size shrub could be compared with means and standard deviations for the five shrubs in each plot measured, both model predictions and validation data were converted to present change in leaf biomass and biomass of reproductive structures per unit biomass of leaf at each sample date:

$$\text{percent change} = (L_n - L_{n-1})/L_{n-1}$$

where

percent change = percent change in leaf biomass

$L_n$  = leaf biomass at time  $n$  (g dry wt)

$L_{n-1}$  = leaf biomass at time  $n-1$  (g dry wt)

### RESULTS

The results of the comparisons between model output and validation data for each of the experimental treatments lead to the same general conclusions. Therefore, only results from three representative simulations are presented here. One is for plot 16, which received no soil moisture augmentation (Figs. 1 and 2). Another is for plot 1, which had its soil water potential, down to a depth of 120 cm, brought to field capacity weekly from April 15, 1973, until April 15, 1974 (Figs. 3 and 4). The third is for plot 8, which had its soil water potential, down to a depth of 120 cm, brought to field capacity weekly from April 15 until July 15, 1973 (Figs. 5 and 6).

The model appears to be reasonably successful at predicting both the timing and extent of vegetative growth for the plants on plot 16. It does not, however, predict the slight and variable growth flush which some of the plants experienced in August 1973. Most of the model predictions do fall within 1 SD of the mean plant response. As with vegetative production, the model appears to accurately simulate the timing of reproductive activity. The extent of reproduction appears to be somewhat underestimated, however.

The timing of simulated vegetative production of plot 1 is relatively close to the actual growth response. As with plot 16, the model does not predict the slight vegetative production on some plants in late summer of 1973. The model predicts, instead, reproductive activity which was not observed in the field plants. For the spring and summer of 1974, the model overestimates vegetative growth and underestimates reproductive effort of plot 1 plants.

Model predictions appear to most closely simulate the validation data from plants on plot 8. As in the case of plot 1, which also received supplemental soil moisture between April 15 and July 15, 1973, the model does not predict the slight vegetative production in August 1973, but predicts a slight amount of reproduction that the plants did not experience. The model also overestimates vegetative and

underestimates reproductive growth during the spring and summer of 1974.

### DISCUSSION AND CONCLUSIONS

The model exhibits excellent behavior in terms of the timing and relative magnitudes of vegetative and reproductive growth over the entire range of soil moisture conditions imposed in the experimental manipulations. The major quantitative disagreement between model predictions and validation data is the frequent underestimation of reproductive allocation and the concomitant overestimation of vegetative allocation. This disagreement appears to be the result of the model allowing only one cohort of reproductive biomass to proceed through the development stages from early buds to mature fruits at any one time. This restriction results in fewer reproductive buds being initiated than would otherwise be the case. It also results in the unrealistic spikes in reproductive biomass evident in the simulations. We are presently attempting to correct this problem by modifying the model so that new reproductive buds can be initiated while other reproductive stages are still developing on the plant.

Another quantitative disagreement between model predictions and validation data is the apparent overestimation of total production during the late fall and winter for shrubs on plots with high soil water contents during that period. This overestimation is most likely a result of not allowing irradiance to limit net photosynthesis when soil water potentials are high. We are presently incorporating an irradiance dependence function into the net photosynthesis calculations which should correct this problem.

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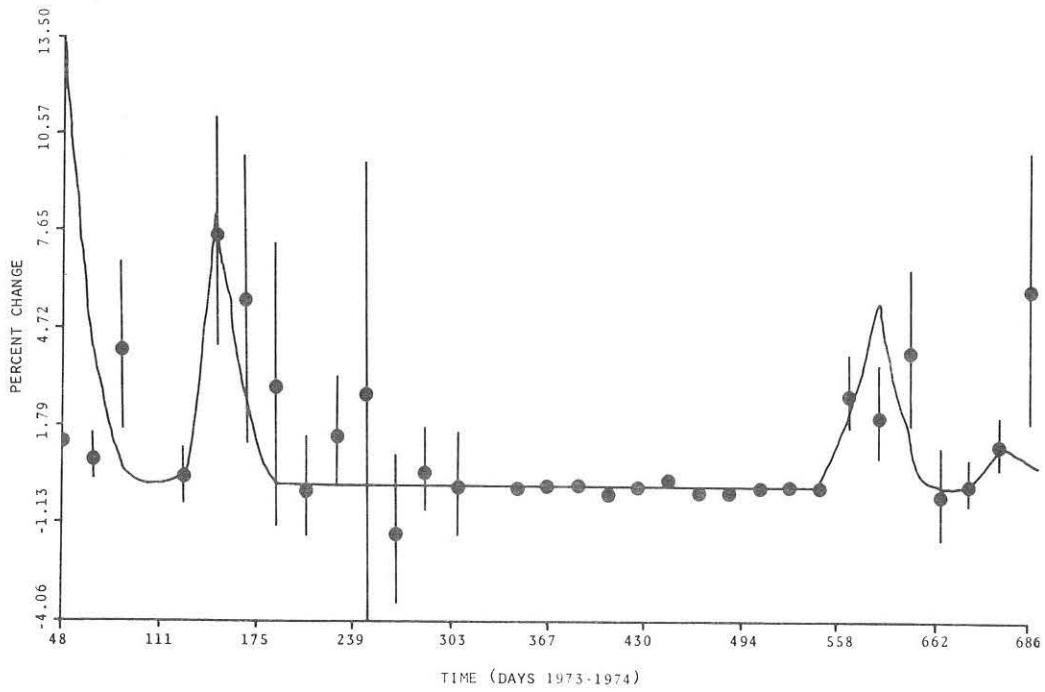


Figure 1. Percent change in leaf biomass during 1973 and 1974 for *Larrea* on experimental plot 16, which received no soil moisture augmentation. Simulation predictions are the continuous lines. Points are the means of the five validation plants and the bars represent  $\pm 1$  SD.

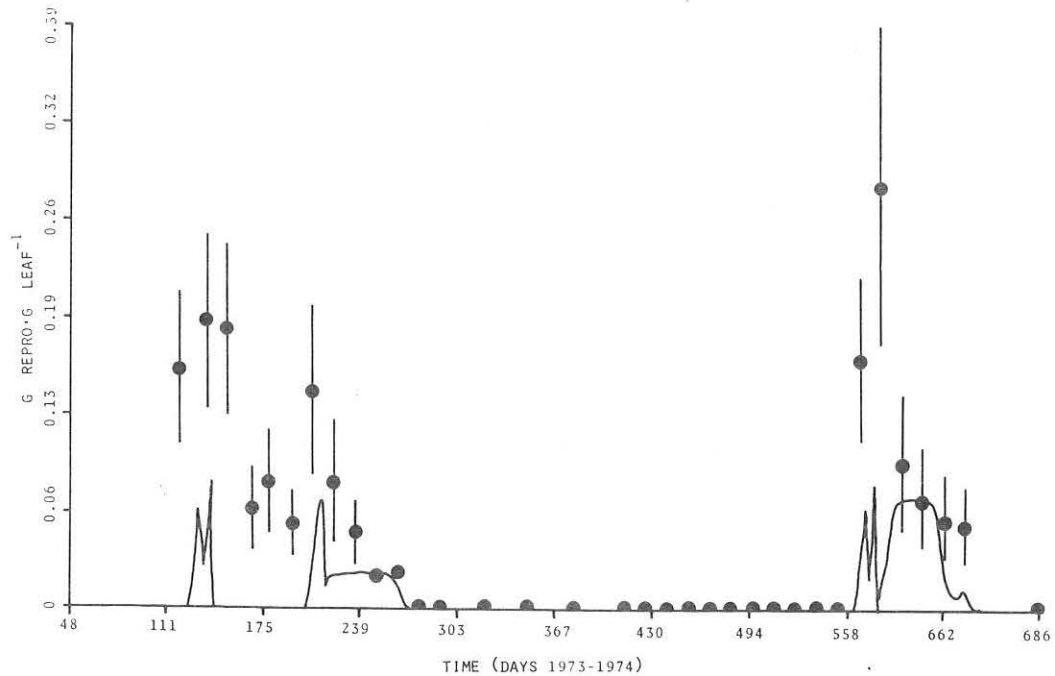
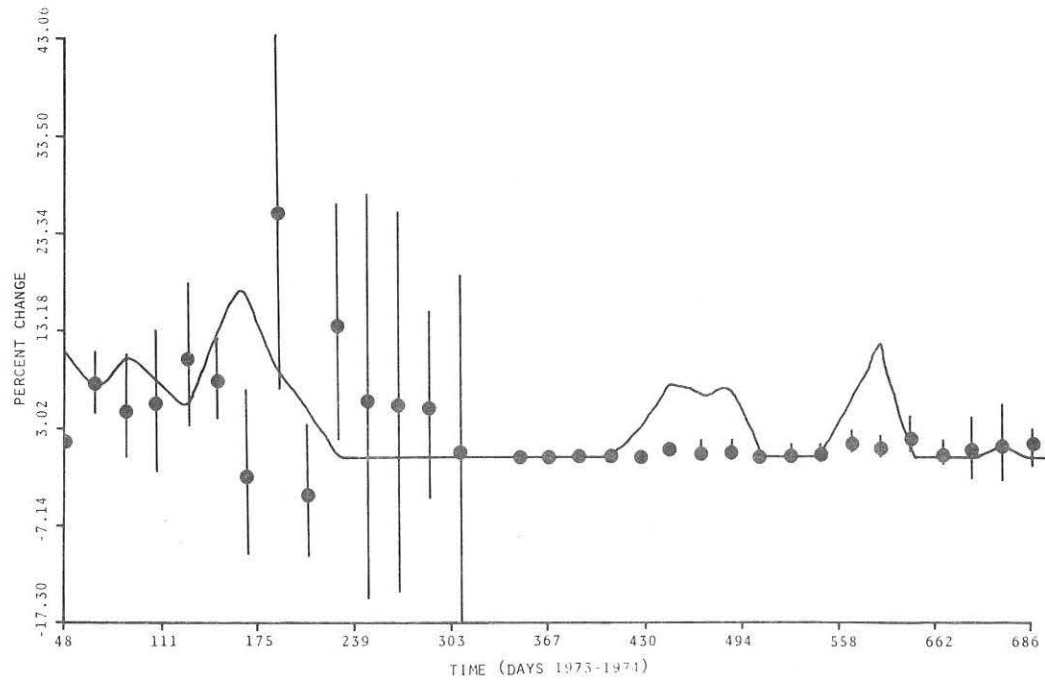
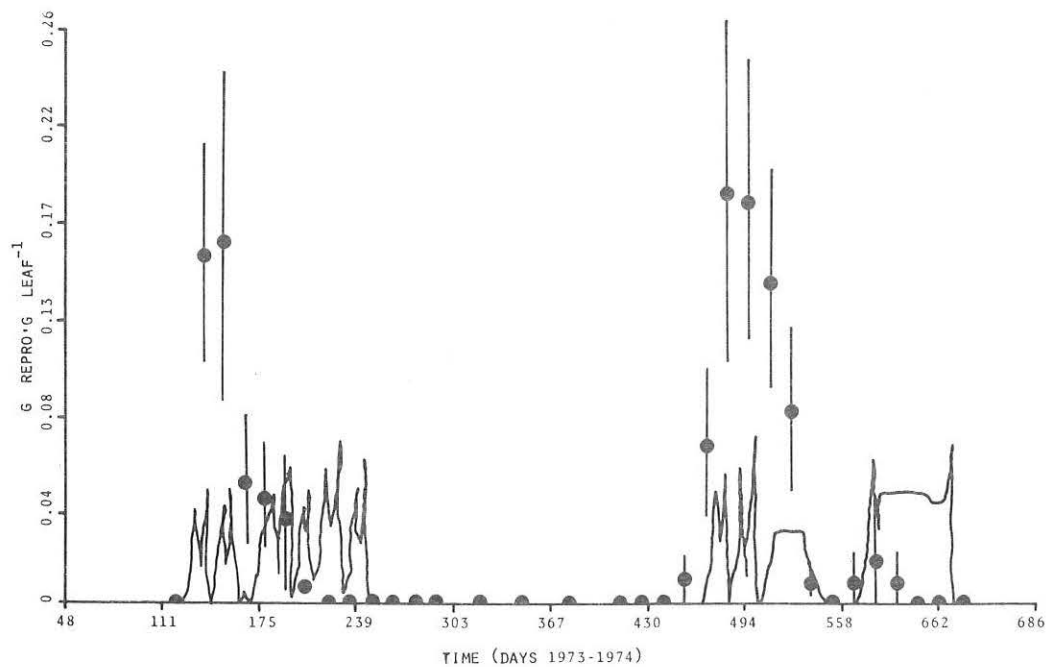


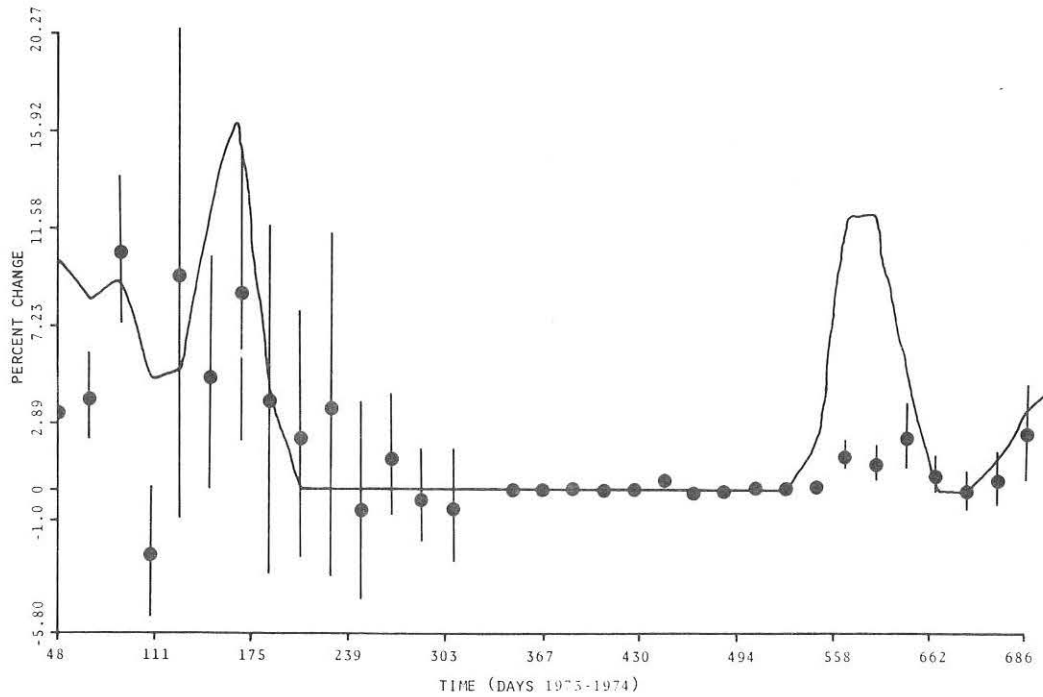
Figure 2. Grams of reproductive biomass per gram of leaf tissue during 1973 and 1974 for *Larrea* on experimental plot 16, which received no soil moisture augmentation. Simulation predictions are the continuous lines. Points are the means of the five validation plants and the bars represent  $\pm 1$  SD.



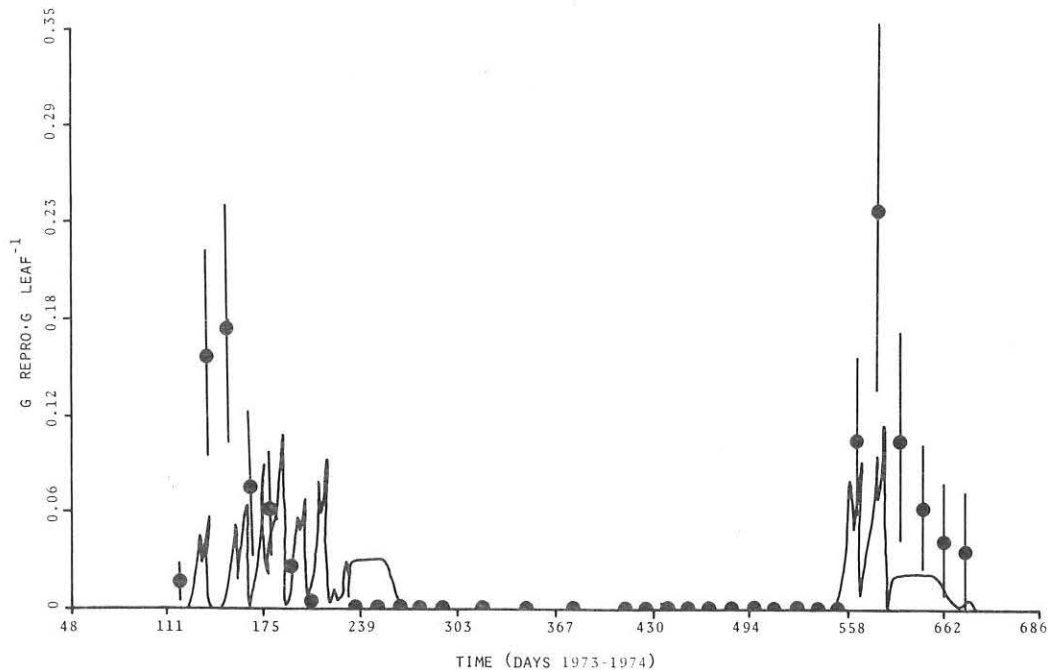
**Figure 3.** Percent change in leaf biomass during 1973 and 1974 for *Larrea* on experimental plot 1, which received soil moisture augmentation from April 15, 1973, until April 15, 1974. Simulation predictions are the continuous lines. Points are the means of the five validation plants and the bars represent  $\pm 1$  SD.



**Figure 4.** Grams of reproductive biomass per gram of leaf tissue during 1973 and 1974 for *Larrea* on experimental plot 1, which received soil moisture augmentation from April 15, 1973, until April 15, 1974. Simulation predictions are the continuous lines. Points are the means of the five validation plants and the bars represent  $\pm 1$  SD.



**Figure 5.** Percent change in leaf biomass during 1973 and 1974 for *Larrea* on experimental plot 8, which received soil moisture augmentation from April 15 until July 15, 1973. Simulation predictions are the continuous lines. Points are the means of the five validation plants and bars represent  $\pm 1$  SD.



**Figure 6.** Grams of reproductive biomass per gram of leaf tissue during 1973 and 1974 for *Larrea* on experimental plot 8, which received soil moisture augmentation from April 15 until July 15, 1973. Simulation predictions are the continuous lines. Points are the means of the five validation plants and the bars represent  $\pm 1$  SD.