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G. L. Cunningham

J. P. Syvertsen

J. M. Willson

T. Donahue

F. R. Balding

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1973 PROGRESS REPORT

PRIMARY PRODUCTION AND CARBON ALLOCATION
IN CREOSOTEBUSH

G. L. Cunningham, Project Leader
J. P. Syvertsen, J. M. Willson, T. Donahue and F. R. Balding
New Mexico State University

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Ecology Center, Utah State University, Logan, Utah 84322

ABSTRACT

The research reported here was undertaken to ascertain the effects of season and soil moisture on the allocation of carbon to reproduction in the creosote bush. Soil moisture augmentation experiments were conducted near the Jornada bajada site. These experiments provided data on extent of reproductive activity at various times of the year under different soil moisture regimes. Measurements of respiration rates were made in the laboratory to ascertain the amount of carbon lost through maintenance of reproductive structures. The results, as they have been analyzed to date, indicate that plants with less than maximal soil moisture divert a significantly greater amount of carbon and energy to reproduction.

INTRODUCTION

An analysis of the function of an ecosystem requires a quantitative evaluation of the acquisition and allocation of resources (energy and material) by each of the component populations of the system. The development and maintenance of the structure of the ecosystem requires energy. This energy is acquired by the system through the photosynthetic processes of the green plants which convert the energy of sunlight to stored chemical energy of carbon bonds. The energy is then available for growth, maintenance and reproduction of the green plants and for possible transfer to consumer populations within the system. The flux of energy through the ecosystem can thus be quantitatively evaluated by evaluating the flux of carbon through the system. It follows that the logical first step in evaluating the functioning of an ecosystem should be a quantitative assessment of the carbon acquisition and allocation of the primary producers as it is affected by the physical environment, competition and predation.

A quantitative assessment of the carbon balance of the primary producer populations is also important in developing an understanding of their survival, reproductive and competitive strategies (Mooney, 1972). The use of carbon balance information to answer ecological and life history questions not directly dealing with the trophic dynamics of ecosystems has only recently been attempted (Harper, 1967; Harper and Ogden, 1970; Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973). The importance of quantitative assessments of the carbon balances of plants in answering diverse ecological questions adds to the value of such assessments in ecosystem studies.

To date, most carbon balance studies have been limited to assessments of standing crop biomass in roots, shoots and reproductive structures at a single point in time. These studies, while extremely valuable, do not provide information on the dynamics of acquisition and allocation of carbon as it is affected by environmental parameters. In addition, little work has been done in assessing the loss of carbon through maintenance respiration of non-photosynthetic organs. In particular, few attempts have been made to quantitatively assess the total carbon balance of a single species even though the value of such an assessment is of unquestionable importance in understanding the ecology of the species (Mooney, 1972).

Our goal is to develop a quantitative description of the carbon balance of the creosote bush (*Larrea divaricata* Cav.). This quantitative description, as it is now envisioned,

will be in the form of a computer model that will describe the acquisition and allocation of carbon by *Larrea* as a function of its physical environment, competitors and predators. *Larrea* was selected because of its wide distribution and dominance in many of the desert areas of North America. An understanding of the functioning of *Larrea* in the desert environment should also provide some insight into the functioning of other species which utilize the evergreen perennial strategy. The quantity of information on *Larrea* in the literature also made it an ideal choice for carbon balance studies.

Our current working version of the *Larrea* carbon balance model will be described so that the reader can more clearly see how the research reported here will fit into the model. The model now makes calculations of biomass in grams dry weight, but this can be easily changed to grams of carbon or calories with the proper conversion factors. The time step of the model is one week but could be changed to any desired time interval. Initial values of root, leaf, stem, and total biomass in grams dry weight per square meter are entered along with appropriate climatological data for the period of interest.

The first step in the algorithm calculates the net daylight CO₂ accumulation. This is done by a limiting factors approach. It is assumed that either soil water potential, irradiance or air temperature is limiting the rate of net CO₂ accumulation. The maximum rate of net CO₂ accumulation that can occur, given the irradiance level, is obtained from a table relating net CO₂ exchange rate (in milligrams CO₂ per gram dry weight of leaf per hour) to irradiance (in watts per square meter) when soil water potential and temperature are optimal. Likewise, the maximum rate that can occur at the given level of soil water potential (in bars) is obtained from a table relating net CO₂ exchange rate to soil water potential at optimum irradiance and air temperature. The maximum rate of net CO₂ exchange that can occur at the given value of air temperature (in C) is obtained from a three-dimensional table which gives values of net CO₂ exchange as a function of present and acclimation temperatures when irradiance and soil water potential are optimal. The mean daytime temperature of the previous week is taken as the acclimation temperature. Two- and three-dimensional interpolation subroutines are used to calculate the irradiance, temperature and soil water potential limited rates if the given values lie between values in the tables. The minimum of these three values is assigned to the actual rate of net CO₂ accumulation. This rate is then multiplied by the number of daylight hours within the period of interest to obtain the net photosynthesis. Dark

respiration of the photosynthetic tissues is calculated in the same manner and subtracted from the photosynthesis value to give the value for CO₂ accumulation during the week.

Values for the net CO₂ exchange rate tables were obtained from the literature (Strain, 1969 and 1970; Strain and Chase, 1966; Ochel, Strain and Odening, 1972a). The Desert Biome process studies being conducted by Bamberg et al. (1973) should provide additional values and allow a comparison of Mohave and Sonoran desert populations. It is also hoped that additional Biome research will allow the calculation of net CO₂ exchange rates by methods having more biological reality, such as that used by Cunningham et al. (1974).

The weekly CO₂ accumulation is converted to biomass by the relationship: 0.00556 g dry weight per mg CO₂ (Larcher, 1969). The dry matter increment is then partitioned in fixed ratios between leaf, stem and root. This is certainly not realistic and can be improved with data such as that recently published by Oechel, Strain and Odening (1972b). Desert Biome process studies on translocation in *Larrea* should also allow this portion of the model to be made more realistic (Bamberg et al., 1973).

The biomass lost by death of roots, stems and leaves is subtracted from the weekly increment of biomass to give a new updated total. In the current version of the model these death rates are given as fixed constants, but could and should be made variables dependent on the environment.

This current version of the model greatly exaggerates the carbon accumulation of *Larrea* when compared with Desert Biome validation data (Whitford and Ludwig, 1972) and values in the literature (Chew and Chew, 1965; Burk and Dick-Peddie, 1973). This overestimate of carbon accumulation and allocation is obviously the result of failure to include several carbon loss and allocation processes:

1. allocation to reproductive activity
2. allocation to volatile and leachable compounds
3. maintenance respiration of nonphotosynthetic organs

OBJECTIVE

The objective of the research reported here was to ascertain for *Larrea divaricata* the extent of carbon allocation to reproductive activity as a function of season and availability of soil moisture.

METHODS

A field soil moisture augmentation experiment was conducted to ascertain the effects of season and soil moisture availability on the timing and extent of reproductive activity. The experiment consisted of 15 treatments and a control. The treatment plots were each given soil moisture augmentation during one or more three-month time periods (seasons). The control received no augmentation of soil

moisture. The treatments were randomly assigned to the plots as shown in Table 1.

The site for the field experiment was on the New Mexico State University College Ranch approximately 0.8 km southeast of the Desert Biome Jornada Validation Site. The site slopes slightly to the east and has a relatively uniform soil structure throughout. The perennial shrub vegetation is almost exclusively *Larrea divaricata*. A few *Prosopis glandulosa* and *Flourensia cernua* also occur on the site. The sixteen 4 x 7 m plots were established along the east side of a small north-south dirt road. This was necessary to facilitate water transport to the plots. The plots were located at least 10 m from the road and 10 m from each other. The plots were fenced to exclude jackrabbits (*Lepus californicus*) which prune *Larrea* stems. Four branches (one in each ordinal direction) on each of five *Larrea* shrubs in each of the 16 plots were randomly selected and tagged with colored yarn. The tagged branches served as the sample units for counts of reproductive structures. Reproductive structures were grouped into six age classes:

1. Early buds; stages from initial to beginning of the splitting of the floral sepals.
2. Mid buds; sepals partially split.
3. Late buds; yellow of corolla visible but still enfolded.
4. Flowers; corolla open and petals separate.
5. Immature fruits; petals withered or absent, ovary swollen to maximum size but still green.
6. Mature fruits; fruits brown.

Table 1. Schedule of soil moisture augmentation for study plots -- an X indicates that the soil moisture of the plot was brought to field capacity to a depth of 120 cm once a week during the indicated time intervals

Plot Number	Spring 15 April- 15 July	Summer 15 July- 15 October	Fall 15 October- 15 January	Winter 15 January- 15 April
1	X	X	X	X
2	X	X		X
3	X	X	X	
4	X	X		
5	X		X	
6	X			X
7	X		X	X
8	X			
9		X		X
10		X		
11		X	X	X
12		X	X	
13			X	X
14				X
15			X	
16				

Soil moisture was measured using two sets of three gypsum electrical resistance blocks (Balding and Cunningham, 1974) per plot. One set of blocks was located near the west (upslope) and one near the east (downslope) end of each plot. Blocks were placed at depths of 80, 40 and 10 cm. A calibration curve was constructed relating soil water content in $\text{cm}^3 \cdot \text{cm}^{-3}$ of soil to electrical resistance of the blocks. This was done by obtaining resistance measurements and water content measurements of a known volume of soil as it dried. Soil from the study site was used so that the resistance values of the blocks could be used to calculate the amount of water required per plot to bring the soil water content to field capacity down to a depth of 120 cm. This volume was assumed to include the entire root zone of *Larrea* as the petro-calcic layer generally occurred at that depth.

The gypsum blocks were read each week and the calculated amount of water was applied to the eight plots scheduled for moisture augmentation (Table 1; DSCODE A3UCG04). Water was transported to the site in a 2,000 gallon water truck and applied to the plots with a garden hose attached to a totalizing flow meter.

The number of each age stage of reproductive structure was counted on all tagged branches every two weeks during the growing season and every four weeks during the remainder of the year. Measurements were begun in February, 1973, and will be continued through June, 1974 (A3UCG02).

Respiration rates of the reproductive structures were measured in the laboratory using a Gilson differential respirometer. Branches bearing the reproductive structures to be measured were harvested in the field. The cut ends were submerged and re-cut under water and transported immediately to the laboratory. The reproductive structures were removed from the branches and placed in the respirometer flasks along with a few drops of distilled water. Three to five structures were used in each flask. A diethanolamine buffer was used to hold CO_2 partial pressure constant in the flasks and respiration was measured in μl of O_2 consumed per min (A3UCG03). Respiration rates were measured at temperatures of 10, 25 and 40 C for one-half hr and volume readings were taken every ten min. Each set of measurements was replicated within 16 to 19 flasks. This gave from 48 to 57 replications of each measurement. At the conclusion of the measurements fresh and dry weights of the reproductive structures were recorded. Carbon loss was calculated as mg carbon per gram dry weight of tissue per hour.

RESULTS AND DISCUSSION

Because of time limitations on the analysis of the data, results will only be presented through the end of October, 1973. As can be seen from the data this includes the major portion of the year in which carbon was allocated to reproductive growth. However, data not included in this report do indicate some reproductive activity after the end

of October. In addition, comparisons will only be made between plots which received supplemental spring water (plots 1-8) and those that did not (plots 9-16).

The mean number of reproductive structures in each of the age categories (stages) per meter of branch length are presented for each of the study plots in Tables 2.01-2.16 (A3UCG02). Only structures produced during the period of observations beginning February 17, 1973, were included in the calculation of these mean values. A regression analysis of variance (Sokal and Rohlf, 1969) indicated that at the 0.05 level of probability, differences in the means exist between dates and plots as well as among plants within plots.

All but two of the plots had branches which were producing buds by April 28, 1973. All plots had branches producing buds by May 17, 1973. There appears to be no difference in the date of initial allocation of carbon to reproduction as a function of soil moisture. It appears that plots which received supplemental soil moisture in the spring did not have branches continuing to produce new buds as late in the year as plots which did not receive supplemental spring moisture. Plants on plots 1-8 did not produce new buds after July 25, 1973. Some plants on plots

Table 2.01-2.16. Mean number of each reproductive stage counted on each of the sample dates (number $\cdot \text{m}^{-1}$ of branch length). Only reproductive structures produced during 1973 were included in the mean calculations

2.01. Plot number 1						
Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	0	0	0	0	0	0
5-17	90	9	3	2	0	0
5-31	20	6	1	30	50	0
6-16	1	0	1	1	50	0
6-28	0	0	0	0	40	0
7-12	0	0	0	0	40	1
7-25	0	0	0	0	7	9
8-9	0	0	0	0	0	9
8-24	0	0	0	0	0	5
9-7	0	0	0	0	0	0
9-21	0	0	0	0	0	0
10-5	0	0	0	0	0	0
10-19	0	0	0	0	0	0

2.02. Plot number 2						
Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	20	0	0	0	0	0
5-17	10	20	6	4	0	0
5-31	20	10	3	50	40	0
6-16	3	2	1	3	70	0
6-28	3	1	0	0	40	0
7-12	6	0	0	1	30	0
7-25	1	2	0	0	1	10
8-9	0	0	0	1	1	8
8-24	0	0	0	0	2	4
9-7	0	0	0	0	0	2
9-21	0	0	0	0	0	0
10-5	0	0	0	0	0	0
10-19	0	0	0	0	0	0

Table 2 (continued)

2.03. Plot number 3

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	50	0	0	0	0	0
5-17	80	10	1	0	0	0
5-31	4	20	5	40	30	0
6-16	0	0	0	0	60	0
6-28	0	0	0	0	20	0
7-12	0	0	0	0	10	2
7-25	0	0	0	0	3	6
8-9	0	0	0	0	0	3
8-24	0	0	0	0	0	2
9-7	0	0	0	0	0	1
9-21	0	0	0	0	0	0
10-5	0	0	0	0	0	0
10-19	0	0	0	0	0	0

2.07. Plot number 7

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	20	0	0	0	0	0
5-17	120	10	1	2	0	0
5-31	9	20	10	20	60	0
6-16	1	0	0	1	60	0
6-28	0	1	0	0	40	0
7-12	0	0	0	0	30	0
7-25	0	0	0	0	9	10
8-9	0	0	0	0	4	20
8-24	0	0	0	0	0	10
9-7	0	0	0	0	0	5
9-21	0	0	0	0	0	5
10-5	0	0	0	0	0	5
10-19	0	0	0	0	0	5

2.04. Plot number 4

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	20	0	0	0	0	0
5-17	70	3	0	0	0	0
5-31	10	20	4	20	30	0
6-16	0	0	0	0	30	0
6-28	0	0	0	0	20	0
7-12	0	0	0	0	20	0
7-25	0	0	0	0	7	6
8-9	0	0	0	0	2	5
8-24	0	0	0	0	0	5
9-7	0	0	0	0	0	2
9-21	0	0	0	0	0	1
10-5	0	0	0	0	0	0
10-19	0	0	0	0	0	0

2.08. Plot number 8

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	10	0	0	0	0	0
5-17	90	10	0	0	0	0
5-31	4	20	10	20	30	0
6-16	2	2	0	2	80	0
6-28	3	0	0	0	40	0
7-12	0	0	0	0	30	0
7-25	0	0	0	0	5	10
8-9	0	0	0	0	5	7
8-24	0	0	0	0	0	6
9-7	0	0	0	0	0	3
9-21	0	0	0	0	0	3
10-5	0	0	0	0	0	1
10-19	0	0	0	0	0	1

2.05. Plot number 5

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	0	0	0	0	0	0
5-17	70	8	3	0	0	0
5-31	10	10	6	20	20	0
6-16	1	0	1	1	30	0
6-28	1	0	1	1	25	0
7-12	1	0	0	1	20	0
7-25	2	0	0	0	5	8
8-9	0	0	0	0	1	10
8-24	0	0	0	0	0	5
9-7	0	0	0	0	0	4
9-21	0	0	0	0	0	2
10-5	0	0	0	0	0	0
10-19	0	0	0	0	0	0

2.09. Plot number 9

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	50	0	0	0	0	0
5-17	80	20	0	1	0	0
5-31	9	20	6	20	40	0
6-16	1	0	0	0	70	0
6-28	0	0	0	0	60	0
7-12	0	0	0	0	40	0
7-25	0	0	0	0	20	10
8-9	0	0	0	0	1	20
8-24	0	0	0	0	2	7
9-7	0	0	0	0	0	10
9-21	0	0	0	0	0	4
10-5	0	0	0	0	0	4
10-19	0	0	0	0	0	4

2.06. Plot number 6

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	10	0	0	0	0	0
5-17	90	6	0	0	0	0
5-31	2	30	7	20	30	0
6-16	1	0	0	1	40	0
6-28	0	0	0	0	40	0
7-12	0	0	0	0	20	1
7-25	0	0	0	0	7	20
8-9	0	0	0	0	1	20
8-24	0	0	0	0	0	10
9-7	0	0	0	0	0	10
9-21	0	0	0	0	0	7
10-5	0	0	0	0	0	2
10-19	0	0	0	0	0	5

2.10. Plot number 10

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	40	0	0	0	0	0
5-17	120	20	2	6	0	0
5-31	10	20	3	30	80	0
6-16	0	1	0	0	80	0
6-28	0	0	0	0	70	0
7-12	0	0	0	0	40	1
7-25	20	0	0	0	10	20
8-9	1	5	7	7	10	20
8-24	1	0	0	0	30	20
9-7	0	0	0	0	20	30
9-21	0	0	0	0	20	10
10-5	0	0	0	0	10	6
10-19	0	0	0	0	0	20

Table 2 (continued)

2.11. Plot number 11

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	70	0	0	0	0	0
5-17	70	30	4	8	0	0
5-31	10	20	6	20	60	0
6-16	4	2	1	3	80	0
6-28	9	10	0	0	70	0
7-12	0	0	0	0	40	0
7-25	70	6	0	0	30	2
8-9	3	5	10	20	50	10
8-24	0	0	0	0	50	9
9-7	0	0	0	0	40	40
9-21	0	0	0	0	30	6
10-5	1	0	0	0	20	20
10-19	0	0	0	0	0	20

2.12. Plot number 12

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	60	0	0	0	0	0
5-17	70	20	4	7	0	0
5-31	2	30	2	10	70	0
6-16	0	2	1	1	80	0
6-28	1	0	0	0	70	0
7-12	0	0	0	0	40	10
7-25	1	0	0	0	10	10
8-9	0	0	0	0	3	10
8-24	0	0	0	0	1	7
9-7	0	0	0	0	0	1
9-21	0	0	0	0	0	1
10-5	0	0	0	0	0	0
10-19	0	0	0	0	0	0

2.13. Plot number 13

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	40	0	0	0	0	0
5-17	10	6	0	0	0	0
5-31	1	40	4	20	50	0
6-16	4	0	1	2	90	0
6-28	1	0	0	0	90	0
7-12	0	0	0	0	80	0
7-25	10	0	0	0	50	30
8-9	2	0	2	4	20	9
8-24	0	0	0	0	10	10
9-7	0	0	0	0	0	10
9-21	0	0	0	0	0	5
10-5	0	0	0	0	0	3
10-19	0	0	0	0	0	7

2.14. Plot number 14

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	40	0	0	0	0	0
5-17	70	9	2	6	0	0
5-31	5	30	4	20	50	0
6-16	1	1	4	1	70	0
6-28	0	5	0	1	60	0
7-12	0	0	0	0	50	0
7-25	8	0	0	0	30	4
8-9	1	6	1	8	30	2
8-24	0	0	0	0	20	20
9-7	0	0	0	0	10	9
9-21	0	0	0	0	20	7
10-5	0	0	0	0	0	20
10-19	0	0	0	0	0	20

2.15. Plot number 15

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	70	0	0	0	0	0
5-17	60	10	2	6	0	0
5-31	0	40	4	10	50	0
6-16	2	1	1	1	50	0
6-28	5	7	2	1	50	0
7-12	0	0	0	0	30	3
7-25	20	0	0	0	20	5
8-9	0	1	0	5	20	8
8-24	0	0	0	0	10	10
9-7	0	0	0	0	10	9
9-21	0	0	0	0	4	10
10-5	0	0	0	0	8	6
10-19	0	0	0	0	0	7

2.16. Plot number 16

Date	Stage					
	1	2	3	4	5	6
2-17	0	0	0	0	0	0
4-28	120	0	0	0	0	0
5-17	80	20	6	10	0	0
5-31	0	30	8	10	80	0
6-16	1	1	1	1	60	0
6-28	10	5	0	2	50	0
7-12	10	0	0	0	50	2
7-25	70	10	3	0	20	5
8-9	1	1	2	10	50	5
8-24	0	0	0	0	60	7
9-7	0	0	0	0	20	30
9-21	0	0	0	0	20	8
10-5	0	0	0	0	2	10
10-19	0	0	0	0	0	10

9-16 were still producing a few buds as late as August 24, 1973. This appears to be the result of all but one of the unwatered plots having branches which exhibited two, rather than one, periods of reproductive activity. In general during this second period, plants did not produce as many reproductive structures per meter of branch length as they did during the first period.

The total amount of carbon allocated to reproduction is the sum of the amount of carbon employed in structure and storage in the reproductive structures and the amount lost by respiration of the structures. Since it is obvious from the data that not all new buds produced ultimately become mature fruits, it was necessary to make some generalizations concerning mortality and carbon loss in order to calculate values for the amount of carbon used in structural development and storage:

1. Buds remain as stage 1 less than two weeks. This means each stage-1 bud is counted only once and it is possible that some of the stage-1 buds may be missed.
2. Stage-1 buds have a high mortality compared to other stages; therefore, it can be assumed that once a bud reaches stage 2 it will produce a flower (stage 4) and a mature fruit (stage 6).
3. All carbon in flowers (stage 4) is lost. No carbon is translocated to the developing fruit from the flower and when the flower parts are dropped that carbon is lost from the plant.
4. The immature fruits (stage 5) are very persistent and are probably counted on more than one sampling date.

The data and our observations indicate that these generalizations are true for the plants on and near the study plots. A minimal value for the amount of carbon allocated to structural and storage functions in reproduction was thus calculated:

$$C_s = [(N_1 - N_5) \cdot C_1] + (N_5 \cdot C_4) + (N_5 \cdot C_6)$$

where

C_s = amount of carbon allocated to structure and storage in reproductive parts during the year (g carbon · m⁻¹ of branch length · year⁻¹);

N_1 = minimum number of stage 1 (new buds) produced during the year (m⁻¹ branch length · year⁻¹). This number was obtained by summing the mean number of stage-1 buds observed per meter of branch length on each sample date. If this value was exceeded by the total number of all stages observed on any one date plus the number of stage-1 buds observed after that date then this larger value was used;

N_5 = minimum number of stage 5 (immature fruits) produced during the year (m⁻¹ · year⁻¹). This value was obtained by taking the maximum mean number observed on any one date. If a second period of reproductive activity produced an increase in immature fruits later in the season this was taken into account by adding the difference between the second maximum and the previous minimum to the total;

C_1 = amount of carbon per stage 1 (new bud) structure (g)

C_4 = amount of carbon per stage 4 (flower) structure (g)

C_6 = amount of carbon per stage 6 (mature fruit) structure (g)

The amounts of carbon per structure in each of the stages were calculated using the mean dry weight per structure (A3UCG03) and assuming all carbon was in the form of carbohydrate (C₆H₁₂O₆). The total amounts of carbon allocated to structure and storage of reproductive structures during the 1973 growing season are given for each of the study plots in Table 3. The mean value for the plots which did not receive supplemental spring moisture was 1.955 g carbon · m⁻¹ of branch length · year⁻¹ for those plots which did receive soil moisture augmentation during the spring. The means are significantly different at the 0.005 level of probability as shown by a "t" statistic of 3.55 (Freund et al., 1960).

The effects of temperature on the respiration rates of the reproductive structures of *Larrea* for stages 1-5 are shown in Figure 1 (A3UCG03). No detectable oxygen consumption was observed in the mature fruits (stage 6). An analysis of variance indicated that significant differences existed between mean rates for the three temperatures and between the mean rates at each temperature for the five stages at the 0.001 level of probability. Respiration rates interpolated from these graphs were used to calculate the quantities of carbon lost through respiration for one week before and after the dates on which reproductive structures were counted (Tables 4.01-4.16):

$$C_{ri} = N_i \cdot W_i \cdot 336 \text{ h} \cdot 2 \text{ week}^{-1}$$

where

C_{ri} = amount of carbon lost by respiration of the i'th stage (mg carbon · m⁻¹ of branch length · 2 week⁻¹);

N_i = number of structures in the i'th stage on the measurement date (m⁻¹ of branch length);

W_i = mean dry weight of the i'th stage (g)

R_i = respiration rate of the i'th stage (mg carbon · g⁻¹ dry weight · h⁻¹).

The respiration rates used were determined for the mean hourly temperature for the month in 1972 (Whitford and Ludwig, 1972). Also given in Tables 4.01-4.16 are the total respirational carbon losses for all stages for each two-week period. These values are probably minimal since the use of mean temperatures will underestimate total respiration due to the logarithmic increase of respiration rate with temperature.

The total amount of carbon allocated to maintenance respiration per meter of branch length is given for each of the study plots in Table 3. The mean value for plots which received supplemental water during the spring (1-8) was 9.100 g · m⁻¹ of branch length. The mean value for the unwatered plots (9-16) was 14.680 g · m⁻¹ of branch length. A t test indicated that these means are significantly different at the 0.005 level of probability.

The total allocation of carbon to reproduction for the year was obtained by adding the carbon used in structure and storage and the carbon lost through respiration of the reproductive structures (Table 3). The mean total carbon allocation for the plots which received spring soil moisture augmentation (1-8) was 10.239 g · m⁻¹ of branch length. A higher mean of 16.624 g · m⁻¹ of branch was obtained by the unwatered plots (9-16). Again, the means are significantly different at the 0.005 level of probability as indicated by a t test.

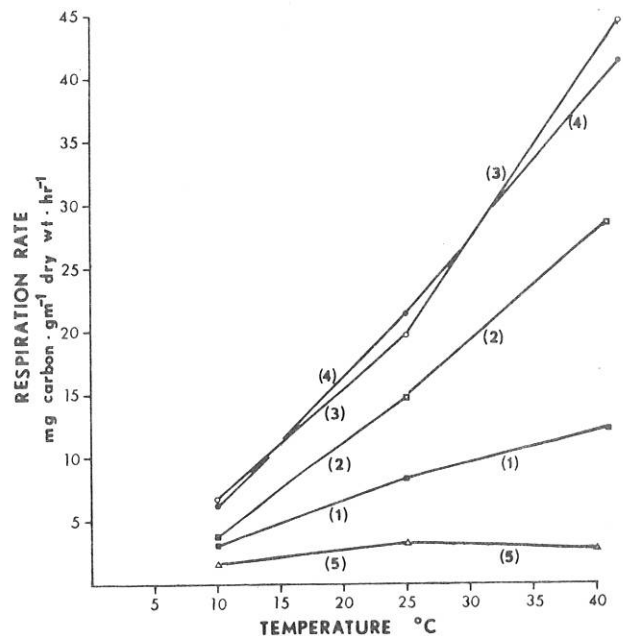


Figure 1. Respiration rate of each of the five stages of reproductive structures of *Larrea divaricata* as a function of temperature.

Table 3. Carbon allocated to structure and storage in reproductive structures, respiration of reproductive structures and total carbon allocated to reproduction during the period of February 2, 1973, to October 19, 1973, for each of the study plots (g carbon · m⁻¹ of branch length)

Plot number	Structure and Storage	Respiration	Total
1	1.147	8.806	9.953
2	1.563	12.953	14.516
3	1.378	9.871	11.249
4	0.763	6.525	7.288
5	0.754	7.175	7.929
6	0.949	8.138	9.087
7	1.414	9.649	11.063
8	1.682	9.147	10.829
9	1.583	9.860	11.443
10	2.227	16.044	18.271
11	2.328	22.233	24.561
12	1.738	10.809	12.547
13	1.913	12.345	14.258
14	1.718	14.421	16.139
15	1.322	12.299	13.621
16	2.811	19.344	22.155

Table 4.01-4.16. Carbon lost in respiration by each stage and total for all stages (mg carbon · m⁻¹ of branch length · 2 weeks⁻¹). Values were calculated from mean hourly temperature for the month of observation and temperature relationship of respiration rates given in Figure 1

4.01. Plot number 1

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	0	0	0	0	0	0	0
5-17	1185	504	273	215	0	0	2177
5-31	263	336	94	3283	579	0	4555
6-16	16	0	123	143	661	0	943
6-28	0	0	0	0	529	0	529
7-12	0	0	0	0	512	0	512
7-25	0	0	0	0	90	0	90
8-9	0	0	0	0	0	0	0
8-24	0	0	0	0	0	0	0
9-7	0	0	0	0	0	0	0
9-21	0	0	0	0	0	0	0
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

4.02. Plot number 2

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	218	0	0	0	0	0	218
5-17	132	1138	562	438	0	0	2270
5-31	263	569	281	5472	463	0	7048
6-16	49	152	123	571	926	0	1821
6-28	49	76	0	0	529	0	578
7-12	104	0	0	157	384	0	645
7-25	17	169	0	0	13	0	199
8-9	0	0	0	135	13	0	148
8-24	0	0	0	0	26	0	26
9-7	0	0	0	0	0	0	0
9-21	0	0	0	0	0	0	0
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

4.03. Plot number 3

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	546	0	0	0	0	0	546
5-17	1054	569	94	0	0	0	1717
5-31	53	1138	469	4378	347	0	6385
6-16	0	0	0	0	793	0	793
6-28	0	0	0	0	264	0	264
7-12	0	0	0	0	128	0	128
7-25	0	0	0	0	38	0	38
8-9	0	0	0	0	0	0	0
8-24	0	0	0	0	0	0	0
9-7	0	0	0	0	0	0	0
9-21	0	0	0	0	0	0	0
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

4.04. Plot number 4

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	218	0	0	0	0	0	218
5-17	922	171	0	0	0	0	1093
5-31	132	1138	375	2189	347	0	4181
6-16	0	0	0	0	397	0	397
6-28	0	0	0	0	264	0	264
7-12	0	0	0	0	256	0	256
7-25	0	0	0	0	90	0	90
8-9	0	0	0	0	26	0	26
8-24	0	0	0	0	0	0	0
9-7	0	0	0	0	0	0	0
9-21	0	0	0	0	0	0	0
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

4.05. Plot number 5

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	0	0	0	0	0	0	0
5-17	922	455	281	0	0	0	1658
5-31	132	569	562	2189	231	0	3683
6-16	16	0	123	143	397	0	679
6-28	16	0	123	143	331	0	613
7-12	17	0	0	157	256	0	430
7-25	35	0	0	0	64	0	99
8-9	0	0	0	0	13	0	13
8-24	0	0	0	0	0	0	0
9-7	0	0	0	0	0	0	0
9-21	0	0	0	0	0	0	0
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

4.06. Plot number 6

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	109	0	0	0	0	0	109
5-17	1185	342	0	0	0	0	1527
5-31	26	1708	656	2189	347	0	4926
6-16	16	0	0	143	529	0	688
6-28	0	0	0	0	529	0	529
7-12	0	0	0	0	256	0	256
7-25	0	0	0	0	90	0	90
8-9	0	0	0	0	13	0	13
8-24	0	0	0	0	0	0	0
9-7	0	0	0	0	0	0	0
9-21	0	0	0	0	0	0	0
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

Table 4 (continued)

4.07. Plot number 7

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	218	0	0	0	0	0	218
5-17	1581	569	94	219	0	0	2463
5-31	119	1138	937	2189	694	0	5077
6-16	16	0	0	143	793	0	952
6-28	0	76	0	0	529	0	605
7-12	0	0	0	0	384	0	384
7-25	0	0	0	0	115	0	115
8-9	0	0	0	0	53	0	53
8-24	0	0	0	0	0	0	0
9-7	0	0	0	0	0	0	0
9-21	0	0	0	0	0	0	0
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

4.11. Plot number 11

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	764	0	0	0	0	0	764
5-17	922	1708	375	876	0	0	3881
5-31	132	1138	562	2189	694	0	4715
6-16	65	152	123	428	1058	0	1826
6-28	147	762	0	0	926	0	1835
7-12	0	0	0	0	512	0	512
7-25	1212	508	0	0	384	0	2104
8-9	47	360	1162	2705	661	0	4935
8-24	0	0	0	0	661	0	661
9-7	0	0	0	0	463	0	463
9-21	0	0	0	0	347	0	347
10-5	0	0	0	0	190	0	190
10-19	0	0	0	0	0	0	0

4.08. Plot number 8

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	109	0	0	0	0	0	109
5-17	1185	569	0	0	0	0	1754
5-31	53	1138	937	2189	347	0	4664
6-16	33	152	0	285	1058	0	1528
6-28	49	0	0	0	529	0	578
7-12	0	0	0	0	384	0	384
7-25	0	0	0	0	64	0	64
8-9	0	0	0	0	66	0	66
8-24	0	0	0	0	0	0	0
9-7	0	0	0	0	0	0	0
9-21	0	0	0	0	0	0	0
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

4.12. Plot number 12

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	655	0	0	0	0	0	655
5-17	922	1138	375	766	0	0	3201
5-31	26	1708	187	1094	810	0	3825
6-16	0	152	123	143	1058	0	1476
6-28	16	0	0	0	926	0	942
7-12	0	0	0	0	512	0	512
7-25	17	0	0	0	128	0	145
8-9	0	0	0	0	40	0	40
8-24	0	0	0	0	13	0	13
9-7	0	0	0	0	0	0	0
9-21	0	0	0	0	0	0	0
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

4.09. Plot number 9

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	546	0	0	0	0	0	546
5-17	1054	1138	0	109	0	0	2301
5-31	119	1138	562	2189	463	0	4471
6-16	16	0	0	0	926	0	942
6-28	0	0	0	0	793	0	793
7-12	0	0	0	0	512	0	512
7-25	0	0	0	0	256	0	256
8-9	0	0	0	0	13	0	13
8-24	0	0	0	0	26	0	26
9-7	0	0	0	0	0	0	0
9-21	0	0	0	0	0	0	0
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

4.13. Plot number 13

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	437	0	0	0	0	0	437
5-17	132	342	0	0	0	0	474
5-31	13	2277	375	2189	579	0	5433
6-16	65	0	123	285	1190	0	1663
6-28	18	0	0	0	1190	0	1298
7-12	0	0	0	0	1025	0	1025
7-25	173	0	0	0	641	0	814
8-9	32	0	232	541	264	0	1069
8-24	0	0	0	0	132	0	132
9-7	0	0	0	0	0	0	0
9-21	0	0	0	0	0	0	0
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

4.10. Plot number 10

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	437	0	0	0	0	0	437
5-17	1581	1138	187	657	0	0	3563
5-31	132	1138	281	3283	926	0	5760
6-16	0	76	0	0	1058	0	1134
6-28	0	0	0	0	926	0	926
7-12	0	0	0	0	512	0	512
7-25	346	0	0	0	128	0	474
8-9	16	360	813	947	132	0	2268
8-24	16	0	0	0	397	0	413
9-7	0	0	0	0	231	0	231
9-21	0	0	0	0	231	0	231
10-5	0	0	0	0	95	0	95
10-19	0	0	0	0	0	0	0

4.14. Plot number 14

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	437	0	0	0	0	0	437
5-17	922	512	187	657	0	0	2278
5-31	66	1708	375	2189	579	0	4917
6-16	16	76	494	143	926	0	1655
6-28	0	381	0	143	793	0	1317
7-12	0	0	0	0	641	0	641
7-25	138	0	0	0	384	0	522
8-9	16	432	116	1082	397	0	2043
8-24	0	0	0	0	264	0	264
9-7	0	0	0	0	116	0	116
9-21	0	0	0	0	231	0	231
10-5	0	0	0	0	0	0	0
10-19	0	0	0	0	0	0	0

Table 4 (continued)

4.15. Plot number 15

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	764	0	0	0	0	0	764
5-17	790	569	187	657	0	0	2203
5-31	0	2277	375	1094	579	0	4325
6-16	33	76	94	109	661	0	973
6-28	82	533	247	143	661	0	1666
7-12	0	0	0	0	384	0	384
7-25	346	0	0	0	256	0	602
8-9	0	72	0	676	264	0	1012
8-24	0	0	0	0	132	0	132
9-7	0	0	0	0	116	0	116
9-21	0	0	0	0	46	0	46
10-5	0	0	0	0	76	0	76
10-19	0	0	0	0	0	0	0

4.16. Plot number 16

Date	Stage						Total
	1	2	3	4	5	6	
2-17	0	0	0	0	0	0	0
4-28	1310	0	0	0	0	0	1310
5-17	1054	1138	562	1094	0	0	3848
5-31	0	1708	750	1094	926	0	4478
6-16	16	76	123	143	694	0	1052
6-28	164	381	0	285	661	0	1491
7-12	173	0	0	0	641	0	814
7-25	1212	847	428	0	256	0	2743
8-9	16	72	232	1353	661	0	2334
8-24	0	0	0	0	793	0	793
9-7	0	0	0	0	231	0	231
9-21	0	0	0	0	231	0	231
10-5	0	0	0	0	19	0	19
10-19	0	0	0	0	0	0	0

CONCLUSION

The results of this study, as they have been analyzed to date, clearly indicate that increased available soil moisture during the spring results in a decrease in the total amount of carbon allocated to reproduction by *Larrea* shrubs. The capacity to divert a greater amount of its resources to reproduction when conditions are less favorable, i.e. less soil moisture, may provide a mechanism that enhances the survival of the population in the desert environment. This is an interesting possibility which we should be able to address in more detail when the information reported here has been more extensively analyzed and incorporated into the *Larrea* carbon balance model. The data will be used in the model to calculate the total carbon allocated to reproduction using the criteria of season and either soil water potential or precipitation. The algorithm for the calculation will follow essentially the method of calculation used in the report.

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