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PRIMARY PRODUCTION AND CARBON ALLOCATION IN CREOSOTEBUSH

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ABSTRACT

This is not a report of completed research but a statement of progress to date in the development of a primary production and carbon allocation model for creosotebush (*Larrea tridentata*). A brief description of the model is given. Progress in the analysis of validation data from field soil moisture augmentation experiments is reported. Progress in measurements of respiration rates of nonphotosynthetic tissues and assessments of mobile carbohydrate pool sizes are also reported.

INTRODUCTION

During 1974 we have continued our work toward the development of a primary production and carbon allocation model for creosotebush (*Larrea tridentata* D.C.). The need for such a model in the analysis of desert ecosystems has been discussed in a previous report (Cunningham et al. 1974) and will not be repeated here. The overall structure of

the model has been modified considerably during the past year and this new structure has dictated some changes in our research efforts. A paradigm of the current working version of the model is presented in Figure 1 so that the reader can see how data presented in this report will be incorporated. A detailed description of the model will be included in a later report.
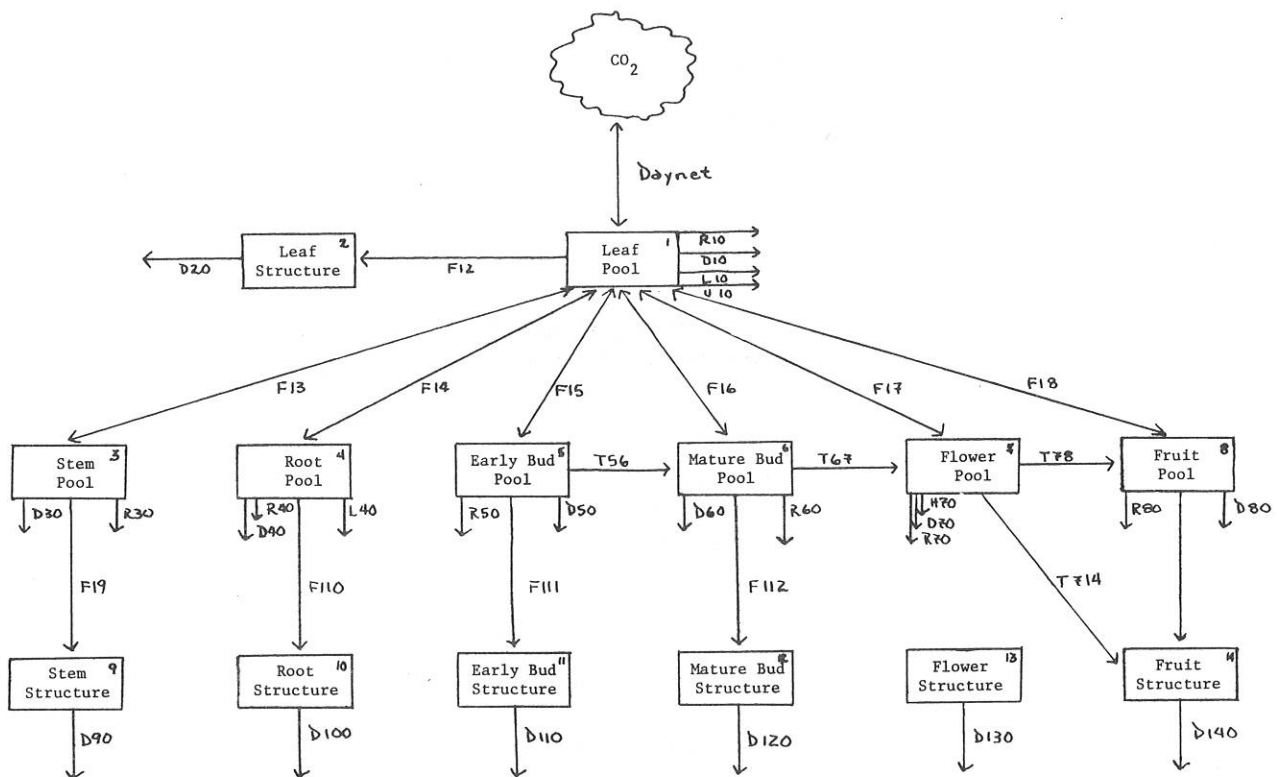
Figure 1. Diagram of possible carbon allocation pathways in the current version of the *Larrea* production and carbon allocation model.

F	-translocation of carbon from one mobile pool to another or incorporation of mobile carbohydrate into non-mobile structure.
T	-transfer from one pool or structure to another due to development processes.
D	-loss of carbon to environment by death.
R	-loss of carbon to environment by respiration.
V	-loss of carbon to environment by volatilization.
L	-loss of carbon to environment by leaching.
Day net	-net daytime CO_2 exchange of photosynthetic tissues.
N	-loss of carbon to environment as nectar.

The essential feature of the current model is that the processes of structural growth and organ death are controlled by physiological conditions of the tissues rather than strictly by physical factors of the environment. The extent of growth of both reproductive and vegetative organs is controlled by the sizes of the mobile carbohydrate pools. Death of organs occurs when mobile carbohydrate pools fall below a critical level. The sizes of mobile carbohydrate pools are determined by the differences between the process of carbon gain (photosynhesis) and the processes of carbon loss (respiration, volatilization, leaching, death). The physical factors of the environment control the rates of carbon gain and loss and provide conditions which make vegetative and/or reproductive growth possible. These basic modifications of the model eliminate the need for some of the unrealistic assumptions made in our original model such as fixed ratios of allocation to various organs and fixed rates of organ death. They in turn require the investigation of physiological processes we did not originally anticipate. We have begun the investigation of these processes during 1974 and they will be the major goal of efforts during 1975.

OBJECTIVES

Our objective has been threefold. The collection and evaluation of data on the vegetative and reproductive growth of *Larrea* on field plots have continued. These data will be used for validation of the model. The second objective of our work has been to develop and use methods for evaluating the sizes of mobile carbohydrate pools and rates of respiration of nonphotosynthetic organs. The third objective was to incorporate the new process information into the model.

METHODS

The methods used for the collection of validation data on the reproductive growth as a function of season and soil moisture availability have been described previously (Cunningham et al. 1974). The soil moisture augmentation experiments were continued through April 15, 1974. Following the completion of the moisture augmentation schedule, measurements were continued through October 15, 1974, in a effort to determine if the moisture augmentation had an effect during the subsequent growing season.

Above-ground vegetative growth was also measured on the 16 experimental plots at two-week intervals from April 1972 through October 1974. This was done by measuring the increase in length of randomly selected growth points on each of the tagged sample branches.

Root respiration rates were measured using the same techniques previously described for respiration rate measurements of reproductive tissues (Cunningham et al. 1974).

Various methods for evaluating the sizes of mobile carbohydrate pools in *Larrea* tissue were tried. The method of Smith (1969) with some modifications appears to give the best results. Field-collected material of reproductive structures and stems was analyzed for percent total nonstructural carbohydrate to evaluate the method and obtain some idea of the variability which might be encountered in later studies.

RESULTS AND DISCUSSION

Root Respiration

Many difficulties were encountered in our attempts to measure root respiration rates. Not the least of these was the difficulty of growing *Larrea* seedlings in carbowax (polyethylene glycol) solutions to control soil water potential. Two different methods failed to give satisfactory results. Seedlings were grown in thin layers of "soil" (Vermiculite and sand). The soil was separated from the carbowax solution by a differentially permeable membrane. Seedlings were also grown in sand and irrigated with a carbowax-Hoagland's solution mixture. Both methods failed to produce satisfactory growth or survival of the seedlings. It appears that the failure was due to inadequate oxygen supply to the roots. Therefore, we are now growing the plants in soil and attempting to regulate soil water potential in a coarse fashion by the timing of irrigation. The meager data available on root respiration were collected from seedlings grown in this manner.

A second problem in the assessment of root respiration rates has been in ascertaining what portion of the root biomass is actually alive and capable of respiring. Many of the root samples tested showed no measurable oxygen uptake and must be considered either dead or dormant. Actively growing roots, although their biomass appears to be very small when compared to total root biomass, have extremely high respiration rates. At 30 C a rate of 21.4 mg $CO_2 \cdot g^{-1}$ dry wt $\cdot hr^{-1}$ has been measured. More work will be needed to assess the proportion of actively respiring roots.

Mobile Carbohydrate Pools

Larrea stem tissue collected during the period of active vegetative growth (May) had a mean percent total nonstructural carbohydrate content of 3.5 with a standard deviation of 1.0. Reproductive structures tended to increase in percent total nonstructural carbon until fruits were produced and then declined to a low point in the mature fruits (Table 1). The values reported here are comparable to the few which appear in the literature for *Larrea* (Strain 1969). These results indicate that the method will be usable for the assessment of the sizes of mobile carbohydrate pools necessary for growth and tissue maintenance.

Reproductive Growth

In last year's report reproductive growth was analyzed through October 19, 1973, but only two treatments, spring moisture augmentation and no spring moisture augmentation, were analyzed. Since that time we have developed computer programs to make the necessary calculations and

perform an analysis of variance of all 16 soil water augmentation treatments. Data have been punched and verified only for the first four treatments through October 1973. The analysis of variance indicates significant differences due to both treatments and time. Least significant differences (P < .05) were calculated to compare each of the treatments at a given sample time. The mean numbers of each reproductive stage per meter of branch length on each of the sample dates are given in Tables 2a-2f. These data indicate that each of the four treatments thus far analyzed had a different effect on the extent of reproductive growth. Reproductive growth was least in the plots which received both spring (April 15-July 15) and summer (July 15-October 15) soil moisture augmentation. Plots which received only spring soil moisture augmentation had slightly greater reproductive growth but less than plots which received no supplemental soil moisture. Thus our original hypothesis that greater soil moisture tends to reduce reproductive activity in *Larrea* appears to be true. Data for the additional months and other treatments will be analyzed in the same manner during the next few months and total carbon allocation to reproduction calculated as described in our previous report (Cunningham et al. 1974).

Vegetative Growth

The vegetative growth data have also only been analyzed for the first four treatments through October 1973. The values presented in Table 3 are the mean change in stem length per growth point for the time period indicated. As with the reproductive growth data the analysis of variance indicated both treatment and time were significant in affecting the means at the 0.05 level of probability. Least significant differences (P <0.05) were calculated to compare each of the treatments at a given time period. Plants which received soil moisture augmentation during the spring showed significantly greater vegetative growth during the spring (April 15-July 15). Supplemental soil moisture in the summer (July 15-October 15) did not signficantly affect vegetative growth.

CONCLUSIONS

The new version of the primary production and carbon allocation model for *Larrea* promises to provide us with a completed version with much more accuracy and biological reality within the near future. Most of the data reported here will be used to validate the model. A great deal of progress has been made in developing the methods needed to obtain the necessary process information for the model. This process information will be obtained during 1975 and the model will be continuously updated and checked against the data from the field experimental plots. A completed production and allocation model is anticipated by late 1975.

The trade-off between vegetative and reproductive growth in *Larrea* which is apparent in the data has caused us to dramatically alter the basic form of the allocation model. When the extent and controls of these shifts in carbohydrate

allocation are incorporated in the model our understanding of the role and success of this species in warm desert ecosystems will be greatly enhanced.

LITERATURE CITED

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Smith, D. 1969. Removing and analyzing total non-structural carbohydrates from plant tissue. Univ. of Wisc., College of Agr. and Life Sci. Res. Rep. No 41.

Strain, B. R. 1969. Seasonal adaptations in photosynthesis and respiration in four desert shrubs growing in situ. Ecology 50:511-513.

Table 1. Percent total nonstructural carbohydrate in reproductive tissues of *Larrea tridentata* sampled during the 1973 growing season at the Jornada Validation Site

Reproductive Stage	Mean	Standard deviation
Early buds	3.6	2.2
Late buds	5.5	2.3
Flowers	12.3	1.6
Immature fruits	3.1	0.5
Mature fruits	1.6	0.6

Table 2 (a - f). Mean number of reproductive structures per meter of branch for each of the soil moisture augmentation treatments from April 30, 1973, to October 30, 1973. Values on each date with the same superscript are not significantly different at 0.05 level of probability

a Early Buds

Date	Water 15 April-15 Oct.	Water 15 April-15 July	Water 15 July-15 oct.	No Water
30 April	16.8			62.2
18 May	89.9			81.7
31 May	9.2			5.5
16 June	1.0^1			1.7^1
28 June	0.8			3.9
12 July	0.9^1			1.5^1
25 July	0.2^1	0.4^1	22.7	28.2
9 Aug.	0.2^1	0^1	1.1^2	0.9^2
24 Aug.	0.1^1	0^1	0.2^1	0^1
7 Sept.	0^1	0^1	0^1	0^1
21 Sept.	0^1	0^1	0^1	0^1
5 Oct.	0^1	0^1	0.2^1	0^1

Table 2, continued

b   Immature Buds

Date	Water 15 April-15 Oct.	Water 15 April-15 July	Water 15 July-15 Oct.	No Water
30 April	0^1			0^1
18 May	11.0			15.9
31 May	16.6			27.1
16 June	0.7^1			0.9^1
28 June	0.3			0.4
12 July	0.1^1			0^1
25 July	0.4	0	1.4	3.0
9 Aug.	0.1	0	2.5^1	2.1^1
24 Aug.	0.1	0^1	0^1	0^1
7 Sept.	0^1	0^1	0^1	0^1
21 Sept.	0^1	0^1	0^1	0^1
5 Oct.	0^1	0^1	0^1	0^1

c   Mature Buds

Date	Water 15 April-15 Oct.	Water 15 April-15 July	Water 15 July-15 Oct.	No Water
30 April	0^1			0^1
18 May	1.9			2.5
31 May	6.2			4.6
16 June	0.5			1.2
28 June	0			0.3
12 July	$< 0.1^1$			$< 0.1^1$
25 July	$< 0.1^1$	0^1	0^1	0.7
9 Aug.	$< 0.1^1$	0^1	5.2	1.2
24 Aug.	0^1	0^1	0^1	0^1
7 Sept.	0^1	0^1	0^1	0^1
21 Sept.	0^1	0^1	0^1	0^1
5 Oct.	0^1	0^1	0^1	0^1

d   Flowers

Date	Water 15 April-15 Oct.	Water 15 April-15 July	Water 15 July-15 Oct.	No Water
30 April	0^1			0^1
18 May	1.1			5.8
31 May	28.2			18.1
16 June	1.3^1			1.2^1
28 June	< 0.1			0.4
12 July	0.2			0
25 July	0.1^1	0^1	0.1^1	$< 0.1^1$
9 Aug.	0.3	0	7.6	7.0
24 Aug.	0^1	0^1	$< 0.1^1$	0^1
7 Sept.	0^1	0^1	0^1	0^1
21 Sept.	0^1	0^1	0^1	0.7
5 Oct.	0^1	0^1	0^1	0^1

e   Immature Fruits

Date	Water 15 April-15 Oct.	Water 15 April-15 July	Water 15 July-15 Oct.	No Water
30 April	0^1			0^1
18 May	0^1			$< 0.1^1$
31 May	37.7			59.9
16 June	53.0			75.9
28 June	32.0			66.3
12 July	25.2			48.2
25 July	5.7	6.4	17.9	31.5
9 Aug.	0.9	2.7	17.4	28.8
24 Aug.	0.7	< 0.1	1.9	24.8
7 Sept.	$< 0.1^1$	0^1	0^1	12.5
21 Sept.	0^1	0^1	12.2	9.6
5 Oct.	0.1^1	0^1	7.6	2.7

f   Mature Fruits

Date	Water 15 April-15 Oct.	Water 15 April-15 July	Water 15 July-15 Oct.	No Water
30 April	3.3			2.2
18 May	0.5			0.4
31 May	< 0.1			< 0.1
16 June	< 0.1			< 0.1
28 June	< 0.1			0
12 July	0.5			2.0
25 July	8.0	11.7	11.2	10.8
9 Aug.	6.6	12.8	14.9	6.1
24 Aug.	3.7	10.0	8.6	11.9
7 Sept.	1.4	5.8	19.7	14.9
21 Sept.	0.8	4.2	6.3	7.2
5 Oct.	0.1	2.1	7.8	9.2

Table 3. Mean change in growth terminal length in mm for each of the soil moisture augmentation treatments from April 30, 1973, to October 5, 1973. Values at each time period with the same superscript are not significantly different at 0.05 level of probability

Time Period	Water 15 April-15 Oct.	Water 15 April-15 July	Water 15 July-15 Oct.	No Water
30 Apr.-18 May	8'			6'
18 May -31 May	16			5
31 May -16 June	23			14
16 June-28 June	3			- 8
28 June-12 July	36			1
12 July-25 July	37'			29'
25 July- 9 Aug.	6'	30'	33'	20'
9 Aug.-24 Aug.	110	47'	59'	20'
24 Aug.- 7 Sept.	3'	- 8'	2'	1'
7 Sept-21 Sept.	44'	32'	68'	5'
21 Sept- 5 Oct.	46'	16'	39'	13'