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1975 PROGRESS REPORT

A SIMULATION MODEL OF PRIMARY PRODUCTION
AND CARBON ALLOCATION IN THE CREOSOTEBUSH,
LARRREA TRIDENTATA (DC) CAV.

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ABSTRACT

A preliminary simulation model of primary productivity and carbon allocation in creosotebush (*Larrea tridentata*) is described. The model utilizes a systems approach in which movement of assimilate within the plant is in response to changes in source-sink strengths of the various compartments representing plant organs or developmental stages (leaves, stems, roots, early reproductive buds, maturing reproductive buds, flowers and fruits). Two distinct compartments per organ or developmental stage are defined to separate assimilate into a pool fraction (labile or translocatable) and a structural fraction (nonlabile). The change 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) is a function of the rates of maintenance respiration and growth as well as a priority scheme governing allocation of assimilates; the dynamics (increases and decreases in dry weight) of the structural compartment is a function of aging and the magnitude of its pool (which determines structural growth and physiological death).

The results of a one-year simulation of a hypothetical *Larrea* plant show that the model exhibits a reasonable behavior, although no validation is attempted at this stage in its development. The heuristic value of the model is illustrated in the sensitivity analysis which shows the need for detailed knowledge of "priority" carbon movement during both vegetative and reproductive growth periods, the importance of substrate-controlled respiration rates and the need for further studies of the dynamics of labile pools in the plant.

The model has proven to be an excellent tool in our initial attempt to integrate the voluminous information on *Larrea* into a complete functional description of the autecology of the species. Further refinement of this model (as data become available from our current research and from that of other investigators) should lead us to a better understanding of the ecological role of *Larrea* in desert ecosystems.

INTRODUCTION

Larrea tridentata (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. The Colorado and Sonoran are generally the warmest and the Chihuahuan the coolest. The Colorado and Mohave have the lowest rainfall, occurring primarily in winter. The Sonoran has the highest rainfall which occurs primarily in summer, but has a significant winter component. Rainfall in the Chihuahuan is intermediate in magnitude and occurs primarily in summer. These climatic variations result in distinct floras in each of the deserts, but *Larrea* has obtained dominance in many portions of each desert.

Although three chromosome races exist -- a diploid ($2n = 26$) in the Chihuahuan Desert, a tetraploid in the Sonoran and a hexaploid in the Mohave (Yang 1967; Barbour 1969) -- there is no evidence indicating that ecotypic variation among the races would account for the widespread success of the species. Much of the available evidence indicates that *Larrea* has achieved dominance in parts of its range only during the past hundred years. This increase in *Larrea* density has apparently been at the expense of perennial grass species, subjected to heavy grazing pressure by cattle (York and Dick-Peddie 1969).

Thus, *Larrea* appears to have evolved a complement of adaptations which are extremely successful in hot arid environments; not only in terms of ensuring its survival, but also allowing it to rapidly achieve dominance on disturbed sites. It also appears to be capable of adapting to a wider variety of environmental conditions than do other potentially dominant plant species. It remains an open question as to whether this capability is a result of ecotypic variation or genetic plasticity. Even though the existence of chromosome races might suggest the former, the acclimation potential exhibited by *Larrea* makes the latter a distinct possibility (Strain and Chase 1966).

The ability of *Larrea* to successfully and rapidly dominate a wide variety of desert ecosystems has led to a great deal of interest in, and investigation of, its adaptations to desert conditions. Information from these investigations has recently been reviewed and summarized (Barbour et al. in press), but no attempt was made to integrate the information into a complete functional description of the autecology of the species. The present paper is a preliminary attempt at such an integration in the form of a heuristic model of primary production and carbon allocation.

Mooney (1972) has effectively pointed out the importance of understanding how plants gain and allocate their resources to evaluating and predicting their success in a given physical environment in combination with specific competitors and predators. He correctly emphasized that, although quantitative models of carbon gain and allocation would be invaluable to such an understanding, we do not

yet have sufficient information to construct such models. It is our feeling that, even though available information is insufficient to construct models in accurate detail, preliminary attempts, such as the one described here, focus attention on the significant gaps in our knowledge and provide a guide for future research.

The successful establishment and maintenance of a population within a given ecosystem is a function of the ability of the individuals of that population to procure the necessary resources (energy and material) from that ecosystem and to allocate those resources in such a manner as to ensure that the population maintains this ability. Both procurement and allocation are functions of the genetically controlled capabilities of the individuals and of the biotic and abiotic constraints placed upon the individuals by the ecosystem. Plants, for example, must obtain carbon from their environments for the development of new structure and the storage of retrievable and transportable energy. The allocation of that carbon to new leaf, stem and root structure affects the individual's capacity to procure more carbon and other materials, as well as energy. The extent to which that carbon is allocated to reproduction will affect the survival of the population as a whole. The use of carbon in the production of pollinator attractants, antiherbivore compounds or allelopathic substances will also affect the survival of the individual and the population. It appears then that both the qualitative and quantitative success of a particular plant species in an ecosystem can be understood from a knowledge of its carbon procurement and allocation. Further, this understanding, if properly conceptualized and quantified, can lead to predictions concerning the success of the population under the influence of perturbations or time-dependent changes in the ecosystem associated with succession.

This same argument holds for any potentially limiting resource for the population. Carbon, however, is a logical choice for investigation since its procurement and allocation are so intimately tied to the procurement and allocation of energy and potentially limiting mineral nutrients and water. Also, the allocation of carbon to some functions within the plant can be ascertained through evaluation of biomass increments making the collection of data and the validation of predictions much simpler. Thus, we have selected carbon gain and allocation as a means of assessing the role of environment in determining resource allocation.

Recent success in the development of computer models to simulate plant growth has shown these models to be valuable tools both for enhancing understanding of the ways in which plants interact with their environment and for predicting the effects which environmental change might have upon the success of the plants. We have relied heavily on these successful models in formulating the general approach to the integration of the information available on *Larrea* into a model of its primary production and carbon allocation. In particular, the corn growth model of de Wit et al. (1970), the cotton growth model (McKinion et al. 1974), the *Calluna* productivity model of Grace and Woolhouse

(1974) and the carbon economy of tobacco model (Hackett 1973) have influenced our approach.

The *Larrea* primary-production and carbon-allocation model was developed with several objectives. First, the model should provide a useful tool to allow a detailed examination of the growth patterns of *Larrea* under an array of variable environmental conditions. Second, the model should include existing knowledge of the physiological responses of *Larrea*, while maintaining a reasonable level of complexity. Third, the model should be structured to serve as a generalized primary production and carbon allocation simulation model for evergreen perennial desert shrubs. Fourth, the development of this model and the subsequent sensitivity analysis should help elucidate the significant gaps in our knowledge of the biology of *Larrea*, thus providing direction for future research and, eventually, refinement of the model.

MODEL STRUCTURE

Carbon flux in a plant is a complex phenomenon involving movements of assimilates in response to source-sink strengths throughout the plant (Wareing and Patrick 1975). To deal with this, a systems approach is adopted in which the movement of assimilates within the plant is conceptualized as an allocation between, and through, various compartments (the "state variables" of DeRusso et al. 1965). These compartments represent the vegetative and reproductive organs of the plant. The dynamics of carbon flux in the plant is then modeled by writing an equation for each compartment which governs the change in the quantity of assimilates through time as a function of the balance between the inputs and outputs. The systems equations are as follows:

$$\dot{C}_i = \sum_j I_{ji} - \sum_k O_{ik} + E_i \quad (1)$$

where \dot{C}_i is the time derivative of compartment i , $\sum_j I_{ji}$ is the sum of all inputs to compartment i from other compartments (e.g., translocation from the leaf to the root), $\sum_k O_{ik}$ is the sum of all losses from compartment i to other compartments or outside the system (e.g., respiratory and volatile losses), and E_i is the input to compartment i from any external sources (e.g., atmospheric CO_2). Each input or output is determined by the product of a transfer coefficient and the content of a compartment (or compartments). These transfer coefficients, which determine the amount of assimilate in a compartment which is transferred, are a function of environmental parameters and internal system conditions. Since analytical solutions are not available for such a system of first-order, nonautonomous linear differential equations (Kowal 1971), numerical approximations are obtained using CSMP III (Continuous System Modelling Program III, IBM 1972), which provides a variety of numerical integration techniques.

SELECTION OF COMPARTMENTS

A compartmental representation of the model is shown in Figure 1. Fourteen compartments are defined, two for each

of seven plant organs or developmental stages of interest: 1 = leaves, 2 = stems, 3 = roots, 4 = early reproductive buds, 5 = maturing reproductive buds, 6 = flowers and 7 = fruits. The two distinct compartments per organ or developmental stage represent a separation of assimilates into a structural fraction (denoted S_i , where $i = 1, 2, \dots, 7$) and a pool fraction (denoted P_i), corresponding to the nonlabile and labile states of carbon, respectively. This distinction is necessary to differentiate between translocatable and structural assimilates.

The structural compartments contain the actual biomass accumulations (g dry wt) for each organ. Positive increments in biomass represent growth or development whereas decreases reflect structural dieback. Associated with each structural biomass compartment is a labile assimilate pool, the dynamics of which determine whether the organ is quiescent, actively growing or dying at any given time. The assimilate pools may fluctuate in size between a maximum (P_i^{**}) and a minimum (P_i^*); these limits are a function of the current structural biomass in an organ compartment. The limits for the pool of the i th organ at time t are defined as

$$P_i^{**}(t) = \delta_u \cdot S_i(t) \quad (2a)$$

$$P_i^*(t) = \delta_l \cdot S_i(t) \quad (2b)$$

where the upper limit is given by δ_u and the lower limit by δ_l . If these limits are exceeded, various consequences are possible (e.g., death of structural biomass, growth, etc.). This is explained in detail below. For the initial simulation,

δ_u was assigned a value of 0.07 for all vegetative organs and 0.25 for all reproductive organs. Vegetative organs were assigned a value of 0.0007 for δ_l and reproductive organs a value of 0.0625. These values, although somewhat lower than might be expected, are, from the small amount of data available, appropriate for *Larrea* (Cunningham and Syvertsen, in review; Strain 1969).

The current version of the model allows only one cohort of reproductive biomass to progress through the maturation stages (from early reproductive buds to mature fruits; Fig. 1) at any given time. Another constraint is that the entire cohort progresses at the same rate (i.e., all buds mature at the same rate). Observations of *Larrea* phenology (Cunningham et al. 1974) indicate that these constraints are realistic. The reproductive status of the plant is thus determined by the presence or absence of a cohort of structural biomass in one of the four reproductive compartments (S_4, S_5, S_6, S_7).

PATHWAYS OF CARBON FLUX

The arrows in Figure 1 represent the possible pathways and directions of carbon flow from the environment to the plant via net photosynthesis, from labile pool compartments to the environment via respiration, leaching and volatilization, from structural compartments to the environment via death, from labile pool to structural compartments via growth, and between labile pool compartments via translocation. The valves on the arrows signify that these flow rates are controlled.

Carbon fixation is a one-way flow (from the atmosphere to the leaf pool) as are the flows involving carbon utilization and death (Fig. 1). Utilization flows are of two types: 1) pool to structure movement, i.e., when labile assimilate is incorporated as structural biomass (growth) and, 2) pool losses to outside the system, i.e., respiratory losses and the formation of volatile and leachable compounds. Death flows are losses of structural biomass from the plant.

Translocation of labile assimilates between organs is achieved by two-way flows from each organ pool through a common labile pool, the leaf pool (Fig. 1). The leaf pool is also the recipient compartment for currently produced photosynthate. Carbon gained by photosynthesis or lost by respiration as CO_2 is converted to or from assimilated carbon by assuming that the ratio of carbon weight to assimilate dry weight is 1:2 (Larcher 1969).

PHOTOSYNTHESIS SUBMODEL

The structure of the carbon allocation model is independent of the photosynthesis submodel; thus any form can be utilized without an alteration of the basic allocation scheme. The photosynthesis submodel we have used for the simulations reported here is quite simple but appears to provide adequate output for the development and testing of the carbon allocation model.

The calculation of photosynthetic rate requires knowledge of its response to irradiation, soil moisture and air

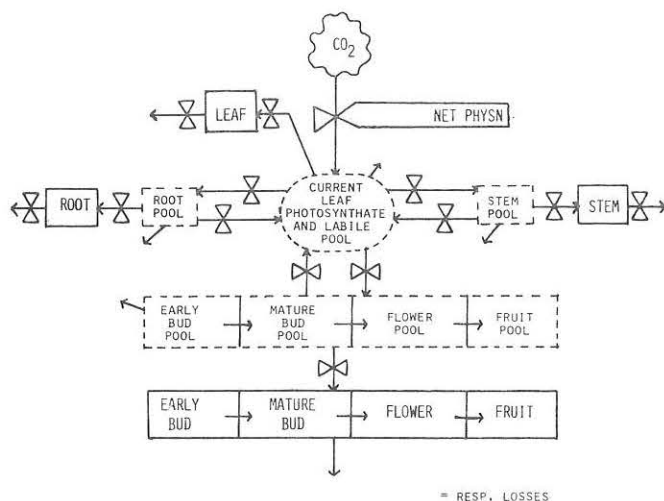


Figure 1. A box-and-arrow representation of the 14 compartments used in the model. Each organ is represented by two boxes, one showing the nonlabile or structural biomass (S_i) and one showing the associated labile or assimilate pool (P_i) for that organ. The arrows between the boxes indicate the possible directions of assimilate flux within the plant.

temperature. Additionally, it is necessary to know the amount of leaf tissue, its age distribution and the associated age-specific photosynthesis rates. The form of the photosynthesis submodel used is the frequently employed "interacting factor approach" (Ares and Singh 1974; Hari and Luukkanen 1973; McIntire 1973):

$$P_{\text{net}} = P_{\text{max}} \cdot n \cdot \left(\frac{1}{\frac{1}{E_1} + \frac{1}{E_2} + \dots + \frac{1}{E_n}} \right) \cdot \bar{S}_1 \quad (3)$$

where P_{net} is net photosynthesis ($\text{mg CO}_2 \cdot \text{g dw}^{-1} \cdot \text{hr}^{-1}$), P_{max} is the maximum attainable level of P_{net} under optimum environmental conditions, E_i ($i = 1, 2, \dots, n$) is an environmental scalar that ranges from 0 to 1, indicating the current effect of the i th environmental factor on the photosynthetic rate (1.0 being optimum conditions), and \bar{S}_1 is a weighted value of leaf biomass reflecting age distribution and age-specific photosynthetic rates. Note that under optimum environmental conditions (i.e., when $E_i = 1.0$, where $i = 1, \dots, n$) P_{net} equals P_{max} . A value for P_{max} of $17.6 \text{ mg CO}_2 \cdot \text{g dw}^{-1} \cdot \text{hr}^{-1}$ was chosen since this is the highest measured rate of which we are aware (Bamberg unpubl.).

Environmental Scalers

Two scalars are calculated, one for the effect of soil moisture (ESM) and one for the effect of air temperature (EAT). The effect of irradiation is initially assumed to be nonlimiting and the irradiation scalar (EIR) is set to 1.0.

Moisture stress is an important determinant of net photosynthesis rate. Its effect in the model at time t is incorporated via data obtained from Oechel et al. (1972) and Odening et al. (1974) relating the relative net photosynthesis rate of *Larrea* to soil water potential (ψ), measured in bars:

$$\begin{aligned} \text{ESM}(t) &= 1.0, \text{ if } \psi(t) > -25 \\ &= 1.804 + 0.033 \cdot \psi(t), \text{ if } -25 \geq \psi(t) \geq -50 \\ &= 0.2176 + 0.00143 \cdot \psi(t), \text{ if } \psi(t) < -50 \end{aligned} \quad (4)$$

From the above it can be seen that water is not limiting to photosynthesis when soil water potential is greater than -25 bars and photosynthesis decreases linearly with soil water potential at values less than -25 bars.

EAT is computed from data obtained by Strain and Chase (1966) which give the relative effect of air temperature on photosynthesis rates under a variety of acclimation regimes. A triple-interpolation table function of CSMP is used to obtain values of EAT at time t from mean daytime air temperature at time t (TEMDAY) and mean daytime air temperature from three weeks previous (ACCDAY). ACCDAY is the daytime temperature to which the plant is assumed to be acclimated at time t . This was felt to be a reasonable first approximation but may require revision when more information is available on the time course of photosynthetic temperature acclimation in *Larrea*.

Weighted Leaf Biomass, \bar{S}_1

The effects of physiological aging of leaves on net photosynthesis are incorporated in the model by calculating a leaf biomass weighted by the effect of physiological age. This weighting is intended to reflect effects resulting from shading by leaves produced distally as well as changes in metabolic potential resulting from senescence. Each cohort of leaf biomass (all leaf biomass produced during a given week) can progress through a maximum of 72 physiological age classes [(PAGE (i), $i = 1, 2, \dots, 72$). Seventy-two potential age classes are used because the maximum life expectancy of *Larrea* leaves is approximately 72 weeks (Chew and Chew 1965; Burk and Dick-Peddie 1973). At the end of each week of a simulation, the biomass in each leaf age class is transferred to the next oldest age class if, and only if, new leaf biomass has been produced during that week. Thus, physiological aging does not occur unless vegetative growth occurs (Ludlow and Ng 1974). For example, if the newest cohort of leaf biomass is 20 weeks old chronologically, it is still contained in the youngest physiological age class. If, however, leaves have been produced during any week following the production of the leaves which are 20 weeks old, the 20-week-old leaves will be in the second physiological age class. If leaf biomass is transferred from the oldest age class, it is transferred to leaf death (see "Death Rates").

The leaf biomass in each physiological age class is weighted from 0.0 to 1.0 according to a linear function (SEN) generated by CSMP using 1.0 for the youngest age class [PAGE (1)] and 0.0 for the oldest age class [PAGE (72)]. A linear decrease in net photosynthetic capacity with physiological age was assumed, but this is certainly a point on which actual data are needed. The value of \bar{S}_1 is calculated from the product of each age class biomass and the associated SEN value for that particular physiological age:

$$\bar{S}_1 = \sum_{i=1}^{72} [\text{SEN} \cdot \text{PAGE}(i)] \quad (5)$$

TIME-VARYING ALLOCATION RATES

The rate-controlled processes of carbon flux to, from and within each organ influencing the carbon balance of the plant are illustrated in the Forrester system notation in Figure 2 (Forrester 1968). This is the fundamental structural unit of the model and can be seen to be consistent with the allocation scheme shown in Figure 1. The amount of carbon in the structure and pool compartment of an organ is a function of processes occurring within that organ and processes occurring in other plant organs which directly influence the total carbon balance.

Maintenance Losses

Maintenance losses include respiration, the formation of volatile compounds by the leaves, the production of leachable compounds by both the leaves and the roots, and the formation of nectar by the flowers.

Table 1. Respiration models. Details of each model are given in the text

i	Organ	Respiration Model	Value of r_i^*	Source
1.	Leaf	$r_1 = r_1^* \cdot T_{\text{mult}}^1 \cdot M_{\text{mult}}^1 \cdot \bar{S}_1$	5.3	Strain and Chase (1966)
2.	Stem	$r_2 = [r_2^*(\text{day}) \cdot M_{\text{mult}}^2 \cdot \bar{S}_2] + [r_2^*(\text{night}) \cdot M_{\text{mult}}^2 \cdot S_2]$	$f(\text{TEMDAY}, \text{TEMNIG}, t)$	Cunningham Unpublished
3.	Root	$r_3 = \{[r_3^*(\text{day}; 10\text{cm}) \cdot M_{\text{mult}}^3 \cdot (\frac{S_2}{2})] + [r_3^*(\text{night}; 50\text{cm}) \cdot M_{\text{mult}}^3 \cdot (\frac{S_3}{2})]\}$	$g(\text{ST10}, \text{ST50}, t)$	Cunningham Unpublished
4.	Early Bud	$r_4 = [r_4^* \cdot T_{\text{mult}}^4(\text{day}) \cdot S_4] + [r_4^* \cdot T_{\text{mult}}^4(\text{night}) \cdot S_4]$	44.77	Cunningham et al. (1974)
5.	Maturing Bud	$r_5 = [r_5^* \cdot T_{\text{mult}}^5(\text{day}) \cdot S_5] + [r_5^* \cdot T_{\text{mult}}^5(\text{night}) \cdot S_5]$	105.4	Cunningham et al. (1974)
6.	Flower	$r_6 = [r_6^* \cdot T_{\text{mult}}^6(\text{day}) \cdot S_6] + [r_6^* \cdot T_{\text{mult}}^6(\text{night}) \cdot S_6]$	152.01	Cunningham et al. (1974)
7.	Fruit	$r_7 = [r_7^* \cdot T_{\text{mult}}^7(\text{day}) \cdot S_7] + [r_7^* \cdot T_{\text{mult}}^7(\text{night}) \cdot S_7]$	11.33	Cunningham et al. (1974)

The respiratory loss of the i th organ (r_i) in $\text{mg CO}_2 \cdot \text{g dw}^{-1} \cdot \text{hr}^{-1}$ is calculated using the general formula:

$$r_i = r_i^* \cdot T_{\text{mult}}^i \cdot M_{\text{mult}}^i \cdot S_i \quad (6)$$

where r_i^* is the maximum respiration rate of the i th organ, T_{mult}^i and M_{mult}^i are multipliers which introduce the effect of air temperature and soil moisture, respectively, on the respiration rate of the i th organ, and S_i is the biomass (g dry wt) of the i th organ.

The value of r_i^* for leaves (from Strain and Chase 1966) and reproductive organs (from Cunningham et al. 1974) are constant values. However, maximum rates for stems and roots are calculated as functions of current air and soil temperatures, respectively, using our unpublished data obtained from CO_2 exchange measurements. All values of r_i^* , which are considered to be the maximum possible rates of respiration for each organ under optimum environmental conditions, are then scaled by the multipliers T_{mult}^i and/or M_{mult}^i to calculate the effects of temperature and/or soil moisture. For example, using this formulation, the effect of temperature (T_{mult}^i) on the respiration rate of the i th organ is given a value ranging from 0.0 to 1.0 to reflect current temperature effects on respiration. Thus, the multiplier T_{mult}^i will be near a value of 1.0 under optimum conditions (i.e., the maximum rate of respiration is achieved) or near 0.0 if conditions are extremely poor (i.e., a small percentage of the maximum rate is achieved). The r_i^* values for each organ and the generalized models for calculating the respiration rates are given in Table 1.

Leaf respiration rate (r_1)—Only nighttime respiration rates are needed for leaves since daytime rates are accounted for in the determination of net photosynthesis. Respiration is a function of the maximum leaf respiration (r_1^*), the weighted dry weight values of leaf biomass (\bar{S}_1) discussed earlier, and two multipliers, T_{mult}^1 and M_{mult}^1 (see Table 2). The value

Table 2. Various maintenance losses calculated as constant rates ($\text{g g dw}^{-1} \cdot \text{day}^{-1}$)

Maintenance loss	Organ (i)	Y_k (constant)
Volatiles	Leaf	0.001
Leachates	Leaf	0.01
Leachates	Roots	0.001
Nectar	Flowers	0.016

of M_{mult}^1 (as well as M_{mult}^2 and M_{mult}^3) is identical to the value of ESM as described in the photosynthesis submodel above. Thus, we are assuming, in the absence of evidence to the contrary, that physiological age has the same effect on both net photosynthesis and dark respiration of leaves and that tissue water status has the same effect on dark respiration of leaves, stem respiration and root respiration.

Strain and Chase (1966) have shown temperature acclimation of respiration in *Larrea*. From their data, regression models were developed to calculate a value of T_{mult}^1 (0 to 1) that would reflect an acclimation of the respiration process to the mean nighttime temperature of three weeks previous:

$$\begin{aligned}
 T_{\text{mult}}^1(t) &= -0.295 + 0.031 \cdot \text{TEMNIG}(t), \text{ if } \text{ACCNIG}(t) < 11.0 \text{ C} \\
 &= -0.270 + 0.027 \cdot \text{TEMNIG}(t), \text{ if } 11 \text{ C} \leq \text{ACCNIG}(t) \leq 20 \text{ C} \\
 &= -0.115 + 0.012 \cdot \text{TEMNIG}(t), \text{ if } \text{ACCNIG}(t) > 20 \text{ C}
 \end{aligned} \quad (7)$$

where TEMNIG is the current mean nighttime air temperature and ACCNIG is the value of TEMNIG three weeks previously. As described in the photosynthesis submodel, the three-week accumulation period is conjectural at this point.

Stem respiration rate (r_2)—Stem respiration rate is a function of the maximum stem respiration rate (r_2^*), an age-weighted stem biomass (S_2) similar to that described for leaves, mean day and nighttime air temperatures (TEMDAY and TEMNIG), and M_{mult}^2 (Table 1). As with leaves, we are assuming that physiological age affects stem respiration to the same extent that it affects net photosynthesis. The maximum rate of respiration is calculated from the following regression model, where T is either the mean daytime (TEMDAY) or nighttime (TEMNIG) air temperature:

$$r_2^* (\text{day or night}) = 0.094 - 0.00467T + 0.000325T^2 \quad (8)$$

Root respiration rate (r_3)—For simplicity, it is assumed here that the root biomass of *Larrea* is evenly distributed at 10- and 50-cm depths. A maximum respiration rate is calculated for both depths as a function of soil temperature at each depth (Cunningham, unpubl. data):

$$r_3^* = -0.1212 + 0.01872ST \quad (9)$$

where ST is either the mean soil temperature at 10 (ST10) cm or 50 (ST50) cm. These values of r_3^* are modified by the effect of soil moisture (M_{mult}^3) as calculated above for leaves (M_{mult}^1) and summed to obtain daily losses (Table 1).

Respiration rates of reproductive organs (r_i , $i = 4, 5, 6, 7$)—The respiratory rate of each reproductive organ is a function of a maximum respiration rate r_i^* as obtained by Cunningham et al. (1974) and a multiplier T_{mult}^i to account for effects of air temperature (Table 1). Each value of T_{mult}^i is obtained using the CSMP curve generating functions AFGEN and NLFGEN from data given in Cunningham et al. (1974).

Substrate-controlled respiration (rs_i)—It has been demonstrated that the respiration rate of a plant may be controlled in part by the current available assimilate pool (McCree 1970). To account for this, a substrate level influence is calculated to modify the respiratory rates of all organs. This is accomplished by scaling the respiratory rates of an organ by a factor which is, in part, a function of the current size of a pool, $P_i^*(t)$, compared to the possible maximum size at that time, $P_i^{**}(t)$, which is a function of the structural biomass. The degree to which this dependence is important in the model is determined by two scalars, ϕ_1 and ϕ_2 , where ϕ_1 determines the base metabolism of the organ and ϕ_2 determines the substrate-dependent respiration. The substrate-dependent respiration rate (rs) of the i th organ at time t is calculated as

$$rs_i(t) = [r_i(t) \cdot \phi_1] + \{r_i(t) \cdot \phi_2 \cdot [P_i^*(t)/P_i^{**}(t)]\} \quad (10)$$

with the following constraints:

$$0. \leq \phi_1 \leq 1., 0. \leq \phi_2 \leq 1., \text{ and } \phi_1 + \phi_2 = 1.0$$

Under the defined constraints, if ϕ_1 is 1.0, the respiration rate is not substrate-dependent; if $\phi_2 = 1.0$, the rate is totally substrate-dependent. As an initial approximation, both ϕ_1 and ϕ_2 are set at 0.50 for the first simulation.

Other maintenance losses—The maintenance losses due to the production of volatile and leachable compounds and the formation of nectar are calculated as donor-controlled, constant coefficient rates. These rates are also substrate-dependent as described for respiration losses. For the i th organ, the total maintenance loss (excluding respiration), m_i , is given by

$$m_i = \sum_k \{[\gamma_k \cdot S_i \cdot \phi_1] + [\gamma_k \cdot S_i \cdot \phi_2 \cdot P_i / P_i^{**}]\} \quad (11)$$

where γ_k is the constant parameter determining the k th maintenance cost (on a $g \cdot g \text{ dw}^{-1}$ basis). The values for nectar production used in the initial simulation are given by Simpson et al. (in press). The other values are only guesses and investigations of their true magnitudes need to be undertaken.

Organ Demand Function

This function is one in which the maintenance requirements of an organ are combined with a priority system of allocation within the plant. "Demand" of organ S_i denotes: 1) the amount of assimilate necessary to maintain the pool size at maximum (P_i^{**}) (this is a function of total maintenance losses); and 2) a growth priority (if any) which specifies that "excess" assimilates are to be allocated to organ S_i . Excess assimilates (EXCESS) are those beyond the amount necessary to fulfill the maintenance requirements of all organs.

The growth priority refers to vegetative growth, reproductive growth or both. There is a priority for allocation to reproductive organs once reproductive growth is initiated. A detailed explanation of the factors involved in the priorities of vegetative and reproductive growth is given under "Growth Rates."

Pool Balance Function

As shown in Figure 2, the movement of labile assimilates from each pool back to the common labile pool (P_1) may occur. These labile assimilates may be subsequently translocated elsewhere in the plant. The pool balance function governs the occurrence of such movements. If, at time t , the current production of photosynthate is not great enough to meet the total maintenance demands of the plant, a "pool balance" occurs. This can occur at any time under any growth conditions, vegetative and/or reproductive.

The pool balancing procedure involves calculating the assimilate that is available (PCA) as a proportion of the necessary pool level that, if available, would bring each pool to maximum size:

$$PCA(t) = [TPOOL(t) - LOSSES(t)]/P_{MAX}(t) \quad (12)$$

where

$$\begin{aligned} \text{TPOOL}(t) &= \sum_i P_i(t) + P_{\text{net}}(t) \\ \text{LOSSES}(t) &= \sum_i rs_i(t) + \sum_i m_i(t) \\ \text{PMAX}(t) &= \sum_i P_i^{**}(t) \end{aligned}$$

$P_{\text{net}}(t)$ is the current photosynthetic input, $\text{TPOOL}(t)$ is the current total labile assimilates in the plant [all pools plus $P_{\text{net}}(t)$], $\text{LOSSES}(t)$ is the total maintenance losses for the plant and $\text{PMAX}(t)$ represents the labile assimilate level that would be necessary to bring each pool to its maximum level based on the current structure of each. Each pool is then allocated a percentage of the available labile pool as follows:

$$\text{PCA}(t) \cdot [\text{individual pool demand}(t)/\text{total pool demand}(t)] \quad (13)$$

where the individual pool demand is the sum of all maintenance losses of the i th organ and the total pool demand is the sum of all maintenance losses of the plant. This procedure results in a pool balance in that the labile assimilate levels are brought to the same percentage of P_i^{**} throughout the plant. Each organ pool either gains or loses assimilates. Note that a pool with a large deviation from its maximum size receives a larger proportion of the available pool reserves than one with a small deviation. Thus, translocation is a function of source and sink strengths among the respective labile pool compartments.

Growth Rates

The growth rate of an organ is a function of the growth priorities and the total amount of assimilate available for growth. Vegetative growth, i.e., structural increments in the leaves, stems and roots, is simply a partitioning of available assimilates in a specific ratio (e.g., 1:1:2) to these organs. In the absence of reproductive organs, all excess assimilate is allocated to the vegetative organs. However, when reproductive organs are present, vegetative growth will occur only if current assimilate levels are above specified values (see below).

Reproductive growth is more complex. As mentioned earlier, the constraints on reproductive growth involve the initialization, development and maturation of only one cohort through the developmental stages ($S_4 \rightarrow S_5 \rightarrow S_6 \rightarrow S_7$) at a rate dependent on available assimilates.

Early reproductive buds—Reproductive growth is initiated if the following two criteria are satisfied: 1) the mean daytime air temperature exceeds 15 C (Chew and Chew 1965) and 2) EXCESS is greater than a certain critical percentage (α) of the leaf structural biomass. The amount of assimilate greater than this percentage is then allocated to initiate early reproductive buds and the remaining assimilate is allocated to the vegetative organs as described above.

Once reproductive growth is initiated, all EXCESS at subsequent times, up to another critical percentage of leaf biomass (β), is utilized for the growth and development of each reproductive organ. If there are assimilates above this amount, they are used for vegetative growth. Therefore, once early reproductive buds are initiated, all of the EXCESS to critical percentage (β) can be used to form reproductive buds. This is allowed to occur only one day past the initiation day. Then the total number of buds (NOBUDS) that were formed is determined on the basis of the following equation:

$$\text{NOBUDS} = S_4/0.0047 \quad (14)$$

where 0.0047 is the average weight of an early bud (g dry weight) and S_4 is the total assimilate allocated to the formation of reproductive buds in the two-day period. Initially, the value of β was set at 0.02 and the value of α at 0.05.

Mature reproductive buds—This stage represents the period of bud maturation. If assimilate is available for reproductive growth, it is allocated to S_5 until the total biomass reaches a level equal to the average weight of a mature bud times the total number of buds (i.e., when $S_5 = \text{NOBUDS} \cdot 0.0178$, where 0.0178 is the average weight, in g dw, of a mature bud).

Flowers—This stage persists for two days. The flowers are not allocated assimilates for structural growth; maintenance losses from the pool are replaced if sufficient photosynthate is available. At the end of the two-day period, the structural biomass (= flowers) is aborted and the pool is used to initialize the structure and pool compartments of the fruit stage.

Fruits—The total flower pool, P_6 , is allocated to the fruit structure and fruit pool in a ratio as follows:

$$\begin{aligned} P_7 &= 0.80 \cdot P_6 \\ S_7 &= 0.20 \cdot P_6 \end{aligned} \quad (15)$$

This initializes the fruit pool and structure levels such that the pool size is at maximum (i.e., 0.25 of structure, δ_{II}). Thereafter, assimilates are allocated to the fruit compartment (as described for the earlier stages) until maturation is reached. This maturation level is based on the average weight of a mature fruit (0.022 g dw; i.e., when $S_7 = \text{NOBUDS} \cdot 0.022$, maturity is reached). Once maturation of a given cohort occurs, a new cohort of reproductive biomass can begin development if conditions are suitable.

Death Rates

The final rate to be considered in the basic structural unit of the model (Fig. 2) is the death rate. This rate has been assumed to be a function of either: 1) the chronological age distribution of the vegetative biomass in the case of vegetative structures; or 2) the attainment of a minimum level of assimilate in the labile pool (P_i^*) for both vegetative and reproductive organs.

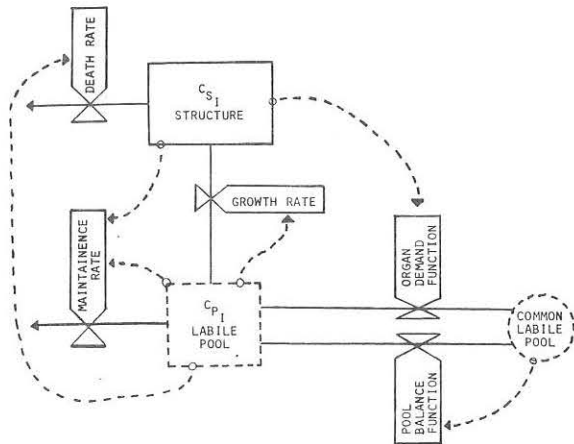


Figure 2. Forrester (1968) system notation of the fundamental structural unit of the model. Movements of assimilates (solid lines) into each organ (from the common labile pool), within each organ (incorporation of assimilates from pools into structural biomass) and out of each organ (via maintenance and death losses or into the common labile pool) are rate-controlled processes (as indicated by valves). Dashed lines denote causal relationships.

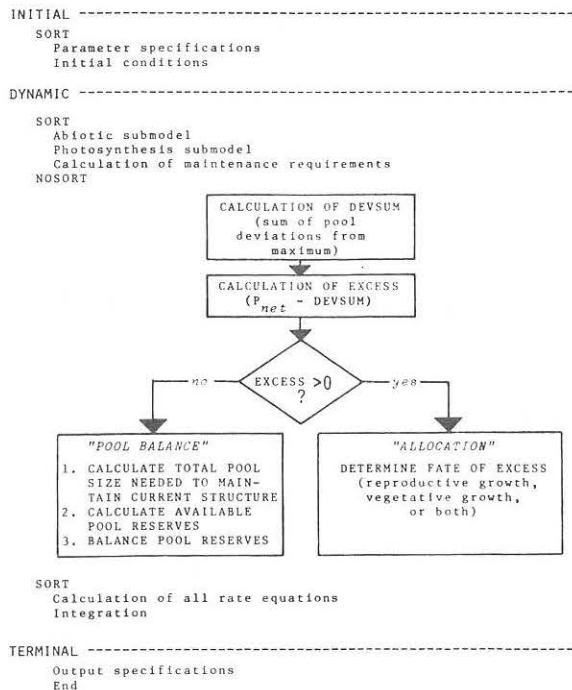


Figure 3. Flow diagram of the CSMP computer simulation model.

Chronological aging—As pointed out above, Chew and Chew (1965) and Burk and Dick-Peddie (1973) have established that the maximum chronological age obtainable by *Larrea* leaves is approximately 18 months. We have assumed that roots and stems have the same life expectancy and have constructed the model so that the structural loss due to chronological age is the same for all three vegetative organs. This can be done by keeping track of only the leaf biomass in each chronological age class because new stem and root biomass are added whenever new leaf biomass is added. Therefore, we account for all structural losses due to aging by placing leaf biomass in 72 age classes, AGE (i), each containing the cohort of leaf biomass produced during a given week. The most recent cohort of leaf biomass is the total amount of assimilate allocated to leaf structure during the latest week. The oldest leaf biomass is dropped and corresponding percentages of the root and stem biomasses are dropped each week.

Minimum pool size—If the pool of any organ drops below a lower limit, a structural loss of biomass occurs at a magnitude which then makes the existing pool size a new maximum. Thus, the biomass lost by death of the i th organ (d_i) in $g \text{ dw} \cdot \text{day}^{-1}$ is as follows:

$$d_i = S_i - (P_i / \delta_u) \quad (16)$$

where δ_u is 0.25 for reproductive organs and 0.07 for vegetative organs and is the upper pool size limit expressed as a percentage of structural biomass. For example, if the current structure size of the maturing reproductive buds (S_5) were 30 g, the minimum pool size (P_5) would be 1.88 g ($30 \text{ g} \cdot 0.0625$, Equation 2b). If the pool size (P_5) dropped to this level, a loss of structural biomass from S_5 would be calculated using Equation 15:

$$d_5 = 30 \text{ g} - 1.88 \text{ g} / 0.25 = 22.48 \text{ g}$$

Thus, the new value for S_5 could be 7.52 g ($S_5 - d_5$, or $30 \text{ g} - 22.48 \text{ g}$), for which a pool size of 1.88 g is exactly the maximum ($P_5^* = 7.52 \cdot 0.25 = 1.88$, Equation 2b).

The loss of structural biomass during the developmental stages of reproductive growth must include a reciprocal reevaluation of the number of reproductive structures that remain. The new number of buds (NEWBUD) is calculated as

$$\text{NEWBUD}(t+1) = \text{NOBUDS}(t) - d_1(t) / \text{NOBUDS}(t) \quad (17)$$

This new number of reproductive structures is then used to determine the maturation biomass levels of the reproductive organs as described previously.

SIMULATION ALGORITHM

A flow diagram of the CSMP model is presented in Figure 3. This scheme provides an overview of the interrelationships between the entire plant model (Fig. 1) and the basic structural unit for each organ in the plant (Fig. 2).

The computer model is composed of three sections: INITIAL, DYNAMIC and TERMINAL. All initial conditions of the model are specified in the INITIAL section, the DYNAMIC section contains all structural statements of the model (e.g., the abiotic submodel, the calculation of the transfer coefficients and the integration equations), whereas the TERMINAL section provides for all output specifications.

The time-step used in the model is one day. Therefore, each day all of the abiotic variables are calculated and used in the calculation of daily net photosynthesis (P_{net}) and maintenance losses. The deviations of all pool sizes from their maximum limits are evaluated and, based on the difference between the sum of these deviations (DEVSUM) and P_{net} , either an allocation of excess assimilate or a balancing of the total pool reserves between the organs occurs (Fig. 3).

The pool balance scheme is straightforward. The allocation scheme involves the partitioning of assimilates to vegetative organs, reproductive organs or both. If any pool drops below its minimum allowable limit, structural biomass losses occur.

Each of the above rates is calculated daily and integrated using Euler approximations to obtain the resulting carbon dynamics of the plant.

SIMULATION RESULTS

It is our intent to evaluate the model at two levels of resolution at this stage in its development. The first level concerns an evaluation of the overall model behavior. This entails considerations of the model's realism (i.e., how closely the model mimics actual processes), its predictive capacity (in view of logical constraints) and its short- and long-term stability. The second level of interest involves an examination of the sensitivity of the model to changes in model parameters that control selected physiological processes in the plant. This is examined below under "Sensitivity Analysis."

The model was tested by simulating the carbon dynamics of one hypothetical *Larrea* plant under environmental conditions similar to those in southern New Mexico. The following are required initial data: 1) initial values (g dw) for the 14 compartments; 2) the initial age distribution of leaf biomass; and 3) abiotic inputs. For the results presented here, both the stem and leaf biomass were arbitrarily initialized at 150 g and the root biomass set at 300 g; this corresponds to a root:shoot ratio of 1:1, which is maintained throughout the simulation. The associated pool compartments for these three organs were initialized at their maximum sizes, i.e., 10.5, 10.5 and 21.0 g, respectively (Equation 2a). All reproductive compartments were initially set to zero. In Figure 4a, the initial age distribution used for the 150 g of leaf biomass is illustrated. This distribution was used to calculate the initial weighted dry weight value (see Equation 5).

The environmental data were generated from records of the Jornada Experimental Range in southern New Mexico (Whitford et al. 1974). The simulation was started on March 14 as day No. 1 and the days numbered consecutively thereafter. Air temperatures, photoperiod and soil temperatures were specified as CSMP trigonometric functions of day numbers:

$$Y = Y_0 + \text{SINE}(C_1, C_2, C_3) \cdot Y_m \quad (18)$$

where Y is the value of the environmental variable of interest, Y_0 is its initial value on March 14, Y_m is the allowable amplitude from Y_0 and C_1 , C_2 and C_3 are CSMP parameters controlling delays, radians per day and time lags. Soil water potential was specified using a table function.

MODEL BEHAVIOR

Output of selected model variables from the 365-day simulation is shown in Figures 5 and 6. In addition, the actual values of the various rates and functions at specific days are summarized in Table 3.

The biomass dynamics of the leaf and reproductive organs are illustrated in Figure 5a and the time-dependent fluctuations of EXCESS are shown in Figure 5b. In Figure 6, P_{net} , during this simulation, is plotted along with the percentage that was allocated to reproductive organs during each day (total maintenance and growth requirements). A day-by-day comparison of the variables plotted in Figures 5 and 6 elucidates the behavioral characteristics of the model as structured in the DYNAMIC section.

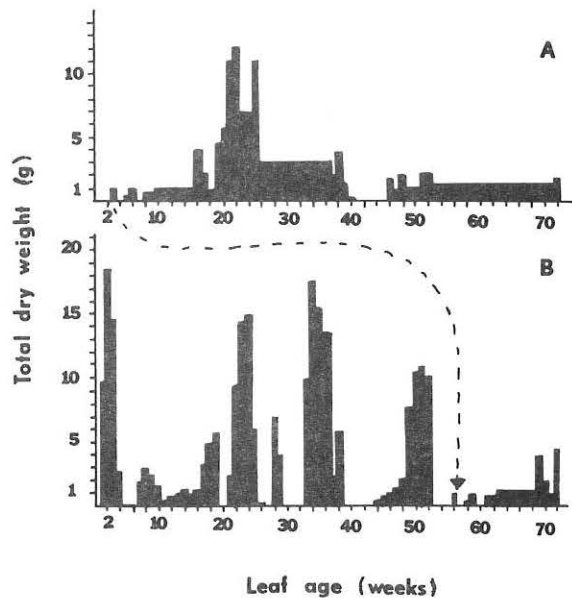


Figure 4. Age distribution of the leaf biomass (a) initially and (b) after the 365-day simulation of the model. Note that the youngest leaf cohorts of the initial distribution are the oldest after the 52-week simulation.

Table 3. Specific values of structure and pool sizes of organs at select times during the one-year simulation of the model. Also shown are the rates controlling the carbon flux in the organ compartments and the resultant net changes (+ or -) due to these rates. See text for details

Day No.	Organ	SIZE		Maintenance Rate	Growth Rate	Death Rate	Organ Demand Function	Pool Balance Function	P_{net}	DEVSUM	EXCESS	PCA	Net Change	
		s_1	P_1										s_1	P_1
0	Leaf	150.0	10.5											
10	Leaf	162.5	11.4	2.54	1.54	0.18	4.19	0.00	10.35	3.74	6.61	1.0	+	+
59	Leaf	183.3	12.8	2.09	0.02	0.18	2.11	0.00	2.78	2.69	0.86	1.0	-	-
53	Leaf	183.0	12.8	2.08	0.00	0.18	2.08	-0.004	2.68	2.70	-0.02	0.99	-	-
134	Leaf	236.3	16.5	3.57	1.74	0.18	5.31	0.00	19.95	7.75	12.19	1.0	+	+
	Early Rep. bud	0.18	0.05	0.09	1.03	0.00	1.12	0.00					+	+
150	Leaf	237.4	16.57*	3.46	0.00	0.28	3.51	-0.009	10.56	19.79	-0.23	0.99	-	-
	Maturing bud	13.8	3.43*	11.81	0.00	0.00	11.83	-1.8x10 ⁻³					o	-
162	Leaf	235.5	15.33*	3.88	0.00	0.14	5.03	-1.16	18.3	27.93	-9.63	0.86	-	-
	Flower	15.0	3.47*	15.50	0.00	0.00	15.78	-0.28					o	-
167	Leaf	238.6	16.70	3.85	0.87	0.14	4.72	0.00	17.2	9.32	7.88	1.0	+	+
	Fruit	15.2	3.80	2.07	3.32	0.00	5.39	0.00					+	+
188	Leaf	243.4	17.0	3.19	0.00	0.26	3.19	-1.14	16.3	21.2	-4.90	0.93	-	-
	Maturing bud	22.6	5.6	14.94	0.00	0.00	14.94	-0.38					o	-
197	Leaf	250.3	17.52	2.77	1.34	0.00	4.11	0.00	16.59	5.80	10.79	1.0	+	+
	Fruit	27.9	6.97	2.40	3.52	0.00	5.92	0.00					+	+
270	Leaf	291.3	20.4	3.28	0.13	0.00	3.41	0.00	4.68	4.13	0.55	1.0	+	+
336	Leaf	266.9	17.7*	2.93	0.00	0.29	3.91	-0.12	2.83	7.22	-4.39	0.94	-	-
365	Leaf	274.3	19.2	3.87	0.28	0.85	4.15	0.00	18.2	11.81	6.39	1.0	-	-

* pool size less than maximum.

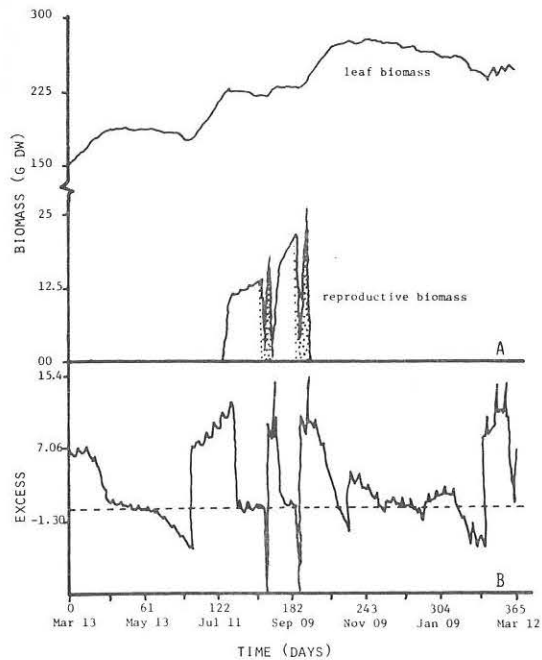


Figure 5. Model output. (a) Dynamics of leaf biomass (S_1) and the reproductive biomass (S_4 , S_5 , S_6 and S_7). The shaded areas under the curves represent the flower and fruit stages, whereas the remaining area is the bud development stages. (b) Time dynamics of EXCESS, the difference between DEVSUM and P_{net} . See text for details.

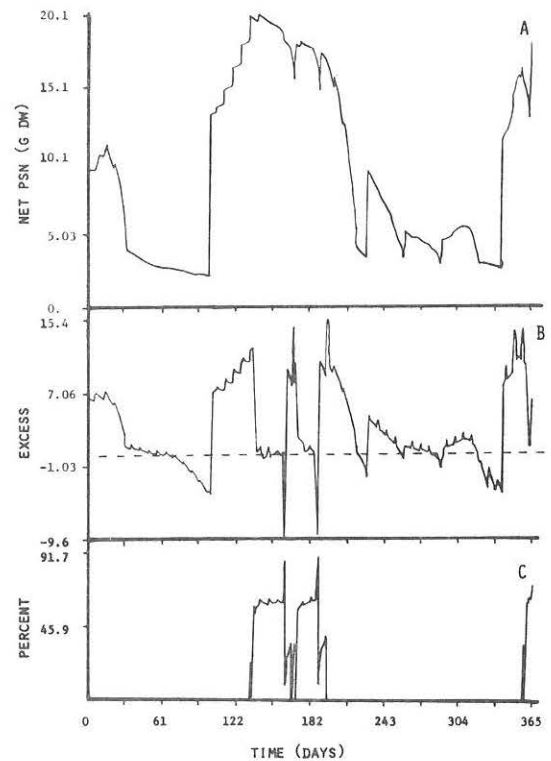


Figure 6. Model output. (a) Net photosynthesis (g dw) during the time course of the simulation. (b) EXCESS, as in Figure 5b. (c) The percentage of net photosynthesis allocated to reproductive organs.

Days 1-122 (March 13-July 11)

No reproductive activity occurred during this portion of the simulation. P_{net} at the start of the simulation (mid-March), was at a relatively high value of around 10 g $\text{dw} \cdot \text{day}^{-1}$ (Fig. 6a); the EXCESS during this period was about 7 g $\text{dw} \cdot \text{day}^{-1}$ (Fig. 6b). Since no reproductive growth was initiated, this EXCESS was allocated to the leaves, stems and roots in portions that would maintain a root:shoot ratio of 1:1. For example, as summarized in Table 3, during day No. 10 the total maintenance demands of the vegetative organs consumed only 36% of P_{net} , leaving an EXCESS of 6.61 g. The leaves were allocated 1.63 g of this (1.54 to S_1 and 0.09 to P_1). However, there was also a structural loss of 0.18 g at day No. 10 due to leaf senescence (see Fig. 4a), making the net leaf biomass increase less than 1.54 g. Both the structural and pool compartments showed positive size increments (“+,” Table 3), indicating that EXCESS was greater than 0.0 and the death rate due to senescence (Fig. 4a) was less than the growth rate.

In the middle portion of this period (days 30-100), photosynthetic production declined in response to dry environmental conditions. As can be seen in Figure 5a, the total leaf biomass steadily declined. This loss was directly attributable to leaf senescence. Structural losses occurred on days 59 and 63 although the pool sizes were at maximum both days (Table 3). At day 59, the small growth rate of 0.02 g only partially offset the death rate of 0.18 g. EXCESS dropped below zero for the first time on day 63; P_{net} was 0.02 g less than DEVSUM. Consequently, a pool balance occurred as evidenced by the small “loss” of 0.004 g from the leaf pool (i.e., the pool balancing resulted in an allocation of 0.004 g less than the organ demand of 2.08 g). Note that in spite of a negative net change for a pool compartment, it could still be at maximum size due to simultaneous losses of structural biomass.

Photosynthetic gains jumped dramatically on day 101 (Fig. 6a). This resulted in rapid growth of the leaves (Fig. 5a) for the rest of this period.

Days 123-213 (July 12-October 10)

Two large reproductive growth flushes occurred in this period, one initiating on day 133 and the other on day 170, resulting in total fruit production of 18.54 g (day 168) and 27.89 g (day 197), respectively (Fig. 5a). The general pattern of allocation during these periods involved: 1) an initial allocation for the formation of buds (days 133 and 170); 2) the maturation period of these buds; 3) the flower development stage with accompanying large respiratory losses; 4) the aborting of flowers (days 164 and 190); and 5) a maturation period for the development of fruits (the duration, as in 2 above, a function of available assimilates).

Comparing Figures 5a and 5b, it can be seen that EXCESS levels dropped drastically once reproductive growth was initiated. This resulted from the large maintenance requirements of the reproductive organs. For example, at days 150 and 162, assimilate pools for both the leaves and the reproductive buds were below maximum

sizes (Table 3). The maintenance demands of the buds alone at these times were 60 and 90% of P_{net} . Because of the pool balance, the net changes in the bud pools were negative, but the bud structures remained unchanged since the pool sizes were still above the minimum allowable levels. The loss of leaf biomass both days was again due to leaf senescence.

Once the reproductive buds reached a mature size, i.e., the flower stage, high respiratory cost drove EXCESS to its minimum levels (see Fig. 5b and day 162, Table 3). Immediately following the aborting of the flowers, a jump in the EXCESS levels is apparent, starting the maturation period for the fruits (days 167 and 197, Table 3). The percentage of P_{net} allocated to reproductive organs is greatest, of course, during the flower stages due to their high respiration rates (Fig. 6c).

Days 214-265 (October 11-March 12)

The remaining portion of the simulation consisted entirely of vegetative activity. EXCESS and, hence, growth responses can be seen to fluctuate in response to increases or decreases in P_{net} (Fig. 6a, Table 3).

The final leaf biomass was 273.7 g, an increase of 123.7 g. The age distribution of this biomass is depicted in Figure 4b. A close inspection of Figures 4b and 5a reveals the weeks of highest leaf biomass increments.

SENSITIVITY ANALYSIS

Once the general structure of a model is defined and the equations describing the system formulated in a manner consistent with the observable behavior of the system being modeled, a sensitivity analysis is a useful next step in refining the model. Sensitivity analysis encompasses a set of techniques which test the effect of a change in a specific parameter on certain response variables. The “parameter” is usually a coefficient which governs the rate of a certain process (e.g., maximum respiration rate, r_i^*), whereas the “response variables” are usually the state variables of the model (e.g., the biomass of fruit). Various approaches to sensitivity analysis have been suggested, some involving complex calculations if the model is itself fairly complex (e.g., Kerlin and Lucius 1966; Brylinsky 1972). The technique used here is described by Smith (1970) and Singh (1973). The parameter of interest is, in turn, varied upward and downward a certain percentage, the model executed, and the behavior of the response variables is observed. Using this procedure, it is simple to ascertain which parameters cause significant system responses by small changes in their values; these parameters are important and must be critically evaluated. This can eventually lead to a better understanding of the cause-effect interactions which take place in the biological system being modeled and suggest where research is needed to develop a better model (Smith 1970).

A sensitivity analysis was conducted on those parameters for which no experimental data were available and whose values were of significant magnitude to lead us to suspect they would have appreciable effect on the model output (α ,

β , ϕ_1 and ϕ_2 , δ_u and δ_l). The sensitivity of the model to maximum allowable respiration rates (r_i^*) was also tested to obtain an appreciation for the relative precision with which rates of physiological processes must be known to obtain realistic model output.

Critical Percentages α and β

These parameters are involved in controlling the initiation of reproductive growth (α) and the subsequent allocation of EXCESS to the developing reproductive organs (β). The sensitivity analysis has shown the model to be highly sensitive to these parameters.

In Table 4, some of the numeric values of α used in the sensitivity analysis are given. The final total vegetative biomass from each run is compared to the results from the initial simulation where α was set at 5%; these comparisons are given as a percent change. The relative sensitivities of the final vegetative biomass to these changes in α were calculated by dividing the percent change for each run by the largest change (ignoring the signs). The same is done for reproductive biomass using total fruit production from each run as the comparison. It can be seen from Table 4 that raising or lowering α 1% from its initial value of 5% has a significant effect on both vegetative and reproductive activity.

The greatest change resulted when α was increased (relative sensitivity = 1.0, Table 4). When α was set at 6%, no reproductive growth occurred (a -100% change) and the final vegetative biomass increased 180% (Table 4). It is evident from this that EXCESS did not exceed the critical magnitude necessary to initiate the formation of reproductive buds and, hence, all assimilates were utilized in vegetative maintenance and growth.

Conversely, a decrease in α allowed reproductive growth to be initiated at lower assimilate levels. This resulted, however, in overall decreases in both reproductive and vegetative biomass (Table 4). The timing of the various phenological stages of reproductive growth is provided in Figure 7.

The dynamics of reproductive growth in the initial simulation are shown in Figure 7a. Note that decreasing α to 3 and 4% resulted in reproductive growth throughout the period of the simulations (Fig. 7b and c). In spite of this, total fruit production (as well as vegetative biomass) decreased substantially (Table 4). This can be explained by examining the following: 1) the total number of buds initially formed at the onset of reproductive activity; 2) the pattern of net photosynthetic gains over the period of the simulations; and 3) the high respiratory costs of maintaining reproductive organs.

Reproductive growth was initiated during the first day of the simulations when α was set to 3 and 4% (Fig. 7b and c). For the same amount of available photosynthate, a value of α at 3% results in a greater number of buds formed than a value of 4%. This was, in fact, the situation here as 825

Table 4. Results of the sensitivity analysis. The different values of each parameter tested are given along with the resulting percent changes in final vegetative and reproductive biomass produced during the simulation. Relative sensitivity was calculated by dividing the change for each run by the largest change (ignoring the sign)

VALUE OF PARAMETER	VEGETATIVE		REPRODUCTIVE		
	% CHANGE	RELATIVE SENSITIVITY	% CHANGE	RELATIVE SENSITIVITY	
α	1%	-85	0.47	-89	0.89
	3%	-83	0.46	-92	0.92
	4%	-81	0.45	-51	0.51
	5%	0	0.00	0	0.00
	6%	+180	1.00	-100	1.00
	7%	+180	1.00	-100	1.00
	β	1%	+62	1.00	-47
2%		0	0.00	0	0.00
3%		-2	0.03	-42	0.50
4%		-24	0.39	-23	0.27
5%		-44	0.71	-84	1.00
6%		-44	0.71	-83	0.99
ϕ_2		0.00	-10	0.20	-88
	0.15	+2	0.04	0	0.00
	0.30	+2	0.04	0	0.00
	0.45	+1	0.02	0	0.00
	0.50	0	0.00	0	0.00
	0.65	-5	0.10	+2	0.03
	0.95	-4	0.08	+2	0.02
1.00	-50	1.00	-100	1.00	
r_i^*	+50%	+81	0.66	-100	0.38
	+20%	+123	1.00	-30	0.11
	+5%	+17	0.14	-33	0.13
	0%	0	0.00	0	0.00
	-5%	+5	0.04	+7	0.03
	-20%	-8	0.07	-63	0.24
	-50%	+30	0.24	+262	1.00
δ_u	+20%	-40	0.05	+100	1.00
	+15%	-18	0.25	-42	0.42
	+10%	-10	0.14	-21	0.21
	+5%	-1	0.01	-23	0.23
	0%	0	0.00	0	0.00
	-5%	-6	0.08	-10	0.10
	-10%	-13	0.18	-12	0.12
-15%	-30	0.42	-30	0.30	
-20%	-71	1.00	-75	0.73	

§ - represents the percent change in the initial values of the parameter.

buds were formed with α at 3%, 601 at 4% (Equation 14). Based on this, flower maturation did not occur until total bud biomass reached 14.7 and 10.7 g, respectively. As can be seen in Figure 7b, both flower and fruit maturation occurred rather quickly at 4% whereas the necessary maturation levels were not reached until day 107 (and at a reduced level) at the 3% value (Fig. 7c).

As mentioned previously, the drop in P_{net} after about 15 days into the simulation as shown in Figure 6a is a response to dry conditions. This same pattern occurred in all runs regardless of the absolute magnitude of P_{net} . Therefore, in the case where α was set at 3%, the buds did not mature into flowers before the drop in P_{net} . In fact, because of the lower P_{net} and the high costs of maintenance, a large loss of reproductive bud material occurred between days 25 and 30 (Fig. 7c). Eventually, when P_{net} increased again (see Fig. 6a), the remaining buds matured into flowers and fruits.

This same sequence of events occurred during the entire length of the simulations for both the 3 and 4% values of α . That is, reproductive growth was initiated at low assimilate levels resulting in continuous reproductive growth with the associated high respiratory costs. Consequently, buds developed up to a certain level only to have periods of low P_{net} drain the assimilate pools of the plant in order to maintain these buds (these are the horizontal lines in Fig. 7c where pool balancing was occurring). This resulted in dieback of vegetative biomass (Equation 17) and, eventually, death of the buds.

The results obtained from varying the β parameter are given in Table 4. Once reproduction is initiated, the percentage of EXCESS that is allocated to reproductive organs is controlled by β (i.e., all excess assimilates up to a maximum percentage, β , of leaf biomass will be allocated to the reproductive organs). Since α is constant, all simulations are similar up to the time reproductive growth is first initiated (day 133, Fig. 7a).

Lowering β to 1% resulted in the greatest deviations from the initial run. As might be anticipated, vegetative biomass increased substantially (a 62% increase) whereas reproductive biomass decreased (a 47% decrease), reflecting the lower allocation of carbon to developing reproductive organs and, hence, more to the vegetative organs.

On the other hand, increases in β resulted in decreases in both vegetative and reproductive biomass (Table 4). Increases in β mean that more assimilates will be allocated during the bud formation period, consequently putting a

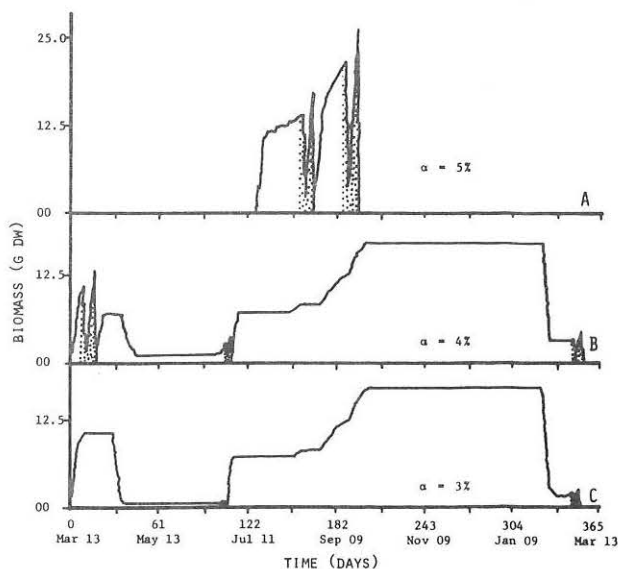


Figure 7. Model output (sensitivity analysis). Biomass dynamics (g dw) of reproductive organs for three values of α : (a) 5%, (b) 4% and (c) 3%. The shaded areas represent the flower and fruiting stages; the remaining is bud developmental stages.

greater demand on the plant to maintain this high-cost biomass. This situation is similar to the initiation of reproductive growth at low levels of EXCESS as discussed above.

Substrate-Controlled Respiration, ϕ_1 and ϕ_2

In Table 4 the range of values used for ϕ_1 and ϕ_2 in the sensitivity analysis is shown (where $\phi_1 = 1.0 - \phi_2$). These values represent conditions of no substrate-controlled respiration (i.e., $\phi_2 = 0.0$) to total control by substrate levels (i.e., $\phi_2 = 1.0$). It is immediately apparent that the model was sensitive to only the extreme situations, i.e., to total control or no control (Table 4).

When there was no substrate dependence, the respiratory rates of all organs were much higher. This resulted in a large decrease in total fruit production (—88%) and a moderate reduction in vegetative biomass (—10%). This pattern was repeated, however, when respiratory rates were made totally dependent on substrate levels; again, higher rates decreased both vegetative and reproductive biomass. Note that the model was consistently unresponsive to all intermediate values of ϕ_2 .

Maximum Respiration Rates, r_i^*

The maximum rates of respiration for all organs were simultaneously increased or decreased to examine their effect on the behavior of the model. The results are presented in Table 4.

Decreases in all rates lead to the expected increases in both the vegetative and reproductive biomass with one exception, the —20% reduction (Table 4). This particular level of reduction led to a higher amount of EXCESS which was allocated for the formation of buds. However, the accompanying high respiratory costs were not compensated for by the reduction in rates resulting in an overall biomass decline. The greater reductions in rates compensated for this increased reproductive demand. Increased rates resulted in a decline in fruit production and gain in vegetative biomass (Table 4).

Upper Pool Size Limits, δ_u

All changes in this parameter, both positive and negative, resulted in decreases in both vegetative and reproductive biomass (Table 4). Lowering this limit lowered the magnitude of the assimilate pools of the plant, which, consequently, resulted in less assimilate for redistribution during periods of pool balancing. Thus, under stress conditions, the minimum levels were reached and biomass losses occurred.

DISCUSSION

The model appears to provide a qualitatively acceptable simulation of the primary production and carbon allocation of *Larrea*. The quantitative validity of the model remains to be tested. It is our hope that the extensive measurements of *Larrea* production and associated environ-

mental parameters which are being conducted at the US/IBP Desert Biome validation sites will provide data for validation of the model. These data, along with numerous studies of rates of physiological processes in *Larrea* being conducted under the Analysis of Desert Ecosystems Program, will provide invaluable information for refinement of the model. In addition, by comparing outputs of the model generated from environmental data from validation sites in each of the warm desert regions with actual production data from the sites, we can gain some insight on the problem of ecotypic variation among the chromosome races of *Larrea*.

In developing the structure and logic of the model we have relied heavily on two assumed characteristics of *Larrea*'s physiology. The first of these assumptions was that the timing of reproductive and vegetative growth is dependent only on the levels of assimilates available and is not induced by external environmental cues such as photoperiod or temperature. The only environmental constraint we have used is to not allow the initiation of reproductive growth unless the mean daytime air temperature is above 15 C. This assumption appears to be justifiable from the frequent observations of *Larrea* flowering at almost any time of year over some part of its range (Kearny and Peebles 1960). The second assumption was that both vegetative and reproductive growth occur at the expense of currently produced assimilates rather than at the expense of stored assimilates. The work of Oechel et al. (1972) indicates that this is a valid assumption. From the available evidence, these assumptions appear to be valid for *Larrea* but may not be valid for other desert evergreen perennials and are certainly not valid for woody perennials in general.

One of our major objectives in developing the *Larrea* model was to focus attention on the significant gaps in knowledge which need to be filled before a complete understanding of its primary production and carbon allocation can be obtained. In this respect, the modeling effort was quite successful. We will discuss here some of the significant gaps which have occurred to us. Others undoubtedly exist and will become more apparent as the model is refined.

Many of the questions which the model raises relate to the senescence of various plant organs. We have assumed that death of leaves, stems and roots can result from senescence due to chronological aging and that the maximum chronological age is the same for all vegetative organs. Leaves were assumed to age physiologically at a rate proportional to the rate of new leaf production. The rate of net photosynthesis and respiration of leaves was decreased linearly with increasing physiological age. Physiological age was assumed to have no effect on the respiration rates of stems and roots. It was also assumed that there are no significant age effects on reproductive structures. Each of these assumptions about senescence needs to be investigated.

The model has pointed out some important gaps in our knowledge of temperature acclimation. Information on the

time course of both photosynthetic and respiratory temperature acclimation is needed. It is also important to know if temperature acclimation occurs in organs other than leaves.

Information is also needed on other factors which may influence photosynthesis and respiration rates. The assumption that there is no assimilate (end product) inhibition of photosynthesis needs to be tested. We need to know if it is logical to assume that plant water status has no effect on the respiration rates of reproductive organs. The assumption was also made that water status has the same relative effect on the respiration rates of all vegetative organs as it has on net photosynthesis. This needs to be investigated. The sensitivity analysis has shown that more information is needed on the substrate dependence of respiration rates.

The model currently maintains a constant ratio of leaves:stems:roots of 1:1:2. This ratio is representative of some measured values for *Larrea* but considerable variation does exist (Barbour et al. in press). More information is needed on the control of assimilate allocation to different vegetative organs. This will be particularly important when simulations of time periods longer than one year are attempted.

The upper and lower limits of assimilate pool sizes (δ_u and δ_l) currently used in the model are based on very few actual data. The actual values of these limits and whether or not they vary with season or organ need to be established. The true values of allocation percentages to reproductive and vegetative growth (α and β) also need to be established.

The actual magnitudes of volatile and leachable compounds produced need to be evaluated. Information is also needed on the effects of environment and physiological status of the plant on their production.

We have made the simplifying assumption that the ratio of carbon weight to assimilate dry weight is 1:2 for all structural and storage assimilates. The actual value of this ratio and the extent to which it varies among structure and assimilate pools in the various plant organs need to be established.

Several questions arise from the model concerning the reproductive activity of *Larrea* which need to be answered before more biological reality can be built into the model. Is it logical to assume that only one cohort of reproductive biomass can occur on the plant at any one time? Is it realistic to make all reproductive structures mature at the same rate? Is the mature weight of each individual reproductive structure the same or should the possibility exist for maturation at different sizes? Should all flower structural biomass be dropped when fruiting occurs or should some of it be converted to fruit structure? Are two-day limits for initiation of new reproductive buds and for maintenance of flowers realistic or should these times be made functions of environmental conditions?

We are currently initiating research to fill some of these obvious gaps in our knowledge of the biology of *Larrea*. Future refinements of the model based on this research and the US/IBP Desert Biome research mentioned above should lead us to a more complete understanding of the adaptations which allow *Larrea* to play such a dominant role in the warm desert ecosystems of North America.

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