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### Recommended Citation

Wilkin, D.C., Lommen, P.W., Robinson, J.V. 1975. Conceptualization and Early Development of a Water Response Ecosystem Model. U.S. International Biological Program, Desert Biome, Utah State University, Logan, Utah. Reports of 1974 Progress, Volume 1: Central Office, Modeling, RM 75-49.

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**1974 PROGRESS REPORT**

**CONCEPTUALIZATION AND EARLY DEVELOPMENT OF A  
WATER RESPONSE ECOSYSTEM MODEL**

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**US/IBP DESERT BIOME  
RESEARCH MEMORANDUM 75-49**

in

**REPORTS OF 1974 PROGRESS  
Volume 1: Central Office, Modeling  
Terrestrial Model Section, pp. 1-21**

1974 Proposal No. 2. 1.3

**Printed 1975**

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Citation format: Author(s). 1975. Title.  
US/IBP Desert Biome Res. Memo. 75-49.  
Utah State Univ., Logan. 21 pp.

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## INTRODUCTION

Ecological modeling within the Desert Biome program has been characterized by two contrasting approaches. The first, often called "question-oriented" modeling, generated a collection of independent models which addressed specific questions about desert ecosystems, such as "What is the annual wood consumption for a colony of termites?" These questions were usually raised by field investigators who expected the resulting model to assist and complement their research program. The second approach, referred to as "general-purpose" modeling, was planned entirely by the central modeling staff and concentrated on a relatively complex model of the entire ecosystem. This ecosystem model was divided into subsystem models (plant, animal, abiotic/soil) which were developed at varying levels of sophistication to provide a set of replaceable modules for each subsystem. The general-purpose model was designed to answer questions about the dynamics of desert ecosystems; a question addressing a facet of soil moisture conditions, for example, would be answered with a model composed of a detailed abiotic module but with relatively simple versions of the plant and animal subsystem models.

There were inherent inadequacies in both modeling philosophies. The question-oriented models, although of considerable interest and utility, sidestepped the original objectives of the Desert Biome program, which focused upon the development of a complete ecosystem model. The general-purpose modeling effort demanded a greater understanding of the biology and ecology of desert organisms than the present state of the science could provide. In order to satisfy the criteria permitting generality in application, the model had to represent many processes and relationships for which the only available data base was derived from more mesic systems or for which there was really no data base at all. The processes of translocation of photosynthate and root growth, for instance, were critical to the plant components of the model, but the modelers could only make reasonable guesses at the appropriate parameters. A positive result of these impediments to model construction was the identification of the most important fields for further research, and this is having an impact on the directions of the field studies. In plant projects, for example, more attention is currently being given to root distribution and turnover.

This report is concerned with a third approach within the Desert Biome modeling studies, which is a compromise between the two enterprises discussed above: a question-oriented ecosystem model. The advantages of question-orientation are retained, so that the model will include only those components and processes which are considered "important" in the context of the question. A further constraint is that guesswork will be minimized, and therefore processes for which there are no data bases will be black-boxed. The characteristics of an ecosystem scale of modeling will be retained by representing abiotic, soil, producer and consumer sections of the system.

The IBP ecosystem studies were intended to attempt an ecosystem-level model of the various biomes. To this end, the spectrum of funded research covers the main functions and entities of each ecosystem. Despite difficulties in implementing the original research design, the Desert Biome has assumed a commitment to ecosystem-level modeling for the duration of the program.

## THE QUESTION

Early in 1974 a model design committee was formed to plan the work on a question-oriented ecosystem model. This committee was chaired by George Innis and was comprised of all the modeling staff plus the Directorate. The committee deliberated on the choice of a suitable question from the following list of three:

*Question 1;* What is the annual effect ( $\pm$  one field-determined standard deviation 80% of the time) of halving or doubling the long-term mean annual precipitation (either natural or irrigated increase) on the above-ground phytomass? [The model answering this question shall be sufficiently parameterized to apply to all Desert Biome sites without structural change.]

*Question 2;* What is the effect of "standard" and perturbed stocking density by domestic herbivores (cattle or sheep) on the pattern of carbon flow in desert ecosystems?

*Question 3;* What is the effect of halving or doubling precipitation or primary production on the distribution of N in the forms of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in interplant spaces and beneath the canopy?

Ultimately, question 1 was selected for a full-scale modeling effort, largely on the basis of the dominant role water plays in determining primary production in arid ecosystems.

A preliminary outline of this model, called the Water Response Model, was presented at the annual Desert Biome Informational Meeting in March 1974. From suggestions and comments received there, and elsewhere, the question the model was to address was refined somewhat as follows:

What is the *effect* on the annual, above-ground *phytomass* on the five validation sites of *increasing* or *decreasing* the annual *water input* above or below the *long-term* pattern now prevailing?

The italicized key words in the question were then defined in order to reduce ambiguity as much as possible:

*Effect:*

Effect is measured on the five validation sites by tracking the above-ground phytomass (in kg carbon/ha equivalent)

of plant species which will, or do, constitute at least 85% of the above-ground phytomass of those classified as non-herbaceous species and of those which will or do constitute 85% of the above-ground phytomass in the herbaceous species.

*Increasing or Decreasing:*

The seasonal patterns of water input characteristic of each site will not be altered. The existing rainfall intensities (e.g., mm/hr for seasonal storms) will also not be changed. The major difference will be in increasing or reducing the number of rainfall events, and/or increasing or reducing the lengths of events occurring at the existing frequency. As long as these conditions are met, the only significant difference between natural and applied water inputs, from the model point of view, will be temperatures of air and water during the precipitation event, and rain-borne nutrient inputs. Assuming extant seasonal patterns and extant storm intensities, any water input scenario can be simulated subject to the constraints outlined below under Water Input.

*Long-term:*

Equals the length of record of a station or stations representative of the site being simulated.

*Water Input:*

The net effect of the simulated modification will be to increase or decrease the annual rainfall totals during the period of modification relative to the existing long-term medians for the five sites. The median has been chosen as a better comparative parameter than the mean because desert rainfall distributions are skewed, and the precipitation falls below the mean in more years than it exceeds the mean. Water inputs can be simulated either by means of preset measured variables, or by pseudo-stochastic generators utilizing appropriate statistical parameters. The only constraints are that extant seasonal patterns are used; extant storm intensities are used; and the median of the generator for a given simulation may not exceed twice the long-term median annual precipitation, nor drop below half the long-term median annual precipitation.

*Phytomass:*

Defined as live plant material, subdivided by organ. Units of measurement will be kg C/ha. Reproductive material will not be included as a state variable, but plant reproduction processes may be included.

Several constraints were also spelled out:

*Accuracy:*

The criterion for success will be that the model can simulate (within plus or minus one field-determined standard deviation of the field-determined mean, 80% of

the time) the amount of carbon (kg C/ha) in the above-ground phytomass.

*Functional Group:*

Plant species will be lumped insofar as possible into functional groups, the members of which are similar enough in life form, phenology or response characteristics to be considered together as members of a homogeneous group.

*Length of Simulation:*

In actuality, long-term changes in precipitation elicit changes in community structure such as successional changes. The processes involved in such changes involve poorly understood competitive interactions and autecological processes which we have not yet researched adequately. Consequently, we are not yet prepared to simulate these longer-term changes. It is for this reason that this simulation will be restricted to a maximum of about five years.

Finally, 14 other conditions and assumptions were listed:

1. The model will be coded in FORTRAN.
2. The time-step of the model will be from two days to one week.
3. The aforementioned time-step was chosen to provide the indicated accuracy at one-month intervals.
4. The CO<sub>2</sub> concentration throughout the plant canopy is assumed constant.
5. The light is assumed constant throughout the plant canopy for photosynthesis and growth.
6. Fresh stems photosynthesize.
7. Runoff of water can be treated either in an average way, considering the topography above and below the site, or simply assumed to equal runoff.
8. The model will contain vertical stratification. Some horizontal spatial heterogeneity may be accommodated.
9. The effects of herbivory on the system will be explicitly modeled where information is available and of significant impact, implicitly where not.
10. Detritus will generally be handled by a "furnace" approach (it will be consumed as a function of moisture and temperature without regard to what is doing the consuming). If sufficient data exist (e.g., for termites) effects of individual species may be considered.
11. Decomposition will also be handled by a "furnace" approach.
12. Nitrogen will be tracked by soil horizon.
13. Soil water potential will also be tracked by horizon.
14. Desert Biome data will be used in the model wherever possible.

## CONCEPTUALIZATION

With the objectives, key word definitions, constraints and assumptions stated so clearly, the conceptualization of model structure proceeded rapidly. The entire model was visualized as shown in the box-and-arrow diagram of Figure 1.

Vegetation and animal submodels were initially conceived as shown in Figures 2 and 3.

The nitrogen and decomposition submodels are represented in Figures 4 and 5. The initial approach to the inclusion of nitrogen as a constraint in the Water Response Model relied heavily on a nitrogen submodel developed by the Grassland Biome program to perform a similar role. [This submodel was considerably modified in the course of programming the vegetation submodel.]

Finally, the two truly abiotic submodels are diagrammed in Figures 6 and 7. Modeling heat transfer and soil water flow has been specifically studied in the Desert Biome since the first year of the program (Hanks et al. 1971). The culmination of this specialized modeling effort in the work of Griffin et al. (1974) was used as the basis for the abiotic section of the Water Response Model.

**VARIABLE NAMES**

In order to facilitate the cooperative effort of the modeling team by reducing confusion from the outset, a convention and hierarchy in the naming of the variables was adopted. The first letter of all variables would be either X, C, T, Z or P, whose meanings are shown in Table 1, along with the hierarchy to be used if a variable has more than one use.

The second letter of a variable name (with the exception of parameters and driving variables) represents the characteristic letter of the submodel of origin (Table 2). The remaining letters of a variable name would be chosen as a phonetic representation of the variable. The state variable names for the various submodels described by the box-and-

arrow diagrams, and the naming conventions, are given in Table 3. Finally, a list of "communication" variables was compiled. These variables are calculated or introduced in one submodel and needed by another to determine a rate of transfer. The preliminary list of these variables is given in Table 4.

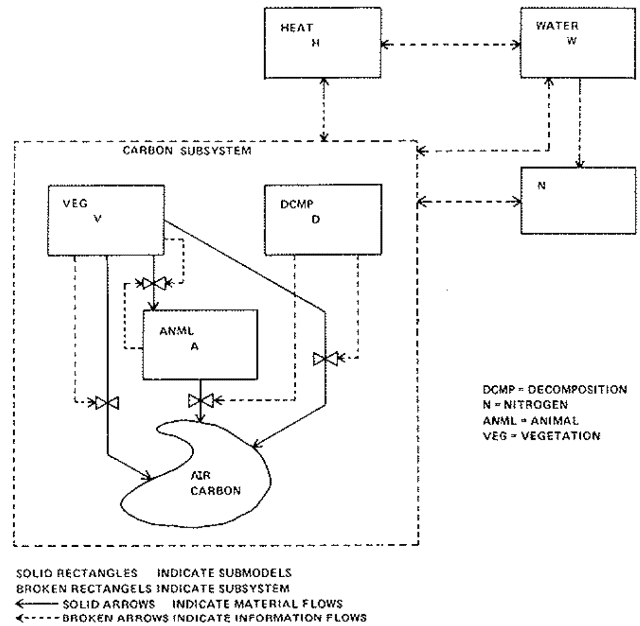


Figure 1. Submodels and subsystems of the Water Response Model.

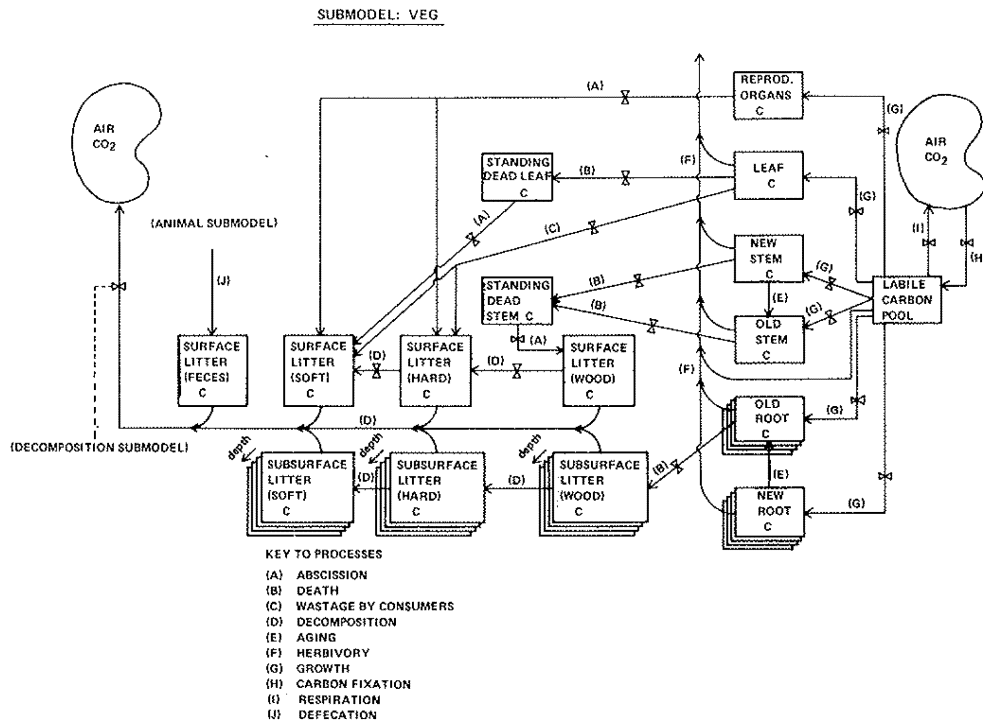


Figure 2. Box-and-arrow diagram of VEG submodel.

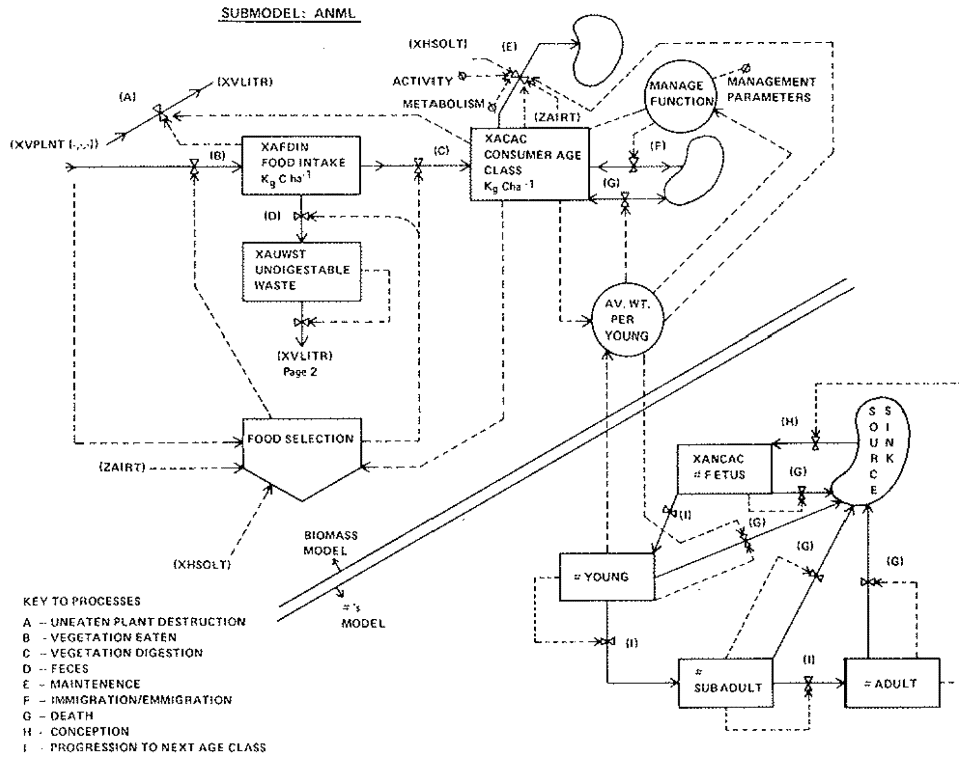


Figure 3. Box-and-arrow diagram of ANML submodel.

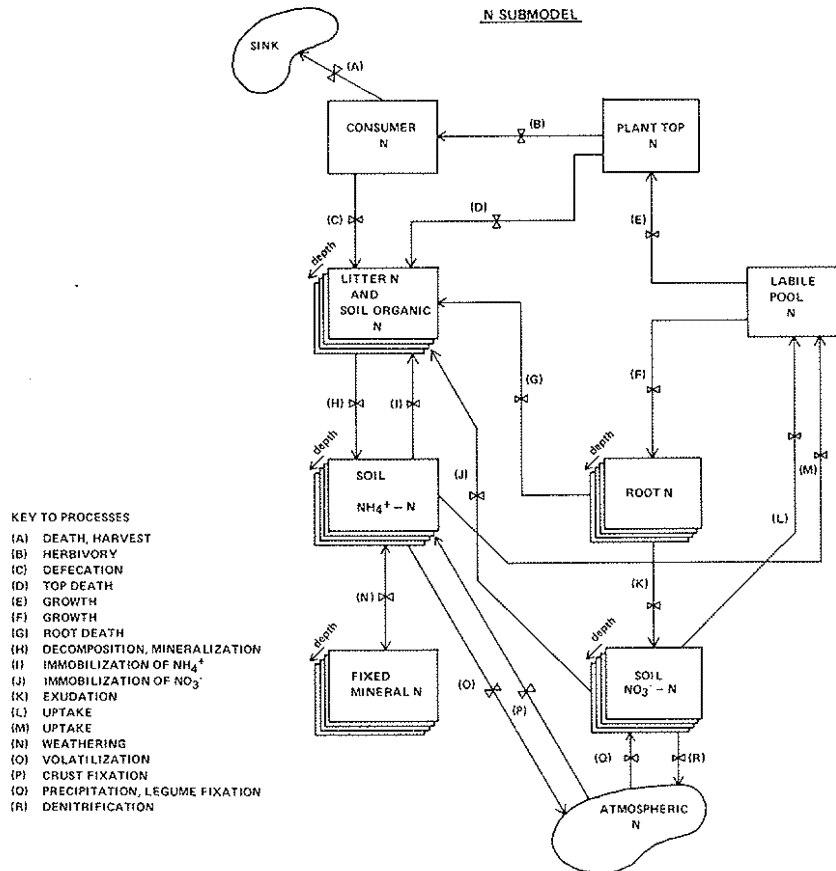


Figure 4. Box-and-arrow diagram of N submodel (nitrogen).

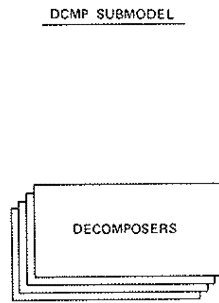


Figure 5. Decomposition submodel. As can be seen, no input or output. Acts only to control flows of decomposition in VEG and N submodels.

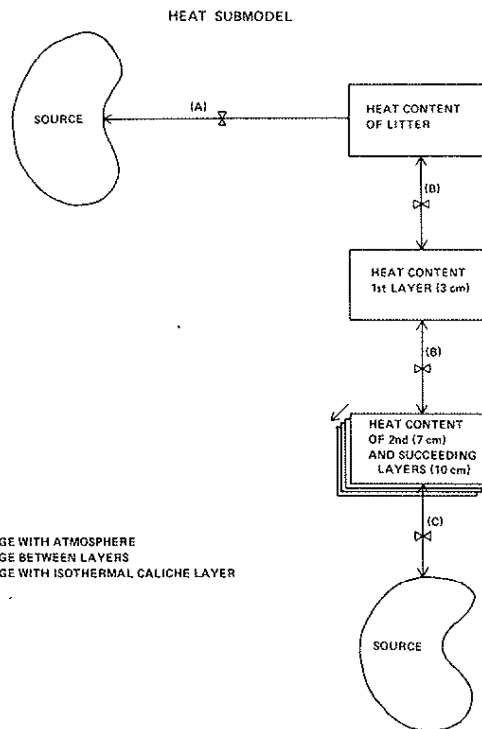


Figure 6. Diagram of HEAT submodel.

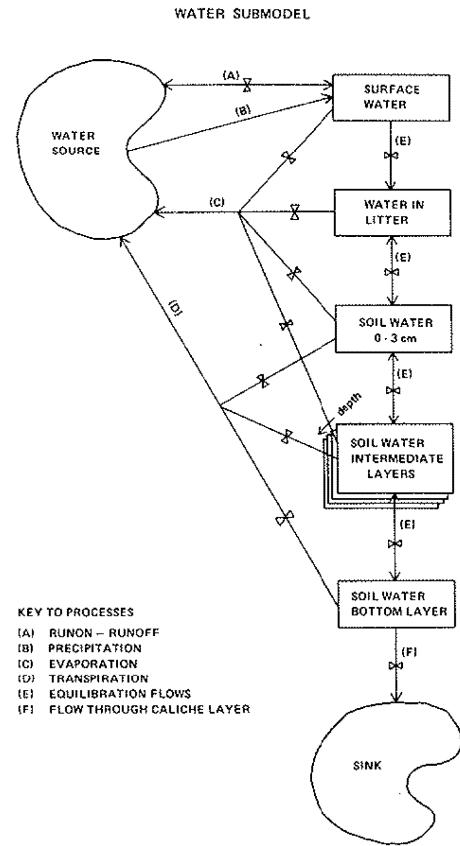


Figure 7. Diagram of WATER submodel.

Table 1. Convention and hierarchy utilized to name variables

X	= State variable
C	= Communication variable
T	= Temporary (internal) variable
B	= Driving variable
P	= Parameter

Table 2. Characteristic letters for submodels

Submodels	Name	Characteristic letter
Heat	HEAT	H
Water	WATER	W
Nitrogen	N	N
Phosphorus	P	P
Decomposition	DCMP	D
Vegetation	VEG	V
Animal	ANML	A

Table 3. State variable names

Submodel	Variable	Name *	Units
N	Consumer N	XNCØNS	kg N/ha
	Plant top N	XNTØP	"
	Labile pool N	XNLBP	"
	Litter and soil org. N	XNLIT (depth)	"
	Root N	XNRØØT (depth)	"
	Soil NH <sub>4</sub> <sup>+</sup> -N	XNNH4 (depth)	"
	Soil NO <sub>3</sub> <sup>-</sup> -N	XNNØ3 (depth)	"
	Fixed mineral N	XNMIN (depth)	"
WATER	Surface water	XWSURF	mm
	Water in litter	XWLIT	mm/mm
	Water in soil layers	XWHTA (depth)	mm/mm
VEG	Live plant carbon (functional group, plant part, phenophase)	XVPLNT (FG,PP,PH)	kg C/ha
	Carbon in litter (location, type)	XVLITR (LOC,TYP)	kg C/ha
HEAT	Heat content of litter	XHLIT	calories
	Heat content of soil layers	XHSOIL (depth)	calories
DCMP	Decomposer biomass	XDBMS (depth)	kg C/ha
ANML	Food intake (species, age class)	XAFDIN (S,AC)	kg C/ha
	Undigestible waste	XAUWST	"
	Biomass (species, age class)	XABSAC (S,AC)	"
	Numbers (species, age class)	XANSAC (S,AC)	"

\* S = species,  
AC = age class,  
FG = functional group,  
PP = plant part,  
PH = phenophase,  
LOC = location,  
TYP = type.



Table 4. Communication variables

Required by	Variable	Name	Units	Source	Time**	Depth
VEG	$[NO_3^-]$ (·)	XNNØ3	ppm	N	T	Every
	$[H_2PO_4^-]$ (·)	XPPØ4	ppm	P	T	Every
	$[NH_4^+]$ (·)	XNNH4	ppm	N	T	Every
	Soil water potential (·)	CWPSI	bars	WATER	$\frac{DT}{DT}$	Every
	Soil temperature (·)	XHSOLT	°C	HEAT	$\frac{DT}{DT}$	Every
	Air temperature	BAIRT	°C	Driving variable	$\frac{DT}{DT}$	2 meters
	Photoperiod	CHPHPD	---	HEAT	$\frac{DT}{DT}$	Soil surface
	Animal removal	CAAR (FG,PP)*	kg C·ha <sup>-1</sup> ·dt <sup>-1</sup>	ANML	DT	---
	Fraction of possible sunlight	CHFØPS	---	HEAT	$\frac{DT}{DT}$	Top of canopy
	No. ungulates	CAUN (FG)*	#/ha	ANML	$\frac{DT}{DT}$	---
	Ave. distance walked	CAAD (FG)*	km	ANML	DT	---
	Feces	CAUWST	kg C/ha	ANML	T	---
	Ave. peak runoff intens.	CWPRI	mm/hr	WATER	DT	---
	Animal veg. dest.	CADEST (FG,PP)*	kg C/ha	ANML	DT	---
WATER	Rainfall	BRAIN	mm	Driving variable	DT	Top of canopy
	Transpiration	CVTSPR (·)	mm·layer <sup>-1</sup> ·dt <sup>-1</sup>	VEG	$\frac{DT}{DT}$	Every
	Solar radiation	BINSOL	langley/dt	Driving variable	$\frac{DT}{DT}$	Top of canopy
	Relative humidity	BRH	%	Driving variable	$\frac{DT}{DT}$	---
	Wind distance	BWIND	km/dt	Driving variable	$\frac{DT}{DT}$	---
	Air temperature	BAIRT	°C	Driving variable	$\frac{DT}{DT}$	2 meters
	Vegetative cover	CVVCØV	---	VEG	T	Vert. proj.
	Litter cover	CVLCØV	---	VEG	T	Surface
	Litter amount	XVLITR (·)	kg C/ha	VEG	T	Surface
	Albedo	CHALBD	---	HEAT	T	Above canopy
N	Litter amount C	XVLITR (·)	kg C/ha	VEG	T	Every
	Legume C	XVPLNT (·)	kg C/ha	VEG	T	Every
	Rainfall	BRAIN	mm	Driving Variable	T (for T +DT)	Top of canopy
	Volumetric water content	XWHTA (·)	---	WATER	$\frac{DT}{DT}$	Every
P	Litter amount C	XVLITR (·)	kg C/ha	VEG	T	Every
	Rainfall	BRAIN	mm	Driving variable	T (for T +DT)	Top of canopy
	Volumetric water content	XWHTA (·)	---	WATER	$\frac{DT}{DT}$	Every
DCMP	Soil temperature	XHSOLT (·)	°C	HEAT	$\frac{DT}{DT}$	Every
	Volumetric water content	XWHTA (·)	---	WATER	$\frac{DT}{DT}$	Every
	Litter water content (or index thereof)	CWLWTC	---	WATER	$\frac{DT}{DT}$	Surface
	Litter amount C	XVLITR	kg C/ha	VEG	T	Surface
Litter amount N	XNLITN (·)	kg C/ha	N	T	Every	
HEAT	Litter amount	XVLITR (·)	kg C/ha	VEG	T	Surface
	Solar radiation	BINSØL	langley/dt	Driving variable	$\frac{DT}{DT}$	Top of canopy
	Relative humidity	BRH	%	Driving variable	$\frac{DT}{DT}$	---
	Wind distance	BWIND	km/dt	Driving variable	$\frac{DT}{DT}$	---
	Air temperature	BAIRT	°C	Driving variable	$\frac{DT}{DT}$	2 meters
	Vegetative cover	CVVCØV	---	VEG	T	Vert. proj.
	Litter cover	CVLCØV	---	VEG	T	Surface
	Temp. of caliche layer	PTØCL	°C	DATA	T	Caliche layer
Volumetric water content	XWHTA (·)	---	WATER	$\frac{DT}{DT}$	Every	

Table 4, continued

Required by	Variable	Name	Units	Source	Time**	Depth
ANML	Food	XVPLANT (FG, PP, PH)*	kg C/ha	VEG	T	Above ground
	Air temperature	#AIRT	°C	Driving variable	$\overline{DT}$	2 meters
	Surface temperature	XHSOLT	°C	HEAT	$\overline{DT}$	0

\* FG = functional group,  
 PP = plant part,  
 PH = phenological state.

\*\* T = model tracks time course of this variable,  
 DT = change occurring during time-step,  
 $\overline{DT}$  = average value during time-step.

### INPUT FROM INVESTIGATORS

At the Desert Biome Information Meeting held in March 1974, several workshop sessions were conducted to explore, among other things, principal aspects of the model in terms of data availability and research needs. These workshops were 1) Primary Production and Water; 2) Herbivory; 3) Granivory; 4) Detritus-based Food Chains; and 5) Nitrogen. The reports from these workshops are presented below in their entirety. It will be apparent to the reader that some sections are more applicable to the Water Response Model than others; no attempt was made to edit out the less pertinent information. A lot of the discussion was directed toward research needs, which is a natural by-product of any modeling investigation.

#### PRIMARY PRODUCTION AND WATER (REPORTED BY B. E. NORTON)

The discussion during this session centered on the following four questions:

1. Given the vegetation standing crop at the beginning of the year, and any given weather pattern, what is the primary production by species and organ on each validation site?
2. Can the above question be answered by going through the causal steps of photosynthesis, translocation and growth within the next two years? If not, can this causation be "black-boxed" by some regression method which bridges the photosynthesis studies and the measured primary production on the sites?
3. How close are we to having the parameters for the Hanks soil water model so that we can simulate the changes in soil water over time on all sites, given the rainfall inputs?
4. What additional research is needed to get whatever parameters we do not have?

#### Primary Production

1. **Phenology**—The role of environmental variables is to switch plant functions from one phenological state to the next, and to be determinants of amount of carbon fixed

during each phenological phase. Within a phenological phase, allocation of photosynthate will be directed by read-in distribution functions modified by photosynthetic rate.

2. **Respiration**—More research is needed to measure respiration rates of stems and roots. It was recommended that this be incorporated into current 1974 studies.

3. **Herbivory**—A critical part of the plant model will be incrementing photosynthetic tissue, because of the compounding effect on photosynthate production. For this reason, insect herbivory on leaf tissue should be treated as an important function in the animal model.

4. **Reserves**—Stored reserves in roots and stems could be an important factor for growth at the beginning of the growing season of perennials. This should be considered as a research project for 1975.

5. **Summary**—In a general answer to questions 1 and 2, the plant meeting believed that we are getting close to predicting primary production by going through the causal steps of photosynthesis, translocation and respiration. This effort should be continued. As a check on the mechanistic model, an index of shrub growth on the validation sites should be obtained at regular intervals (2-4 weeks) during the growing season. Some data on this are already available from Curlew Valley and Jornada. It was agreed that Rock Valley should also be included.

#### Soil Water and Plant Production

1. The Hanks soil water model is not equipped to handle horizontal heterogeneity. All validation sites are currently measuring soil water potential beneath shrub canopies and in interspace soils. Curlew Valley and Silverbell sites report no significant difference in soil water potential between canopy and interspace zones, but Rock Valley data indicate a difference in the soil water regimes. The meeting recommended that the soil water profiles beneath canopy and bare areas be integrated (weighted according to percent shrub vegetative cover) to provide model input. More detailed information on the horizontal variation in soil water potential was identified as a research need on all validation sites.

2. Soil temperature variation is sufficiently predictable to permit the use of read-in sine curves for modeling purposes, so that it would not be calculated by the model per se.
3. Root distribution (either as biomass or root density per profile interval) is an input requirement for the soil water model. The roots do not need to be differentiated by species. The raw data for this are already available.
4. Potential transpiration (transpiration rate when soil moisture is not limiting) and potential evaporation data through the annual seasons are input requirements to the soil water model. Data on potential transpiration are limited at present, and measurements should be taken this year by plant investigators where necessary. Ecophysicologists suggested that relative photosynthetic activity could be used as an index of transpiration rate, and hence root extraction of soil water.
5. The meeting agreed to omit plant water potential from the model. The driving moisture variable for plant function will be soil water potential, as calculated by the Hanks model. Where plant water potential has been measured in the past as a variable in gas exchange rates, additional research may be required to relate carbon fixation rates to soil moisture status.

#### *Soil Water*

1. In answer to question 3 (How close are we to having the parameters for the Hanks model so that we can simulate the changes in soil water over time on all sites, given rainfall input?), the water group concluded that data collected to date and laboratory analyses are probably adequate to run the model. Some field calibration still needs to be done, however, to adjust lab-measured variables to field situations.
2. The water group specified as a research need the examination of the significance of temperature-induced soil water flux as it affects soil water potential.

#### HERBIVORY

(REPORTED BY J. A. MACMAHON)

The questions considered were

1. What is the rate at which herbivores are utilizing the vegetation production -- or reducing that production through girdling, sucking, etc. -- on each of the validation sites? To what extent can we apportion this utilization among the different insect species, functional groups or taxonomic blocks?
2. To what extent do these effects influence the vegetation structure and function?
3. What are the constraints on herbivore populations?

It was concluded that

1. If vertebrate populations are known accurately, amount of food required can be estimated and *generally* the kinds of food.
2. The same is thought to be true for our knowledge of insects. This feeling was not unanimous.

3. Obviously, we need to know more about preference arrays.
4. We do not know the values for gross consumption vs. wastage for any species.
5. We do not, in general, know the consumptive or non-consumptive effects of animals on vegetation structure and function, or even the response of individual plants.
6. Constraints on herbivore populations are moderately known.

Two themes evolved during discussion:

1. If we are going to model suckers and nematodes as part of the plant because we have no data separating the two, then we probably should ignore all consumers (see 5 above) in our models for the same reason.
2. The most judicious plan for future work revolves around manipulation of the system by exclosure, defaunation, etc., etc. Creative experiments along these lines would answer our most pressing questions with regard to herbivores in the desert ecosystem.

#### DETRITIVORY

(REPORTED BY F. H. WAGNER)

The detritivory workshop addressed itself to several questions on the degree to which granivores utilize seed production and reserves, and 1) affect vegetation production and/or structure thereby, and 2) are themselves limited by the quantity of seeds available to them. Among the major points made by the participants were the following:

#### *Seed Reserves and Vegetation Expression*

1. Goodall reported that seed production rates exceed the measurable seed reserves in the soil by several orders of magnitude. Whitford stated that, on the Jornada, annual production rates approximate  $10^{12}$  seeds, whereas measured standing crops typically approximate  $10^6$ . Clearly, the output is very high, probably approximating the input. Goodall also pointed out that in some instances, seedling numbers approach the number of seeds in the soil. Mechanisms of seed removal are physical (wind, water, burial within the soil below where they can germinate) and biotic (fungal, bacterial, granivorous).
2. Whether or not the reserves are ever reduced to where primary production and/or vegetation composition are affected is not known. The point was generally agreed upon that the sequence from seed deposition to vegetation expression involves a series of processes, and granivory is influential at only one or two. Graivory affects seed survival, but has nothing to do with germination rates and seedling demography.
3. None of the participants cared to generalize much about germination rates. These need to be studied species by species. Both Whitson and Reichman stressed the importance of the concept of "available" seeds for germination -- those at suitable depths, sites, moisture and temperature conditions. Many seeds get moved to depths where they cannot germinate and, therefore, should not be

thought of as part of the germinable (or forageable, for that matter) seed reserves. Whitson has begun detailed, experimental work at Jornada on annual germination and demography.

4. Although only a fraction of the "available" seed reserves germinate at one time, the group discussed the possibility that this reserve could be depleted in a low-probability series of wet years when a high proportion germinated, and the seedlings were grazed off by high populations of herbivores before seed production. Nagy suggested an experiment with continuous, high irrigation, and continuous removal of seedlings to develop a seed extinction curve. Other participants suggested research into such variables affecting germination as soil depth and scarification.

#### Granivory

1. Soholt reported on his small rodent study. He estimated that use, primarily by *Dipodomys merriami*, totaled about 10,200,000 seeds·ha<sup>-1</sup>·yr<sup>-1</sup>, and that this approached the production on the site. Some 76% of the diet was filaree (*Erodium*). Reichman reported seed use at 12,500,000·ha<sup>-1</sup>·yr<sup>-1</sup>; amazingly close agreement to Soholt's data. For the pocket mouse, 38% of the consumption was perennial seed, mostly *Larrea*. For the kangaroo rat, 13% was perennials and insects. Individual kangaroo rats collected as many as 4000 seeds per night, a feat which could be accomplished only by foraging from seed clumps, in Reichman's opinion. He also inferred rather strongly that the number of seeds foraged approximated a major fraction of the reserve.

2. Brown discussed the partitioning of the seed reserve among different granivorous species, this being accomplished on the basis of seed size, among other things. Birds select from the large end of the size spectrum, ants from the small and *Perognathus* from the midrange with considerable overlap with birds and ants. Brown sketched a regression line of seed size consumed on rodent body size for sandy areas in the Mohave and Great Basin deserts, and one for the Sonoran. The two lines had the same slopes, but the Sonoran line had a lower Y-intercept. Brown also sketched regression lines for two Y variables -- number of rodent species, and rodent population density -- on his index of rainfall predictability, namely the rainfall mean, minus the standard deviation. Two such lines were drawn each for the Mohave-Great Basin areas and for the Sonoran. For each of the two desert types, the two lines had essentially the same slope, and all had zero intercepts. However, the slopes for the two Mohave-Great Basin lines were substantially steeper than the two lines for the Sonoran, with a widening area between as the two pairs of lines diverged to the right. Brown postulated that the Sonoran slope might be lower because of lower seed availability and this could conceivably be due to foraging (and competition) by ants. In a concluding remark, Brown stated: "There isn't any doubt that desert granivores are food limited."

3. Gould reported that birds on the Silverbell site consume 70,000 to 90,000 seeds (7-9 kg) per hectare. Seed availability has a large influence on the numbers of birds on the site. Raitt reported that the breeding avifauna on the Jornada is primarily insectivorous while the winter migrants are

primarily granivorous. The number of wintering species tends to increase in years with above-average moisture, with playa species responding more than bajada and grassland inhabitants. There is some evidence that large overwinter populations can influence vegetation composition the following year. Brown has observed a nomadic pattern in overwintering desert birds, with the flocks tending to seek out and follow what were storm tracks during the year, and consequently had blishes of annuals. In so doing, they heavily exploit the seed reserves in areas of high production, and reduce overall variability of seed reserves. 4. Some summary statistics on the resource and its rate of use: a) production, 10<sup>12</sup> seeds·ha<sup>-1</sup>·yr<sup>-1</sup> (Jornada); b) typical standing crops, 10<sup>6</sup> (Jornada); c) rodent consumption, 10<sup>7</sup> (Reichman, Soholt); d) collection by rodents, 10<sup>10</sup> (Whitford, Jornada); by ants, 10<sup>10</sup> (Whitford, Jornada); by birds, 10<sup>8</sup> (Gould, Silverbell).

#### Vegetation Effects

1. Whitford's hypothesis is that foraging intensity is not sufficient to affect total primary production, but that preferential foraging may reduce the numbers of some plant species, and affect the distribution of others: a) ants utilize the small seeds heavily, may reduce the densities of those plant species which produce them; b) birds (primarily wintering concentrations) make heavy use of large seeds, may reduce the density of these plant species; c) rodents cache in clumps of seeds, may thereby produce clumping vegetation. In 1974, Whitford will start enclosure experiments to test this hypothesis.

2. Maza had some observations of seedling clumps that were probably produced by caching. Soholt questioned that this leads eventually to mature vegetation clumping because of the competition induced for the seedlings.

#### DETRITUS-BASED FOOD CHAINS (REPORTED BY J. F. McBRAYER)

Studies on detritus-based food chains, the animal component of decomposition, are probably the least advanced of all the areas funded for process studies. For the most part, workers from the various validation sites were unacquainted with one another and a good deal of the workshop time was invested in a review of the projects represented. Below-ground studies at Curlew Valley and Rock Valley have been in progress for just over a year. Investigations on the role of termites in desert ecosystems are more advanced, with well-established studies being carried on at both the Santa Rita and Jornada sites. Work on ground-dwelling beetles at Rock Valley has been in progress for three years and is now being integrated with the below-ground work. Nematode populations at Rock Valley are being intensively studied, with less frequent validation-type assessments being carried out at Curlew Valley, Jornada and the Tucson Basin.

Four questions were circulated to workshop participants in advance of the meetings. The questions and our responses to them are as follows:

1. What is the rate of detritus production on the validation sites by class (e.g., dead wood, leaf and plant reproductive material, dead roots, dead animal material)?

Only one site, Curlew Valley, reported measuring the rate of above-ground litter production (wood and leaf material). In addition, rate of dead wood production has been measured for Santa Rita. Standing crops of below-ground litter are being measured at regular intervals at Rock Valley and litter traps are due to be installed this season. No site is measuring below-ground inputs, although most are interested if a feasible technique can be demonstrated.

2. What proportion of this detritus is consumed by detritivores, by species or functional groups?

Nutting considers it a conservative estimate that termites consume 50% of the woody litter at Sant Rita. Other studies aimed at establishing litter consumption rates are not yet ready to report.

3. Given the detritus consumption by animals, what is the amount of material delivered by them to the decomposition processes in the form of partially macerated, but not consumed, detrital material and of feces?

We obviously cannot yet answer this question.

4. What are the constraints on detritivore populations?

We can only offer a hypothesis on what constrains detritivore populations. It is accepted that detritus is a "low quality" food source, being both deficient in nitrogen and rich in compounds (e.g., cellulose and lignin) for which animals commonly lack appropriate digestive enzymes. It was suggested that low ecological growth efficiencies may be characteristic of detritivores as a consequence of food quality and, thus, detritivore populations may be unusually susceptible to predation pressures.

Microbial-invertebrate synergisms, particularly as they apply to nitrogen balances, permit detritivory to occur and must be investigated before this question can be answered.

#### *Recommendations*

We feel it should be profitable for all concerned to convene this group with representatives of the microbial decomposer group and the modelers having responsibility for decomposition and mineral cycling. This group should develop a statement of objectives which will lead to parallel studies with ordered objectives on each of the sites. The priorities should be determined by potential importance and probability of success.

For the time being, we recommend at least a minimum program at each site which will measure detritus input and both microbial and detritivore standing crops.

#### NITROGEN (REPORTED BY N. E. WEST)

The discussion was centered around the question of what research should be undertaken in the remaining 2½ years of the formal Biome effort. We used the operational model of the nitrogen cycle of cool deserts and examined the possibility of obtaining data similar to those taken in Curlew Valley from other intensive sites so that the model could be used for comparative purposes. We used the matrix in Table 5 as a checklist of available data. The "x" means that this information is available from the data pool for the intensive sites. Names in the boxes refer to pre-Biome process study or non-Biome data available for filling our needs. Question marks mean that this information is not now available in any known source. Our conclusion was that we are within striking distance of obtaining data to fill this matrix. Available manpower (with a modest amount of budget) could generate the data to make possible the use of the existing model as a comparative tool in two years' time. Consequently, we are recommending that the Biome Directorate consider the support of the following projects, in order of priority:

1. Determination of N fixation rates at sites other than Curlew Valley for: a) Cryptogamic crusts; b) Rhizosphere or nodulated organisms.
2. Decomposition rates for major litter components at Silverbell and Rock Valley.
3. Interactions are needed with the other working groups on several fronts: a) We need to understand more fully the transfers wrought by animals working on the litter component. There is the distinct possibility that termites and mites may have a far greater role in nitrogen cycling than has been previously judged. b) We are missing data on litter fall from all of the sites except Curlew Valley. We would like to know the litter production rates for the major plant species at our intensive sites.
4. We need to know the soil clay content by depths at all of the sites in order to understand the exchange complex for ammonia and nitrate. Perhaps these data exist but we were not sure at the meeting.
5. Denitrification and volatilization rates need to be measured at Rock Valley and Jornada.
6. The chemical species of nitrogen and their respective amounts in soil pools must be better understood at Silverbell and Jornada.
7. There are a few other miscellaneous missing items that show up in the matrix. They should take only minor effort to pull out of existing data banks or by original research.

If the above effort is funded at a moderate level (probably somewhat less than what the decomposer group has been getting for the last three years), we feel that a comprehensive and comparative analysis of nitrogen cycle will be possible for four examples of desert ecosystems. This comparison should be of considerable basic and practical value.

Table 5. Data availability

	Curlew	Rock Valley	Silverbell	Jornada
<b>Pools</b>				
Above-ground biomass	x	Wallace & Romney	---	---
Below-ground biomass	x	Wallace & Romney	---	---
Fixed N in soil	x	Nishita	Westerman	?
Litter biomass	x	Bamberg	?	?
Cryptogam biomass	x	Not important	Not important	Not important
Consumer biomass	x	---	Weak	---
<b>Fluxes</b>				
N in ppt	x	NCAR	---	---
Cryptogam fixation	x	?	McGregor & Mayland	?
Decomposition	Comanor	?	?	Staffeldt
Above-ground litterfall	West	Bamberg	?	?
Below-ground litterfall	Fernandez	?	?	?
Symbiotic fixation	?	?	?	?
Plant uptake	New growth N content	Wallace	New growth Klemmedson	?
Denitrification	Eberhardt	Romey	Westerman & Dutt	?
Volatilization	Eberhardt	? difference	Insignificant	?

### ABIOTIC MODEL -- DATA REQUIREMENTS

With the design of the Water Response Model well in hand, it was thought desirable and useful to draw up a list of data needs for the abiotic section. The list is presented below. It is an idealized list in the sense that the modelers knew it was unrealistic to expect to be provided with full data on all of the items, and so some priorities are indicated. It was hoped, however, that it might be useful to the site personnel in their data collection, starting with the 1974 season:

1. Air temperature, °C at 2 m plus occasional profiles.
2. Precipitation by event, amount and intensity (average rate, or length of time over which event occurred).
3. Soil temperatures: a) prefer surface temperature by radiometer of some kind plus temperatures at 3, 10, 20, 30 cm . . . down to caliche layer; b) or acquire temperatures at the center of layers to be used (i.e., 1½, 6½, 15, 25 cm); c) frequency -- not too important but should include at least one diurnal series (e.g., at 0400 or 0500 hr and at 1300 hr).
4. Wind speed at 2 m: some profiles of characteristic situations would be useful (e.g., at 1400 and 1300 hr, obtain speeds at 0, 10, 20, 50, 100, 200 cm); profiles of wind, air temperature and dew point would be especially useful.
5. Dew point at 2 m (same comments as under "wind speed").
6. Soil characteristics: a) thermal conductivity with depth and water content ( $\text{cal}\cdot\text{cm}^{-1}\cdot\text{hr}^{-1}\cdot\text{C}^{-1}$ ); b) heat capacity with depth and water content ( $\text{cal}/\text{g}$ ); c) hydraulic conductivity with depth and water content ( $\text{cm}^2\cdot\text{hr}^{-1}\cdot\text{unit water tension}^{-1}$ ); d) soil water potential with depth, especially before and after rain, if a, b and c above are too involved and/or time consuming -- depths of 1.5, 6.5, 15,

25, 35 . . . cm.

7. Runon, runoff and standing water -- some general ideas (e.g., runon  $\cong$  2x runoff if rainfall  $\geq$  20 mm and intensity  $\geq$  40 mm/hr but for smaller storms, no runon or runoff; negligible amount of litter carried on).

8. Nitrogen requires: a) the amounts of ammonium, nitrate (nitrite?) by horizon (0-3, 3-10, 10-20 cm, etc.); b) it would be useful to be able to relate activity to biomass by horizon if possible, at least at the surface; c) the dependence of processes on temperature, water availability, substrate concentration (e.g., for immobilization, nitrification, denitrification, volatilization, mineralization).

9. Decomposition: activity by horizon and dependence on temperature, water and substrate.

### SITE VISITS

Following the information meeting, the modeling team decided to visit the intensive research sites in order to get a firsthand impression of the systems for which the model was being constructed. A certain level of familiarity with the sites had been acquired through the study of annual site reports, and some modelers had been acquainted with the sites on previous occasions, but it was now necessary to examine the ecosystems in the context of the Water Response Model. The general design and data needs of the model were fairly clear at this stage. During the site visits, the modelers were able to discuss the site data records with on-site personnel and evaluate the availability of data required to develop and implement the model. In the course of these site visits, rapport between modelers and field personnel was considerably enhanced and this has improved the working relationships during the later stages of modeling.

One of the major outcomes of these visits was the great amount of helpful ideas, opinions and suggestions that were received. Information and speculations on the mechanisms of various processes were contributed, as well as their relative importance to the system; often, the relative difficulty which we might expect in simulating them was expressed.

#### ANIMAL SUBMODEL -- PRELIMINARY STRUCTURE

As work progressed, various reports of a preliminary nature were written. The following material constitutes such a report written to help guide the actual coding of the animal submodel.

It will be necessary to model animal numbers (per unit area) and individual animal weights in order to cover the needed features. Total population consumption (and thereby impact on the producer community) will depend on energetic requirements which means we must have weight per individual. Weight per individual and total population yields a basis for determining total consumption.

The flows in the numbers submodel (Fig. 8) will be quite like those of the weight submodel with a few exceptions. We shall discuss here the numbers submodel. The flows are

1. Conception: Formation of fertile eggs. This flow will be controlled by adult population, adult conditions at conception, genetics and abiotic factors
2. Loss of fetuses: This flow will be controlled by the number of fetuses available, adult conditions and abiotic factors.
3. Birth: Those fetuses that are not lost will, at the end of the gestation period, be born. Abiotic factors and adult condition may affect the gestation period.
4. Loss of young: Young may be lost to predation, cannibalism, abiotic factors, nutrition (mal) and unexplained causes.
5. Recruitment to subadult: Young which are not lost develop, in time, to subadults. The time required may depend on genetics and abiotic factors.
6. Loss of subadults: Subadults may be lost for the same reasons but in different amounts as young.
7. Recruitment to adult: Subadults which are not lost are, in time, sexually mature. Factors affecting the time required are genetic and abiotic.
8. Loss of adults: Adults may be lost for the same reasons but in different amounts as young. Adults are also lost as a result of old age.

#### SOME KEY POINTS NEEDING ATTENTION

1. Fetus data are scarce in many species, yet their treatment seems worthwhile (biologically). Default techniques to treat data shortages will be needed.
2. Adult condition will be computed as a ratio of average weight to expected weight. Low adult condition reduces conception rate and birth rate. However, for many mammals the females breeding in their first season are

lightweight but in perfect health. To deal with this we may need a "lightweight adult" or "young adult" class as distinct from the adult class.

3. For multiple litters, the fetus, young, subadult and young adult sequence of compartments will be repeated for each cohort. (Cohort shall designate a group of individuals of approximately the same age.)

#### MORE DETAILS ON THE FLOWS

1. Define:

OMFPF = Observed maximum number of fetuses per female per litter (a species-specific variable). OMFPF shall be doubly indexed for species and litter-within-a-year.

FCE = Female condition indicator = weight/expected weight, dimensionless.

PPBF = Proportion of the population composed of breeding females, dimensionless. PPBF may be indexed doubly for species and litter-within-a-year.

PBFBUT = Proportion of breeding females breeding/unit time; female/time. PBFBUT may be doubly indexed for species and litter-within-a-year.

BWF = Breeding window function. This is a piecewise constant function which is one when breeding may occur and zero otherwise.

The number of fetuses formed per unit time will be given by the product of the number of adults, PPBF, PBFBUT, OMFPF, BWF and FCI.

2. The first draft should be a constant rate, FDR (fetus death rate), increased by extremes of temperature and moisture (no.·female<sup>-1</sup>·unit time<sup>-1</sup>).

Define:

TEFDR = Temperature effect on fetus death rate, dimensionless.

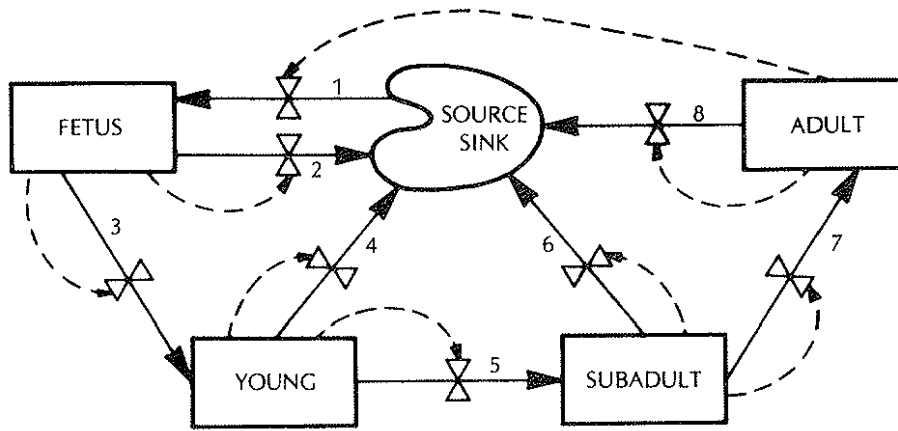
MEFDR = Moisture effect on fetus death rate, dimensionless.

The number of fetuses lost per unit time will be given by the product of the number of fetuses, FDR, TEFDR, MEFDR and FCI.

3. The fetuses that survive the gestation period are born (unless losses at birth are to be included). The gestation period may be constant (as is approximately true for most large mammals) or may depend on environment.

4. Loss-of-young definitions:

YDR = Young death rate due to unexplained causes (no.·young animal<sup>-1</sup>·time<sup>-1</sup>).



**Figure 8.** Box-and-arrow diagram for model structure for mammals, birds and lizards (compartment names are different for birds and mammals). Young are dependent (on adults) for some or all of their food, shelter, . . . Subadults are independent but sexually immature.

YCI = Young condition index = young weight/expected young weight.

YDRMT = Young death rate modifier for temperature, dimensionless.

YDRMM = Young death rate modifier for moisture, dimensionless.

YAGE = Age of the youth as a fraction of the expected time as a youth.

ENY = Effect of nutrition, dimensionless ( $ENY = YAGE * YCI + (1 - YAGE) * FCI$ ).

The number of young lost per unit time is given by the number of young multiplied by the sum of YDR, YDRMT, YDRMM and ENY. Note that the factors YDRMT, YDRMM and ENY are not independent.

5. Animals that do not die as young become subadults as soon as they become independent of the adult. This development time may or may not depend on environmental factors.

6. The loss of subadults will be handled, formally, exactly as the loss of young.

Define:

SADR = Subadult death rate due to unexplained causes ( $\text{no.} \cdot \text{subadult}^{-1} \cdot \text{time}^{-1}$ ).

SACI = subadult condition indicator = subadult weight/expected subadult weight.

SADRMT = Subadult death rate modifier for temperature, dimensionless.

SADRMM = Subadult death rate modifier for moisture, dimensionless.

SAAGE = Subadult age or a fraction of the expected time as a subadult.

ENSA = Effect of nutrition, dimensionless.

The number of subadults lost per unit time is given by the number of subadults multiplied by SADR multiplied by the sum of SADRMT, SADRMM and ENSA. Again, SADRMT, SADRMM and ENSA are not independent.

7. All subadults that survive to sexual maturity are recruited into the adult class. The time required to achieve sexual maturity may or may not depend on environmental factors.

8. Adult losses will parallel (computationally) the subadult losses except that an age factor must be included.

Define:

ADR = Adult death rate due to unexplained causes ( $\text{no.} \cdot \text{adult}^{-1} \cdot \text{time}^{-1}$ ).

ACI = Adult condition indicator = adult weight/expected adult weight.

ADRMT = Adult death rate modifier for temperature, dimensionless.

ADRMM = Adult death rate modifier for moisture, dimensionless.



AAGE = Adult life expectancy, time.

AAF = Adult age effect. A loss rate due to age which assures that fewer than 10% of the population exceed the age of AAGE (no.  $\cdot$  adult<sup>-1</sup>  $\cdot$  time<sup>-1</sup>).

ENA = Effect of nutrition, dimensionless.

The number of adults lost per unit time is given by the number of adults multiplied by the sum of AAF and ADR multiplied by the sum of ADRMT, ADRMM and ENA (no. of adults \* (AAF + ADR \* (ADRMT + ADRMM + ENA))). Note the way in which lightweight adults would affect birth rate. Also note that, in general, any of these effects may be omitted if desired by setting the appropriate function to zero or one.

### VEGETATION SUBMODEL -- FIRST DRAFT

The first submodel of the Water Response Model to be actually running and simulating its part of the ecosystem was the perennial vegetation submodel. A report was written at this stage by D. C. Wilkin. It shows the way the main processes have actually been simulated, as well as many of the decisions and difficulties involved. There is also a section describing how the submodel was parameterized for Curlew Valley.

The "VEG" submodel of the Water Response Model has been coded in Fortran IV for the Burroughs 6700 computer at Utah State University, and is compiled as a separate subroutine which must be bound to the other subroutines comprising the model. Two other subroutines are of special importance to its operation, titled F1 and F2, which are interpolative subroutines defining the majority of functional relationships between and among variables. These three subroutines compile in 12.2 sec CPU time, and are punched on 858 cards, including comments.

The VEG submodel has been designed specifically to simulate as many as six plant functional groups at present. Any more than six will require minor changes to the code. A functional group would consist of plant species similar enough in the specific response items to which this model addresses itself as to be considered as one characteristic group. Most usually, a plant functional group will consist of only one species. The model simulates eight plant parts within each functional group; the first seven are structural parts: leaf, flower, fruit, new stem, old stem, old root, new root. The final plant part is a pool of labile material which is theoretically capable of translocation from one structural plant part to another. The object of the model is to provide a reasonable predicting tool for the above-ground biomass of the plant functional groups being simulated. Biomass is in kg/ha.

The various litter categories are also tracked by the VEG submodel. These are broken down into, at present, four categories corresponding to rates of decomposition and each category is broken down according to location in the system: standing dead, surface and by the soil horizons that are defined by the abiotic submodels.

Interactions with other submodels are as follows: the various abiotic drivers are passed from the abiotic submodels. These are air temperatures, soil water potentials at various depths in the soil, relative humidity, mineral nitrogen levels, fraction of possible sunlight hours, photoperiod and soil temperatures by depth.

The ANML submodel passes values for herbivory of various plant parts, and for transfers from live plant part categories to litter, as in wastage. The DCMP submodel (called from the N submodel) actually decomposes the litter that is being tracked by VEG.

The VEG submodel, in turn, supplies to the ANML submodel the amounts of vegetation and litter by category, plus a phenological index of the material to give some index of palatability of various plant parts. To the abiotic submodels, it passes such values as the total transpiration requirement, the photosynthesis occurring during a time-step and the root distribution among soil horizons.

The first call to the VEG submodel, when running the Water Response Model, is to an entry point labeled VINIT. Each subroutine in the model reads its own input and then prints out what it reads as a check. In VINIT, certain variables not in the common block are dimensioned and/or declared, in addition to the reading and writing of input variables. Virtually no parameters are included in the code itself (of the submodel), but are, rather, read as input.

After the initializing entry points for all the submodels have been called, the iteration begins. The submodels are called in order, with the abiotics called first, the ANML and, finally, the VEG. The time-step is set at the beginning of the run and can be any integral number of days. The internal timing of the model keeps track of Julian day. Within the VEG submodel, at each call, one pass is made through for each functional group being simulated, before control is passed back to the main program.

All state variables are updated within the appropriate subroutine. (This is as opposed to systems wherein the "changes" to the state variables are computed in subroutines, but the changes are made ultimately in some other bookkeeping subroutine.)

The mechanisms incorporated in the VEG submodel were decided upon by the modeler after lengthy discussions with a large number of Desert Biome investigators. These were: S. Bamberg, A. Vollmer and T. Ackerman at the Rock Valley site in Nevada; A. Wallace and E. Romney at UCLA; J. Ludwig, G. Cunningham and J. Reynolds at Las Cruces (Jornada); D. Patten at Tempe; and M. Caldwell, E. DePuit and R. Shinn at Utah State. Although there is no absolute agreement or consensus among these individuals on any part of the model, a general pattern of agreement has emerged which, in conjunction with the photosynthesis modeling work of Schultze and Lange, produces a model that appears to begin approximating the plant function for present purposes. It was conceived and designed as a general plant model whose

specificity for any site depends on parameters furnished as input data. A general description of the internal mechanics of the VEG submodel follows.

#### GENERAL DESCRIPTION OF THE VEG SUBMODEL

##### *Year's End -- Beginning*

On an arbitrary date each year, usually during the middle of the yearly dormant season, plant materials are transferred, where appropriate, from current year's growth to prior years' categories. Thus, new stem and new root become old stem and old root.

##### *Labile Storage Capacity*

A labile storage capacity has been hypothesized for each plant functional group, and the actual amount of labile material in relation to the storage is monitored. Although this is called "storage capacity," it is actually more correctly called the maximum observed labile storage. The plant may be capable, in fact, of storing even more. Nonetheless, the maximum observed labile storage is considered the plant's capacity for labile material. The actual level of labile material, in relation to this capacity, is used as a driving variable for various phenological events, such as establishing priorities between growth or storage of photosynthate, and for triggering the growth of various plant parts.

The first value calculated is this storage capacity, and is used later in the submodel. It is calculated here before any plant part changes have occurred.

##### *Wettest Soil Horizon*

The submodel then iterates through the various defined soil horizons testing for the wettest, since this is what drives plant photosynthesis.

Since the soil water potential does not distinguish, in this model, between a frozen soil and an unfrozen soil, a test is made for the soil temperature in each soil horizon. If the temperature is less than, or equal to, 0 C,  $-50$  bars is added to the soil water potential of that particular horizon.

Having found the wettest soil horizon on this basis, the soil horizon number is recorded and held.

##### *Photosynthesis*

For each above-ground plant part, there is a value provided as an input parameter indicating the maximum possible rate of photosynthesis in  $\text{kg} \cdot \text{kg}^{-1} \cdot \text{hr}^{-1}$   $\text{CO}_2$  exchange (net) as would be measured in a Siemans chamber. For most above-ground plant parts, this is, incidentally, zero. Then, applied to these various photosynthetic rates, are scaling factors, usually from zero to one (although some can be slightly negative, because these photosynthetic rates are net rates). These scaling factors depend on several environmental variables.

The first scaling factor is dependent on air temperature and soil water potential (of the wettest soil horizon). The air

temperature used is a corrected air temperature, which allows for the temperature acclimation of the plant. This optimum acclimation temperature is taken simply as a function of Julian date. Rather than using the mean air temperature, a value is used that is two-thirds of the way from the daily minimum to the daily maximum air temperature. This value has been shown to correlate more highly with net daily photosynthesis than does the mean.

The second photosynthesis scaling factor depends on mineral nitrogen levels in the soil profile. This function is generally rhomboid, such that, at very low and very high levels, photosynthesis may be limited.

The third scaling factor depends on relative humidity. Relative humidity is converted to the water vapor difference in mg/liter between the inside of the leaf and the outside of the leaf (assuming the inside of the leaf is saturated at the current mean air temperature). The greater the difference in water vapor between the inside of the leaf and the outside air, the slower the rate of photosynthesis.

The three factors could be multiplied together as they were in the Schultze and Lange modeling work (Schultze et al. 1974). The present modeler has chosen not to do so. The factors are searched for the minimum single factor and that one is used. It could be argued that, if we looked at enough factors, even though each factor by itself was slightly less than one, we could multiply enough of them together to bring the ultimate product very close to zero. Further work is needed to present a compelling case for one approach over another. Here, we have used only the minimum of the three as scaling the photosynthetic rate.

The resultant factor is then multiplied by a factor that scales the rate down according to fraction of overcast hours during the photoperiod. At this point, the net photosynthate production is calculated by multiplying the maximum possible rate by the composite scaling factor, by the biomass of the photosynthesizing part, by the photoperiod in hours, by the number of days in the time-step and by a conversion factor that converts net  $\text{CO}_2$  gas exchange to biomass increment or decrement.

##### *Respiration*

It is convenient to divide respiration between above-ground plant parts and below-ground plant parts. This is primarily because the first may have been measured, while the latter almost surely has not been. For above-ground plant parts, each plant part has a characteristic respiratory rate, in  $\text{CO}_2$  flux per unit biomass per hour ( $\text{kg} \cdot \text{kg}^{-1} \cdot \text{hr}^{-1}$ ). The characteristic respiratory rate is defined as that which would occur in the dark at  $-1$  bar stem water potential, 35 C. To this rate, a scaling factor is applied depending on air temperature and soil water potential of the wettest soil horizon. Total respiration for the plant part is obtained by multiplying the characteristic rate by the scaling factor, by the biomass of the plant part, by 24 hr, by the number of days in the time-step and by the factor that converts  $\text{CO}_2$  gas exchange to biomass change (.74).

Below-ground respiration of plant parts is handled quite similarly, there being characteristic rates for new roots and old roots, identically defined; that is, at  $-1$  bar stem water potential and 35 C. The scaling factor for below-ground respiration, however, depends on the soil water potential -- weighted by the root distribution of the plant functional group among the various soil horizons, and on the soil temperature, similarly weighted.

To compensate for the fact that the net photosynthesis value previously obtained has respiration included in it, the respiratory loss during the photoperiod of photosynthesizing parts is calculated (assuming dark respiratory rates) and the net photosynthesis value is converted to gross photosynthesis.

At this point, the gross photosynthesis is added to and the gross respiration is subtracted from the labile pool (plant part #8).

#### *Transpiration*

Only because they fit the limited data available so well, and because they obviated the necessity for talking in terms of transpiration efficiency, the absolute values of gross photosynthesis and gross respiration are added and multiplied by a constant.

#### *Growth*

The growth functions in the submodel boil down to two types. The first which determines the total amount of material to be transferred from the labile category to structural, and the second which determines the allocation of growth among the various plant parts, if growth occurs.

Without, for the moment, reference to where the growth is going, consider the functions for the total amount of growth. Basically, the growth can come from two places, conceptually (in this submodel). It can come either from the net labile material produced during the time-step, or from the existing labile pool at the beginning of the time-step. First, consider net production.

Net production is either going to remain labile material for the time being, or it can be allocated immediately to growth. In the submodel, the basis for this allocation depends on the size of the existing labile pool. If the existing pool is very low, then a sizable proportion of the net production will be used to build up the pool. If, on the other hand, the pool is quite full (in quotes), the majority will be committed to structural growth. The only constraint on this is the labile pool is only allowed to increase (in proportion to the plant) by a characteristic fraction or percent per day. Thus, although the allocation of net production to building up the labile pool is very large, if the pool is constrained from growing that large that fast, the excess is committed to structural growth. Normally, however, the proportions of the net production going to structural growth and to labile pool growth are a function of the level of the pool at the beginning of the time-step.

If there is negative net primary production, no allocation of net primary production is made to structural growth. Growth can occur, however, if environmental conditions are appropriate for leafing out. This is the only time the existing pool is allocated to growth. Regardless of whether net primary

production is positive or negative, if conditions are right for leafing out and there is not enough leaf out, a few percent per day of the existing pool can be allocated for growth. There is a given leaf value expressed as a percentage of the total structure of the plant, below which the plant will try to put on leaf. This presumes the environmental conditions have attained a certain minimum value. Assuming proper environmental conditions, if the actual leaf structure in relation to the total plant structure falls below the given leaf value, some fraction of the existing pool can be allocated to growth.

Having calculated the total amount of growth, it is then allocated among the various plant parts. At all times, leaf growth will have a priority so long as it falls below the given leaf number. Otherwise, if growth occurs, it follows the allocation described below.

For this submodel, characteristic fractional allocations are assigned the above-ground plant parts. These are constant values, read in as input. They could be as follows, for example: Leaf, .30; Flower, .05; Fruit, .08; New Stem, .50; Old Stem, .07.

Assuming that there is enough leaf out so that leaf growth does not need a priority, these proportions are the basis for allocation; but, only the basis. Other factors impinge. The proportion for each plant part can become zero unless certain phenological tests are passed. The phenological tests depend on the length of the photoperiod, whether the photoperiod is increasing or decreasing and the level of the labile pool. For each plant part, parameters have been fed in as regards conditions under which it will grow. If those conditions are all met (proper length of photoperiod, proper slope of photoperiod and proper minimum level of the labile pool) the allocation is as above. Otherwise, failing any of the phenological tests, the allocation is zero.

Once the proportional allocations are calculated for the above-ground plant parts, the below-ground growth is calculated. This is a variable fraction of the above-ground allocation, depending on environmental conditions during the time-step. If the conditions are favorable, a smaller proportion of the growth will be assigned to roots. If conditions are not so favorable, a rather larger proportion goes below ground.

At this point, allocations have been made (at least proportionally) to the various plant parts. If, however, the existing leaf material stands at, for example, only 20% of the given leaf value, the proportional allocation to each of the nonleaf plant parts is multiplied by .2. Although there is no substantiation for this sort of mechanism, indeed for this whole phenological section, it is the only way in this submodel to get the plants going in the spring.

Finally, the resulting proportions are then multiplied by the total growth derived earlier and the structural plant part categories are incremented, while the labile pool is decremented.

#### *Herbivory and Wastage*

The ANML submodel passes two kinds of values to the VEG submodel. Animal removal is that material actually

ingested by the animal, or true herbivory. Animal destruction is considered to be that material that is removed from the plant but not ingested, becoming surface litter. The plant part categories are decremented by both animal removal and animal destruction, and animal destruction is transferred into the surface litter category.

#### *Death of Plant Parts*

There are two kinds of death rates applied to plant parts in this submodel; one depends on environmental conditions while the other does not. The first photosynthesis scaling factor, which depends on air temperature and soil water potential of the wettest soil horizon, will have a value usually between zero and one. This is the environmental index that drives plant death. The lower the environmental index, the greater the death rate due to it. Maximum death rates (fraction per day) are read in as input. If the environmental index is zero, the maximum death rate is applied. This death rate decreases linearly as the environmental index increases to one. It is possible to distinguish, in this submodel, between death rates of new and old material, but it is a special distinction and depends on a special definition. In this case, new material is that existing at the beginning of the current year, and it does not become "old" material, or subject to the "old" material death rate, until it has been replaced by new growth. This is quite a separate distinction from that made between new and old stem, for instance. All material, for purposes of death, is new at the beginning of each year and becomes old only when growth occurs to replace it. In that instance, new and old material may have different maximum death rates.

The second death rate applied may have nothing to do with environment. It is taken as a characteristic daily fractional death rate depending solely on Julian date. This was incorporated only to allow simulation of the death of annuals or perennial grass parts after seed-set.

Following the application of death rates, dead materials are transferred to the appropriate litter categories, depending on the rates of decomposition of various plant parts, and on their location (some to standing dead, some to soil horizons). At this point, the iteration through one plant functional group is complete, and the next pass, beginning with calculation of the next plant's labile capacity, is begun.

#### *Litter Distribution*

After all plant functional groups have been completed, fecal litter is passed from the ANML submodel and accounted for in the proper litter category. Then, transfers of litter from location to location are effected. These transfer rates are simply taken as characteristic constant daily fractional transfers. They occur from standing dead to surface, from surface to the first soil horizon, from the first soil horizon to the second, and so on. There is no transfer among the litter kinds.

#### *Summations*

Because the model will, ultimately, be validated on the basis of above-ground plant parts alone, these separate summations of above-ground structure are made after each pass to provide output for graphs and printouts of simulated plant values. Control is, at this point, transferred back to the MAIN calling program.

## CURLEW VALLEY IMPLEMENTATION

### *General*

The Curlew Valley simulation is meant to represent the *Artemisia-Atriplex-Sitanion* association found on the southern shrub site. The plant species simulated are *Artemisia tridentata*, *Atriplex confertifolia* and *Sitanion hystrix*. The roots are distributed among six soil layers.

### *Growth Transfer Day*

For the purposes of this simulation, the first day of January is considered the day on which current year's growth becomes prior-year's growth. This is in the middle of the annual winter dormancy.

### *Labile Storage Capacity*

Coyne and Cook (1970) have studied seasonal fluctuations of the labile carbohydrate pool in eight desert shrub and grass species. These studies divided plants into root, crown and stem material. The crown consisted of the woody material between the first branch above the ground and the first significant branching of the roots. The maximum percentage values for total available carbohydrate (TAC) observed in Coyne and Cook's work were applied as the storage capacity of the simulated plants, their stem storage being applied to all above-ground plant parts, and the root storage to all below-ground plant parts.

### *Photosynthesis*

Gas exchange measurements have been done on all three plant species under a variety of conditions by M. Caldwell and his students (Caldwell et al. 1971, 1972, 1973, 1974), and by Hironaka and Tisdale (1971 and 1972). DePuit and Caldwell (1973) worked and reported extensively on *A. tridentata*. From this work, the temperature optima as a function of date were derived. The modeler's analysis of these *Artemisia* data yielded both the probable maximum photosynthetic rates of leaves and stems, and the scaling factors attributable to temperature. Because this work dealt with stem water potential rather than soil water potential, stem and soil water potentials are considered the same. The decision to use a driving air temperature two-thirds of the way from the daily minimum to the daily maximum was based on diel temperature and photosynthesis curves published in the DePuit and Caldwell (1973) work. The scaling factor for mineral nitrogen levels was derived, in a general sense, from a report published by Jurinak and Griffin (1973) on effects of applying nitrogen and phosphorus to Curlew Valley soils on plant growth. The scaling factor for water vapor difference was derived from plant data published on the Negev desert shrubs by Schultze et al. (1974). The scaling factor for overcast light attenuation is an approximation after observation of radiometer readings, and the effect of light intensities on *A. tridentata* as published in DePuit and Caldwell (1973).

The scaling factors for soil moisture, air temperature, mineral nitrogen levels, water vapor difference and overcast light attenuation for *Atriplex* and *Sitanion* are identical to those used for *Artemisia*; in part because the available data for these two species are not nearly as complete and are not reduced appropriately, plus the fact that the *Sitanion* gas

exchange measurements (1971, 1972) are done on an area basis rather than on a dry weight basis. Probable maximum photosynthetic rates for various plant parts of *Atriplex* and *Sitanion* are approximations by the modeler based on principles discussed with Caldwell and Hironaka.

#### Respiration

DePuit and Caldwell (1973) also give dark respiration rates for *Artemisia* leaf and stem under a variety of conditions of moisture and temperature. These were used for the above-ground plant parts of all three species. Because respiration rates of the below-ground parts have not been studied, hypothetical rates have been supplied by the modeler that are pure guesses, approximating one-tenth the dry-weight rates of above-ground plant parts, but modified in the course of tuning the model to balance the labile pool fluctuations.

The conversion factor from CO<sub>2</sub> gas exchange to biomass changes was derived by the modeler from a detailed photosynthesis chemical formula as published in Odum (1959).

#### Transpiration

As stated before, the mechanism for predicting transpiration water requirements was developed principally from data. The work of DePuit and Caldwell (1973) gives transpiration efficiencies under a variety of conditions for *Artemisia*. When those conditions are used to drive the photosynthesis part of the model and the respiration part, the actual transpiration measured for those conditions approximates a value obtained by multiplying the sum of the absolute values of the predicted photosynthesis and the predicted respiration by a constant. This was considered identical for all plant species.

#### Growth

Since 1972, Shinn and his coworkers (Balph et al. 1972, 1973, 1974) have been taking detailed plant measurements at various times in the year on the Curlew Valley site. These plant measurements have been, for the most part, broken down into categories that correspond almost exactly with the plant parts being simulated. These plant measurements have indicated the dry-weight biomass of various plant parts, both above and below the ground, with confidence intervals, for all the species being simulated. All growth parameters and phenological keys for switching among plant parts have been induced, by the modeler, based on the Curlew Valley data.

#### Death

All death rates, just as the growth rates, have been induced by the modeler based on the Curlew Valley data. Whenever possible, the death rates were taken as a function of the environmental conditions, directly related to the first scaling factor for photosynthesis. Where that was not possible, a priori death rates were involved such that the Curlew Valley data could be reproduced as a function of date.

## UNANSWERED QUESTIONS AND FUTURE DATA NEEDS

In the course of constructing the various models and running them with field-gathered data, it became clear that certain data were not presently available and not likely to become available in the next year or two. In addition, a number of processes were obviously not very well understood and hence were difficult to simulate. Pointing out these deficiencies is a major contribution that modeling can make to ecosystems analysis. It is hoped that the following list may serve to help guide future research efforts:

1. Rates of mineralization, decomposition: Our lack of precise knowledge of these rates and the factors controlling them is the biggest gap in the data for the "abiotic" models. Without this information it is impossible to accurately model these important steps in carbon and nutrient cycles.
2. Photosynthesis: a) Effects of leaf polymorphism and leaf age on photosynthetic rates; b) Stem photosynthesis; role of and extent of; c) How is photosynthetic rate related to varying soil water potential values through the soil profile? Does the wettest soil horizon drive the rate or does some integration over the profile, possibly weighted by root distribution, do a better job? d) What are the effects of various ion concentrations in the soil on photosynthetic rate, especially nitrogen in its various inorganic forms? Also the effects of salt concentrations at various depths; e) How much is the photosynthetic rate attenuated by cloud cover? f) What are the appropriate conversion factors for CO<sub>2</sub> gas exchange to biomass?
3. Respiration: a) What are the general effects of tissue age on respiration rate? b) Which moisture level drives respiration? (Maybe both of these moisture driving questions could be answered by relating plant water potential in various organs to soil water potentials through the rooting profile.); c) Need respiration rates for *all* plant parts, especially roots, under a variety of temperature (soil and air) and moisture conditions; d) Is respiration rate affected by soil ion concentrations? e) Biomass conversion factors again?
4. Growth: a) What conditions trigger the growth response of various plant parts? b) (Maybe the same question.) How is growth allocated to keep the plant in proper proportion and balance (i.e., the right amount of shoots, leaves, roots, etc.)? c) How much growth occurs below the ground and under what conditions? d) How does the plant know when to allocate material to growth and when to keep it to build up the labile pool? e) When can leafing out occur if the plant is defoliated during the year? How does that relate to total available carbohydrate (TAC) levels in the plant at the time of defoliation (assuming conditions for growth are good).
6. Litter: a) What drives the transfer of standing dead material to surface litter? b) Same for surface litter to subsurface litter? c) What are appropriate categories for

litter so that characteristic decomposition rates can be applied to each category (given proper moisture and temperature conditions)? d) What are proper moisture and temperature conditions for decomposition?

7. Herbivory: What are the secondary effects of herbivory and how do they accumulate, if they do? For instance -- under intense grazing, how do plants accumulate the damage -- does the labile pool get too depleted to properly flush out the photosynthetic material -- does it allocate too much material to growth of nonphotosynthetic plant parts, especially roots, under grazing -- do the remaining parts have a substantially higher respiratory rate in order to repair the damage, thus resulting in an additional drain on the TAC pool?

8. Death: a) What environmental factors determine death rates of plant parts? b) What internal factors determine death rates of plant parts (senescence, hormone production, depletion of labile pool, sensitivity to photoperiod or something else)? c) What are the overwintering processes? How are all rates and pool levels affected during "dormancy"? d) Does the plant retain a skeletal root structure that can quickly provide the framework for rapid exploitation of soil moisture by the production of root hair and rootlet material, without having to lay down the heaviest part of the root structure each episode? e) In modeling, things have a tendency to be unstable -- the labile pool goes below zero under certain conditions -- the plant gets entirely out of balance with too much root and not enough leaf, and a million kg/ha of flowers and no fruits, etc. What is the nature of the homeostatic mechanisms that don't allow such things to happen? f) How do differential root distributions affect plant interrelationships (competition for moisture, space, temperatures, etc.)? Will this explain why, after a rain event, we will see one plant species turn on, and the other just sitting there? g) Can we characterize the rooting strategies of various plants with a few relatively easily measured parameters that will allow some prediction of plant association and competitive and/or symbiotic interactions in a community? h) What is mineral uptake proportional to? i) What is the pattern of TAC pool size through the year?

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