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# A MODEL FOR PREDICTING THE EFFECTS OF SEWAGE EFFLUENT ON WETLAND ECOSYSTEMS

by
Kenneth Randall Dixon

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Wildlife Management)
in The University of Michigan
1974

Doctoral Committee:

Professor John A. Kadlec, Chairman
Associate Professor Archibald B. Cowan
Professor Robert H. Kadlec
Professor Richard L. Patterson
Dean H. Urie, U. S. Forest Service

Dedicated to Fred

He ain't heavy -- He's my brother!

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# CHAPTER I

# INTRODUCTION

A mathematical model for a wetland ecosystem is developed in this thesis. The objective is to provide a working model based primarily on data in the published literature. It is anticipated that this model will be updated and validated by data collected from laboratory and field studies. The emphasis in this thesis is on modeling the biomass dynamics of vascular plants, standing dead material, litter and organic soil. These models later will be combined with models of water and nutrient components in a macromodel to predict the effects of sewage effluent on a wetland ecosystem.

Terrestrial disposal of sewage wastewater has been practiced and studied, a posteriori, for several years (Kardos 1967; Larson 1960; Little, et al. 1959). Wetlands provide an alternative to terrestrial and aquatic ecosystems for effluent disposal, but have not been used or studied extensively for this purpose.

A wetland ecosystem possibly will have some advantage over both terrestrial and aquatic ecosystems for use as tertiary treatment of sewage effluent. First, organic wetland soils, with a high adsorptivity and low hydraulic conductivity, provide a nutrient sink, reducing the probability of groundwater contamination and eutrophication of surrounding surface waters. Also, wetland ecosystems,

although important ecologically, have relatively low economic value. The low cost of wetland disposal as tertiary treatment together with the relatively low land value make this method especially advantageous for rural or seasonally low density areas which might not be able to afford more expensive methods.

In order to investigate, a priori, the feasibility of using wetland ecosystems for effluent disposal, a long-range study was established involving a series of laboratory and field experiments and an ecosystem model and simulation. The study area is a wetland site being considered for sewage effluent disposal by Houghton Lake in northcentral lower Michigan. The marsh, or bog, has developed on organic soil, consisting mainly of Houghton muck and Greenwood peat, with a watertable at or above the soil surface most of the year. The major plant species are bog birch (Betula pumila), leatherleaf (Chamaedaphne calyculata), willow (Salix sp.), and sedge (Carex sp.). It was determined that an ecosystem model would be a necessary and integral part of the study for two major reasons. First, the feasibility of this disposal method depends on the ability of the ecosystem to maintain its structural and functional integrity. This cannot be determined from short-term field studies. The second reason is that the model can be used to design an optimal disposal scheme over time and space if the simulation results are favorable.

## Model Description

The purpose of the modeling and simulation is to make long-range predictions of the changes in biomass and nutrient concentrations in the ecosystem. To exercise the simulations on the computer, a largescale, module-oriented process simulator was developed by Parker (1974). This simulator handles the input, output, and numerical integration routines required in the simulation. For the purpose of model development in this thesis, the simulation language CSMP was used.

Spatial variation is handled by dividing the ecosystem into geographical volumes called blocks. Within each spatial block, the ecosystem is further divided into a set of units, or compartments (Figure 1), each of which represents the behavior of a biotic or abiotic variable. Water and nutrients, but not biomass, transfer across the system boundaries and among blocks. The simulator requires that a unit be represented by a time-varying differential equation. Therefore, a set of ordinary, first-order, nonlinear differential, mass balance equations comprises the model.

Ecological modeling strategies have been categorized recently (Walters 1971:285) as following either a compartmental system approach or an experimental components approach. According to Walters (1971), "The compartmental system approach emphasizes the quantities of energy and materials in ecosystem compartments" whereas "The experimental components approach emphasizes detail analysis of

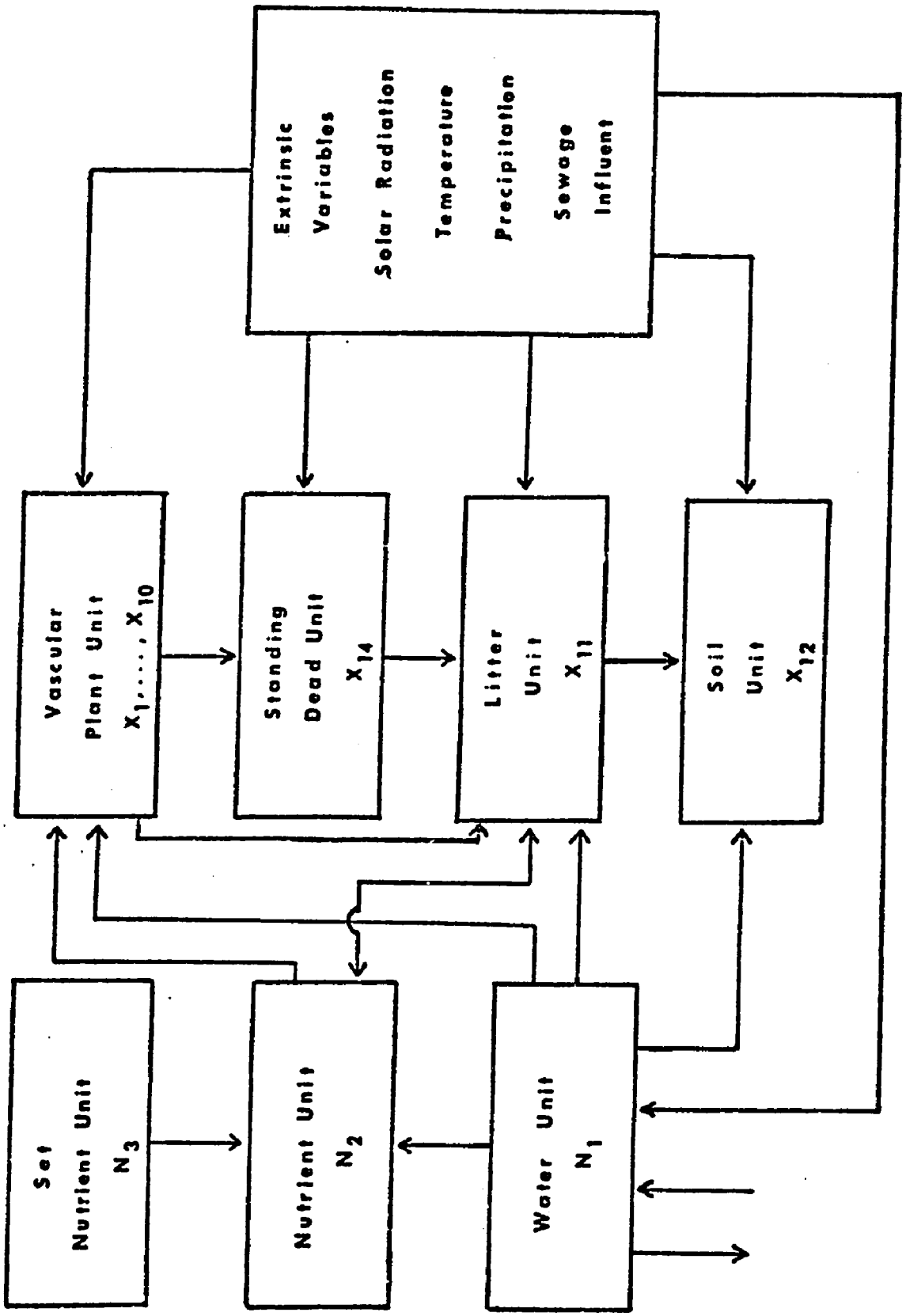



Figure 1. Flow diagram for wetland ecosystem.

ecological processes." This distinction between approaches stems from the development of each approach within a different area of ecology. The compartmental system approach became established through the work in radionuclide cycling in ecosystems (Olson 1965; Patten and Witkamp 1967) while Holling (1963) is credited with developing the experimental components approach in his studies of insect predation.

This distinction between approaches should not be accepted as a necessary dichotomy. In fact, Walters (1971: 287) allows that "Features from both approaches are combined in largescale, integrated studies of whole ecosystems." This artificial classification, however, has led to criticism of the compartmental approach. Bunnell (1973:420) states:

> First, the very data used to test the predictive power of the model are generally involved in determining the functional relations and parameter estimates. The nature of the [compartmental] modeling process makes it very difficult to escape this limitation. Inevitably, these models have high predictive power for the range of data that provided the initial formulation. The circularity of the approach, however, makes extrapolation beyond the range of the original data extremely suspect. Second, by avoiding examination of the underlying processes one's understanding of the dynamics are significantly limited, even though these dynamics may be accurately simulated. The compartment approach is a powerful descriptive device, but weak in understanding the rules of causation that are needed to predict effects of disturbance (for instance, management) into ecological systems."

These criticisms may be made of any modeling approach. They pertain to compartmental models only as they have been used in particular instances. In recent compartmental modeling, the emphasis has been on a total ecosystem model, although process models may be incorporated. The Grassland

Biome model, PWNEE (Bledsoe, et al. 1971), includes four trophic levels and follows the biomass dynamics of each. Parton (1972) has developed an urban-rural ecosystem model which combines detailed meterologic models with some of the PWNEE process models. Some of these process models largely are descriptive, however, and not designed to respond to system perturbations.

In other ecosystem modeling efforts the emphasis has been on detailed process or component models. Models of photosynthesis with relatively high resolution have been developed by Curry (1971), Duncan, et al. (1967) and Kuroiwa (1968) among others. Other ecosystem processes have not received as much attention, although models of decomposition (Olson 1963; Kirita and Hozumi 1969) and nitrification (McLaren 1969a, 1969b, 1971; Cho 1971) are becoming increasingly complex. These models generally are of such high resolution that a total ecosystem model which included a sufficient number of such models to have any utility would be largely intractable. High resolution models applied on an ecosystem scale not only would be intractable but may be less accurate than models of lower resolution (O'Neill 1971).

Equating high resolution models with the experimental component approach, Walters (1971:291) states "The problems of applying such an approach to whole ecosystem would indeed be formidable." The concept of using components or subprocesses in defining the links between compartments is not

negated however. Highly accurate process models can be developed at levels of resolution which are not formidable to a computer. As Patten (1971:8) states, "the degree of abstraction permissible is a value judgement to be made in context of the purpose at hand."

Once a purpose for the model is established (such as the prediction of effects of sewage effluent disposal on a wetland ecosystem), the significant variables, or what have been termed "key factors," can be selected for inclusion in the model. Some of these factors are determined by the variables which are necessary inputs into the system, such as temperature and solar radiation. Other factors are set by the model's purpose. In the present model, in order to predict the effects of sewage effluent on ecosystem processes, the variables of added nutrients and water must be included in those component process models.

The modeling approach used in the present ecosystem model is a combination of the compartmental and experimental component approaches. Circularity is avoided by using one set of data to define functional relations and estimate parameters, through experimental component analysis, and a second set to validate the values of the state variables representing the output from system compartments.

The level of resolution used in defining the ecological process models is determined by several factors. As the resolution of a process model is increased, the complexity involved in computer programming also is increased.

Therefore, one limitation to the amount of detail incorporated in a process model is computer space. It should be pointed out that models which include spatial variation by division of the ecosystem into several spatial blocks increase the complexity in programming considerably. A second factor involved in determining the level of resolution is the logistic capability of conducting field and laboratory studies to collect the data for parameter estimation and model validation. Coordinating the modeling effort with the design of field and laboratory experiments is necessary if the requisite data for the process models are to be collected.

In this study, an attempt was made to maintain constant interaction between the modelers and field biologists. The modelers were aware of what data were feasible to obtain, and the field biologists knew what data were required for predictive models.

Notation

There are no conventional standards for notation in ecosystem models, although there is an effort made to be consistent within any given model. This consistency is essential for communication between modelers and biologists working in the ecosystem, although not necessary for programming on the computer.

Seven general types of variables are used in the models, each with a specific notation.

Extrinsic variables. The extrinsic variables in the models are solar radiation, air temperature, precipitation,

and sewage influent (Figure 1). The notation adopted for these variables is any capital letter except X and N.

Unit and component variables. These variables are the primary dependent variables which describe the mass in each unit or nutrient stream. Examples of unit variables are the biomass of plant species and mass of the organic soil. The notation for these unit variables is a capital N for abiotic components and a capital X for biotic unit variables, followed by modifying numerals. These numerals are dropped from the notation when the unit is clear from the context.

Unit rate variables. These are rates of increase or decrease which when summed are equivalent to the mass balance rates for a unit. An example of a unit rate variable is the net photosynthetic rate. The notation used for these variables is the small letter r, followed by qualifying numbers.

Independent variables. A system which has flow components and is time-dependent can be described as a function of four independent variables: time and three spatial variables. In the marsh ecosystem model time is considered the prime independent variable. Since these models are written for a given spatial block, and the various processes are assumed to function uniformly within a block, space in a horizontal plane is not considered here. Vertical space in the vegetative canopy and the soil profile is represented by integration of the expression for ecosystem processes as functions of vertical height. Time is represented by the

the small letter t in steps of any size, typically one day.

Parameters. A variable whose value is constant or step-wise constant for a block or a unit throughout the simulation is termed a parameter. Parameters appear as constants or coefficients in system equations. The notation utilized for a parameter is a small letter p, followed by a set of numbers which are indicators for the process or function in which the parameter appears. An example of a parameter is p1, the maximum leaf resistance to $CO_2$ diffusion.

Constants. A variable whose value is constant for all blocks or units in which it occurs is termed a constant. The small letter c, followed by integer indicators, is used to denote this variable. Carbon dioxide concentration in the air, c1, is such a constant. In addition, constants without any specific meaning attached are used in some equations. These constants are denoted by small letters without numerical indicators.

Functional variables. These variables are used to represent various process functions or indexes which are incorporated into unit rate variables. The notation adopted for this type of variable is the small letter f, followed by numerical indicators. One such variable is f1, the index of translocation to roots.

A metric system of standard physical units is used, with the basic units being grams for weight, meters for length, days for time, and kilocalories for energy.

# CHAPTER II

## MODEL DEVELOPMENT

In this chapter, models are developed for the biomass units; vascular plants, standing dead biomass, litter, and organic soil. Also, models of the extrinsic variables of light and temperature are developed as driving functions for the biomass models (Figure 1). More complex extrinsic variable models and models of water and nutrient components will be combined with the biomass models in a macromodel using the dynamic simulator of Parker.

The models are developed using data primarily from the published literature. Where it is possible, parameter values are determined from data collected from the marsh study area. Initial condition values for the biomass units are taken from preliminary samples taken in the marsh study area in September 1971, and are presented in Table 1.

### 1. Extrinsic Variable Models

The extrinsic variables used to drive the model include solar radiation, temperature, and precipitation. Models of these variables have been developed by Parker (1974) for use in the macromodel. For developing this ecosystem model, a constant value for daily solar radiation (R) of $5.0 \times 10^9$ $kcal \cdot km^{-2} \cdot day^{-1}$ (Jeník and Rijmanék 1969) is used to estimate maximum daily radiation intensity (I*), which is used in the vascular plant unit model. A constant value of I* is used here, although the variable function of Monteith (1965) can

Table 1. Initial conditions of biomass for simulations starting on January 1.

| Variable | | Initial Condition ($gm/m^2$) |
|---|---|---|
| X1 | Vascular plants (birch) | 2,426.0 |
| X1a | Leaves (birch) | 1.0 |
| X1b | Stems (birch) | 2,425.0 |
| X14 | Standing dead | 1,684.7 |
| X11 | Litter | 218.1[a] |
| X11a | Woody litter | 109.0 |
| X11b | Leaf litter | 109.0 |
| X12 | Organic soil | 31,400.0[b] |

a Total litter assumed half woody and half leaf litter.

b Organic soil biomass calculated on basis of 0.157 $gm/cm^3$ to a depth of 20 cm.

be used, given variables R and d:

$$I^* = \frac{\pi R}{2d} \qquad (1.1)$$

where: R = daily solar radiation

d = duration of daylight

Several temperature variables may be desirable. For example, dark respiration may be a function of nighttime temperature only, whereas litter decomposition may be a function of average daily temperature. Equations are written for these temperature variables based on daily minimum and daily maximum temperature values collected by the Houghton Lake Weather Station. Assuming daily minimum and daily maximum temperatures follow a sinusoidal curve on the average, these variables are expressed by the following equations:

$$Tmin = 0.111 + 10.778 \sin [2\pi(305-t)/365] \qquad (1.2)$$

$$Tmax = 11.389 + 15.278 \sin [2\pi(305/t)365] \qquad (1.3)$$

where t = time in days from January 1. The average temperature during daylight, Tday, and the average temperature at night, Tnite, respectively are written as (Patefield and Austin 1971):

$$Tday = 2 + Tmid + \frac{2}{\pi}(Tmax - Tmid) \qquad (1.4)$$

$$Tnite = Tmid - \frac{2}{\pi}(Tmax - Tmid) \qquad (1.5)$$

where Tmid is the arithmetic mean of the minimum and maximum temperatures. The average daily temperature, Tavg, is the

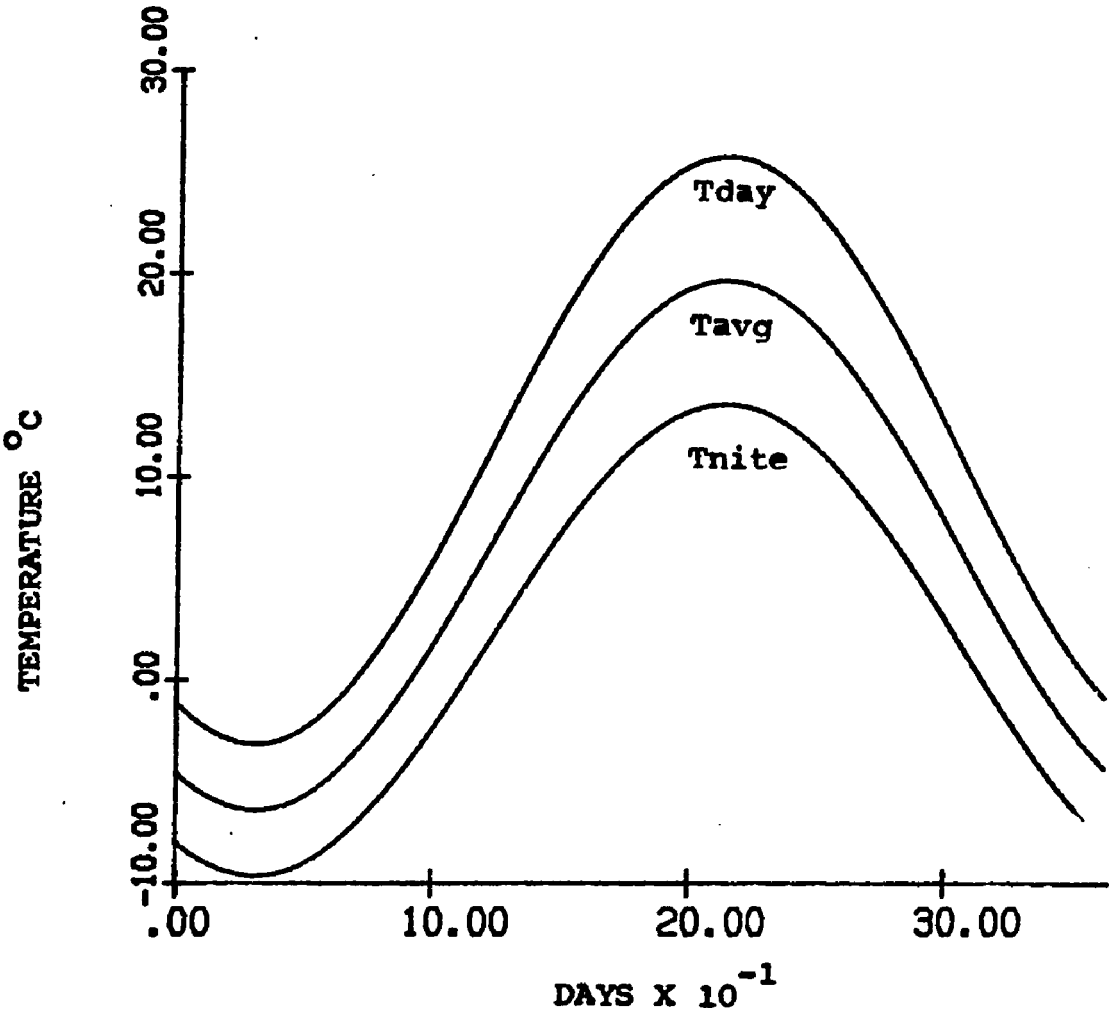



Figure 2. Temperature curves for average daytime (Tday), 24 hour (Tavg), and nighttime (Tnite) temperatures.

arithmetic mean of Tday and Tnite:

$$Tavg = \frac{Tday + Tnite}{2} = Tmid + 1 \qquad (1.6)$$

Figure 2 shows the respective curves for Tday, Tnite, and Tavg.

Precipitation is predicted using a double Monte Carlo technique developed by Parker (1974). First, the length of a rainy or non-rainy period is predicted. Given that rainfall occurs, the rate of rainfall then is predicted for that period. As rainfall rate was not found to be important in the ecosystem processes modeled here, an average rainfall rate was used in the model development. The complex stochastic function will replace the average value in the macromodel simulation.

2. Vascular Plant Unit Model ( X = X1, X2, ..., X10)

The rate of accumulation of biomass of vascular plants is considered only for aboveground biomass. In the case of woody plant species, the aboveground biomass is further divided into leaf biomass and stem biomass. In general, the plant biomass unit is written as:

$$X_i = \int \dot{X}a_i + \int \dot{X}b_i \qquad (2.1)$$

$$\dot{X}a_i = p3 \cdot r1 - r3 - r4 - r10 \qquad (2.1a)$$

$$\dot{X}b_i = (1 - p3)\ r1 - r2 + r10 \qquad (2.1b)$$

where: $X_i$ = aboveground biomass of $i^{th}$ plant species

$Xa_i$ = leaf biomass of $i^{th}$ plant species

$Xb_i$ = stem biomass of $i^{th}$ woody plant species

p3 = fraction of growth apportioned to leaves

r1 = growth rate

r2 = stem mortality rate

r3 = leaf mortality rate

r4 = dark respiration rate

r10 = translocation rate

Leaf and stem rates of biomass accumulation are integrated separately since leaf biomass and stem biomass both appear separately as variables in several process models.

The rates for increase and decrease of plant biomass in equations (2.1) are described in the following sections. Results of the plant biomass simulation are presented at the conclusion of the vascular plant unit model.

Growth rate (r1). The equation for growth rate, r1, is derived from the analagous equation for a gaseous diffusion system, as expressed by the equation:

Net flux = concentration gradient/transfer resistance

This approach to modeling growth rate is used for two reasons. First, the effect of key factor variables, such as temperature, can be measured with greater precision on $CO_2$

uptake rate than on changes in plant biomass. The responses can be measured over a wide range of values for a variable more easily in the laboratory than in the field. Once the form of the response has been determined it can be adjusted to field conditions with data collected periodically from the marsh. The second reason for using this approach is to avoid using the same data set for both model development and validation (see page 7).

The rate of $CO_2$ uptake by plant leaves is determined by the concentration gradient between the leaf and the surrounding air and the transfer resistance in the gas exchange pathway. It is assumed that the $CO_2$ concentration at the chloroplast is zero. For a discussion of this assumption see Gaastra (1959).

An equation which expresses $CO_2$ uptake per unit of leaf area at a given point z in the canopy is:

$$f3(z) = c1/f4(z) \qquad (2.2)$$

where: c1 = $CO_2$ concentration within the plant canopy, assumed constant

f4(z) = leaf resistance at depth z

z = depth into canopy, measured downward

This type of equation has been used in leaf photosynthesis models by Penman and Scholfield (1951), Gaastra (1959), Monteith (1963), and Heath (1969). A partial fraction form of the equation has been used to model plant communities by

Monteith (1965) and Curry (1971). All of these models have been written primarily as a function of light intensity, although Curry added a temperature function. A hyperbolic form of equation, also a function of light intensity, is used to model plant production in communities by Monsi (1968) and Sollins, et al. (1973).

The equation used here, with leaf resistance written as a product function, has the advantage of simplicity of form which facilitates integration over time and space. It also allows investigation of several variables and their individual or combined effects on the photosynthetic process.

This rate is expressed in terms of photosynthate production per unit of ground area ($m^2$) by multiplying the right side of equation (2.2) by the appropriate conversion factors:

$$r1(z)' = c2 \cdot Xa(z) \cdot f10 \cdot f3(z) \qquad (2.3)$$

where: $r1(z)'$ = net photosynthate production rate per unit of ground area at height z in the canopy

$c2$ = stoichiometric coefficient to convert $CO_2$ uptake in $cm^3$ to biomass in grams

$Xa(z)$ = biomass of the leaves of this species per unit ground area at height z

$f10$ = empirical function to convert leaf area to leaf biomass

$f3(z)$ = $CO_2$ uptake rate per unit leaf area at height z

In equation (2.3) the parameter c2 converts a unit volume of $CO_2$ ($cm^3$) taken up by the plant leaf to grams of

photosynthate. From the standard general summary equation for photosynthesis:

$$6CO_2 + 6H_2O \longrightarrow C_6H_{12}O_6 + 6O_2,$$

it is apparent that six molecules of $CO_2$ are required to make a single molecule of sugar. Using the molecular weights of $CO_2$ and starch ($C_6H_{10}O_5$), a factor for converting a unit weight of $CO_2$ to a unit weight of starch is:

$$\frac{\text{Molecular wt } C_6H_{10}O_5}{6 \text{ x molecular wt } CO_2} = \frac{162.14}{6 \text{ x } 44} = .614$$

The conversion factor 0.648 was obtained by Sestak, et al. (1971) using the average of the molecular weight of a starch unit and glucose:

$$\frac{162.14 + 180.14}{2(6 \text{ x } 44)} = .648$$

These factors must be multiplied by the density of $CO_2$ in the air to obtain a factor which converts volume of gas to weight of photosynthate. At 20°C, $CO_2$ density is $1.842 \times 10^{-3}$ g/cm$^3$. Therefore the value of c2, in the same units, is:

$$1.842 \times 10^{-3} \times 0.648 = 1.194 \times 10^{-3}$$

The function f10 which is used to convert leaf area to leaf biomass is the ratio of two variables--leaf area and leaf weight:

$$f10 = \frac{f11}{f12} \qquad (2.4)$$

where: f11 = leaf area function

f12 = leaf weight function

The functions for leaf area and leaf weight are written using data from Hughes (1971) on birch which are presented in Table 2 and Figure 3. Assuming leaf area approaches a maximum, p12, asymptotically, function f11 is written as:

$$f11 = p12(1-e^{-b(t-t2)}) \qquad (2.5)$$

where: p12 = maximum leaf area

t = time

t2 = time of initial leaf area growth

b = a constant

A graph of this function is shown in Figure 3 as line A. Assuming values of p12 and t2 as 4.85 and 121 respectively, the constant b is estimated by linear regression of the leaf area data after a logarithmic transformation. This function is adjusted to the birch species in the marsh study area using data collected in September 1971 (Figure 3, line B).

A similar procedure is used in determining the leaf weight function, f12, using the data in Table 2. These data are plotted in Figure 4. A simple quadratic function is fitted to the data with an $r^2$ of .83 (Figure 4, line A). The resulting equation, adjusted for birch leaf weight data from

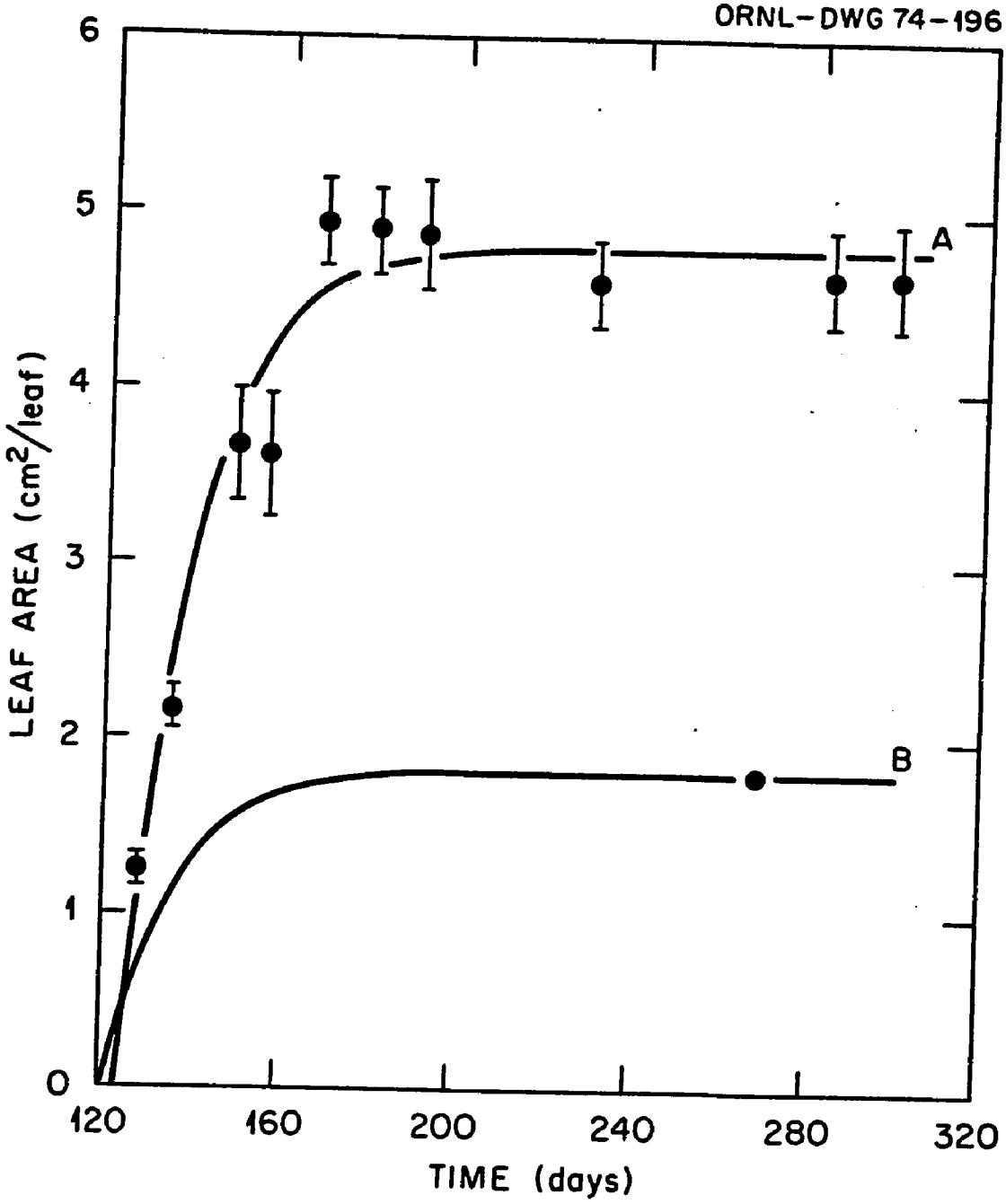



Figure 3. Leaf area per leaf as a function of time (Data from Hughes).

Table 2. Birch leaf area and leaf weight data (From Hughes, 1971).

| Day | area/leaf ($cm^2$) | weight/leaf (gm) |
|---|---|---|
| 128 | 1.25 ± 0.09 | .0120 ± .0007 |
| 135 | 2.17 ± 0.12 | .0136 ± .0009 |
| 149 | 3.68 ± 0.32 | .0210 ± .0015 |
| 156 | 3.62 ± 0.35 | .0211 ± .0014 |
| 168 | 4.94 ± 0.25 | .0215 ± .0012 |
| 180 | 4.91 ± 0.24 | .0216 ± .0011 |
| 191 | 4.88 ± 0.31 | .0213 ± .0014 |
| 230 | 4.62 ± 0.25 | .0258 ± .0014 |
| 284 | 4.65 ± 0.27 | .0235 ± .0021 |
| 299 | 4.67 ± 0.30 | .0219 ± .0040 |

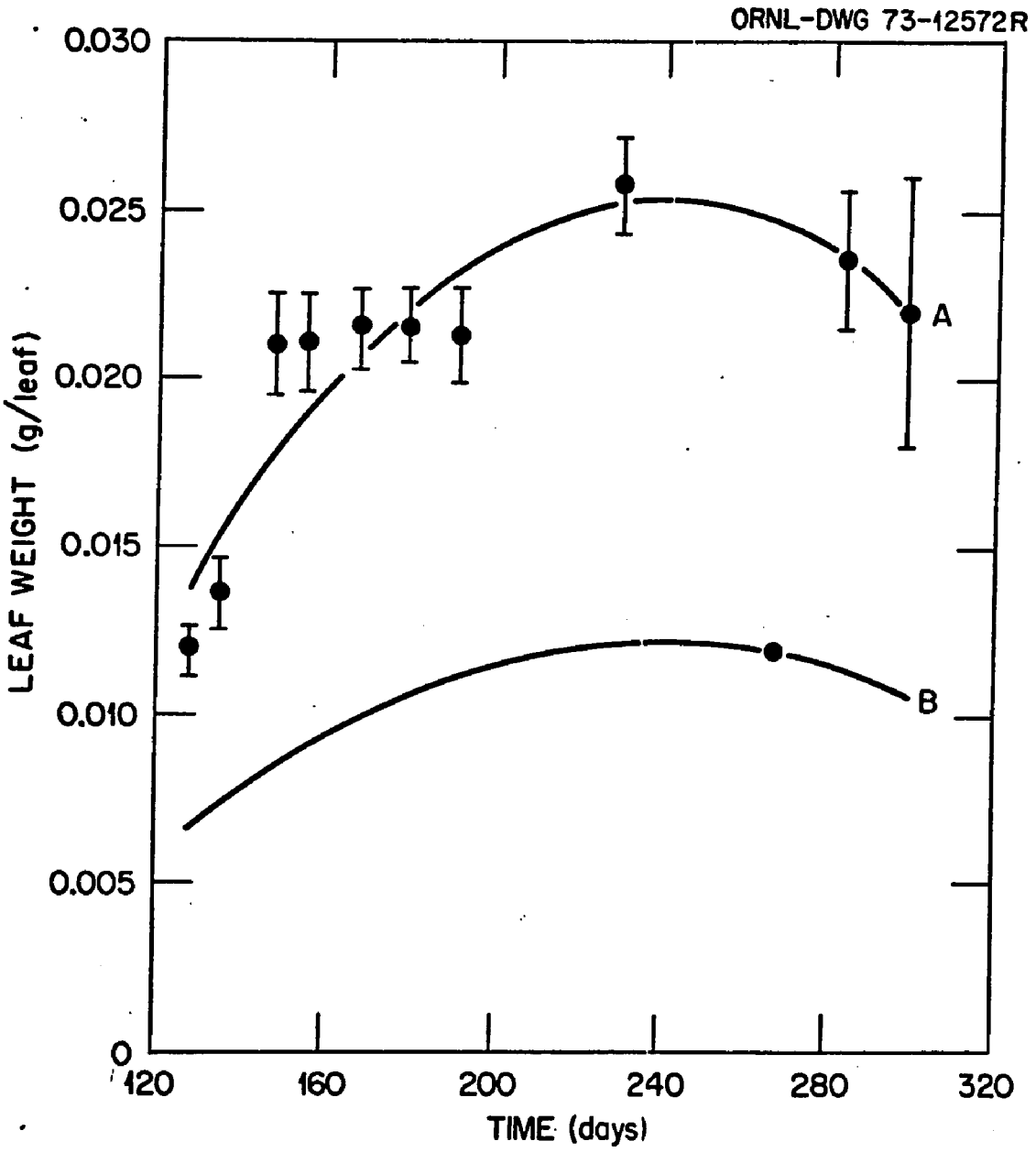



Figure 4. Leaf weight per leaf as a function of time (Data from Hughes 1971).

the marsh study area is:

$$f12 = -0.0137 + 2.167 \times 10^{-4} t - 4.5 \times 10^{-7} t^2 \quad (2.6)$$

where t is time in days from January 1. The graph of this function is shown as line B in Figure 4. The function, f10, which results from the ratio of the leaf area function and leaf weight function, is shown in Figure 5.

The leaf resistance is defined in terms of its response to light, temperature, and the nitrogen content of the leaf:

$$f4(z) = p1 \cdot f5 \cdot f6(z) \cdot f7 \quad (2.7)$$

where: p1 = maximum leaf resistance

f5 = leaf resistance response index for nitrogen content of leaves

f6(z) = leaf resistance response index for sunlight

f7 = leaf resistance response index for temperature

The photosynthetic response to nitrogen concentration in rice plants is shown in Figure 6 (Murata 1969). The effects of low nitrogen levels on $CO_2$ transfer in maize (Zea mays L.), cotton (Gossypium hirsutum L.), and bean plants (Phaseolus vulgaris L.) were studied by Ryle and Hesketh (1969). The maximum rate of photosynthesis was reduced and the $CO_2$ diffusion resistance increased with reduced nitrogen availability in sugar beets (Beta vulgaris L.) (Nevins and Loomis 1970). In general, the resistance response will have the form of the inverse of the

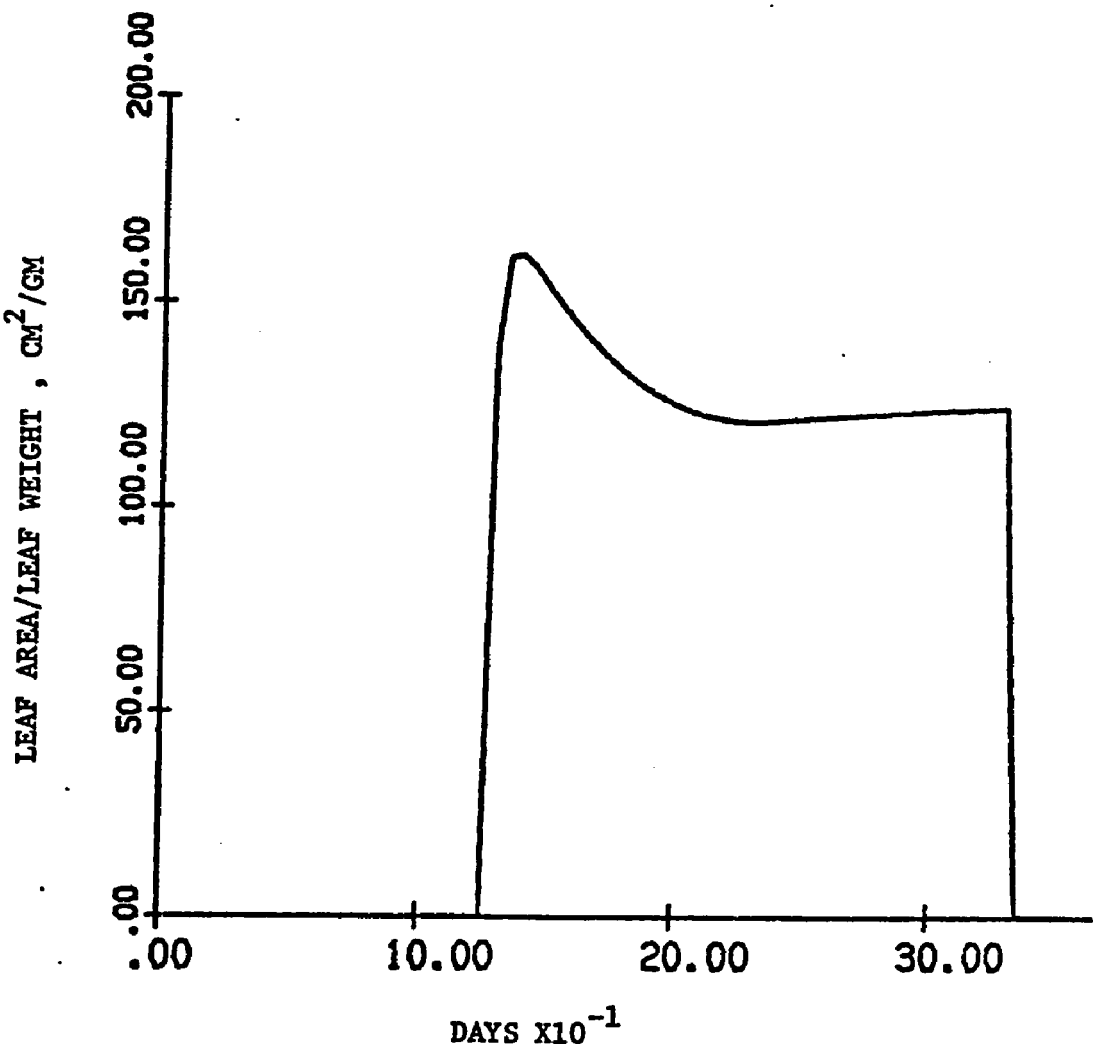



Figure 5. Leaf area/leaf weight ratio function (Data from Hughes 1971).

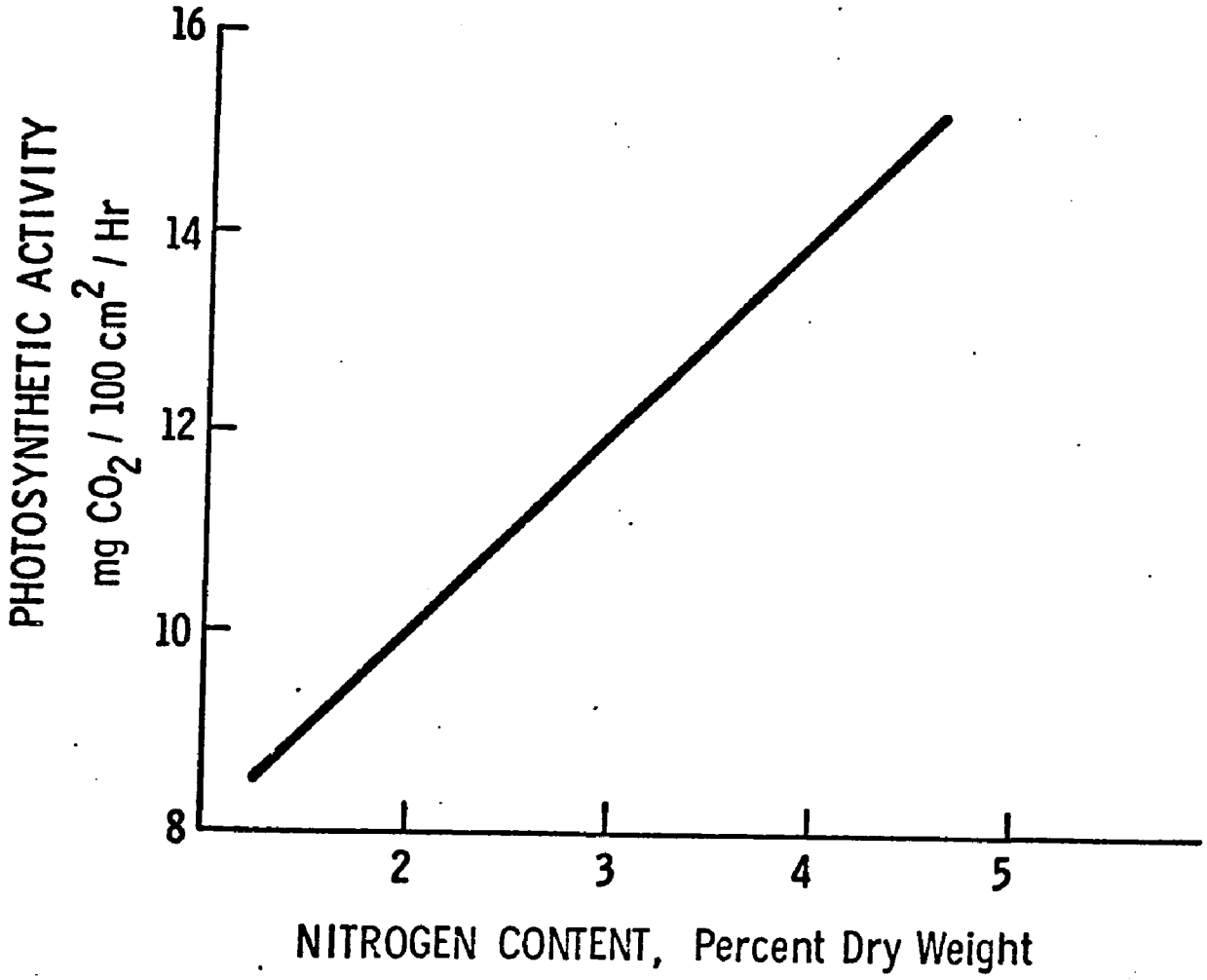



Figure 6. Photosynthetic response to leaf nitrogen content in rice plants (After Murata 1969).

photosynthetic response. The approximate $CO_2$ resistance response for sugar beets, based on the data from Nevins and Loomis, is shown in Figure 7. The resulting response index of the $CO_2$ resistance to leaf nitrogen (f5) is:

$$f5 = 1.117 - .0646 \cdot c3 \qquad (2.8)$$

where c 3 = percent leaf nitrogen. The constant c3 can be replaced (in the macromodel) by a variable written as a function of soil nitrogen.

The influence of leaf temperature on leaf resistance of birch (Betula verrucosa) was measured by Holmgren, et al. (1965). The $CO_2$ resistance was estimated as 1.7 times the transpiration resistance at zero illumination. The $CO_2$ leaf resistance response index due to temperature, based on their data, is given in Figure 8. The curve is extrapolated linearly to zero to obtain the maximum leaf resistance value. The following piece-wise linear equation appears to be valid for this function over the range of temperatures encountered in the marsh:

$$f7 = \begin{cases} 1.0 - .04647\ Tday & Tday \leq 19.5 \\ 0.092 & Tday > 19.5 \end{cases} \qquad (2.9)$$

where Tday = average temperature during hours of daylight. Equation (2.9) may be replaced by a continuous hyperbolic function when this response is measured for the bog plants.

The photosynthetic response to light intensity has been reported for several bog species (Small 1972). The

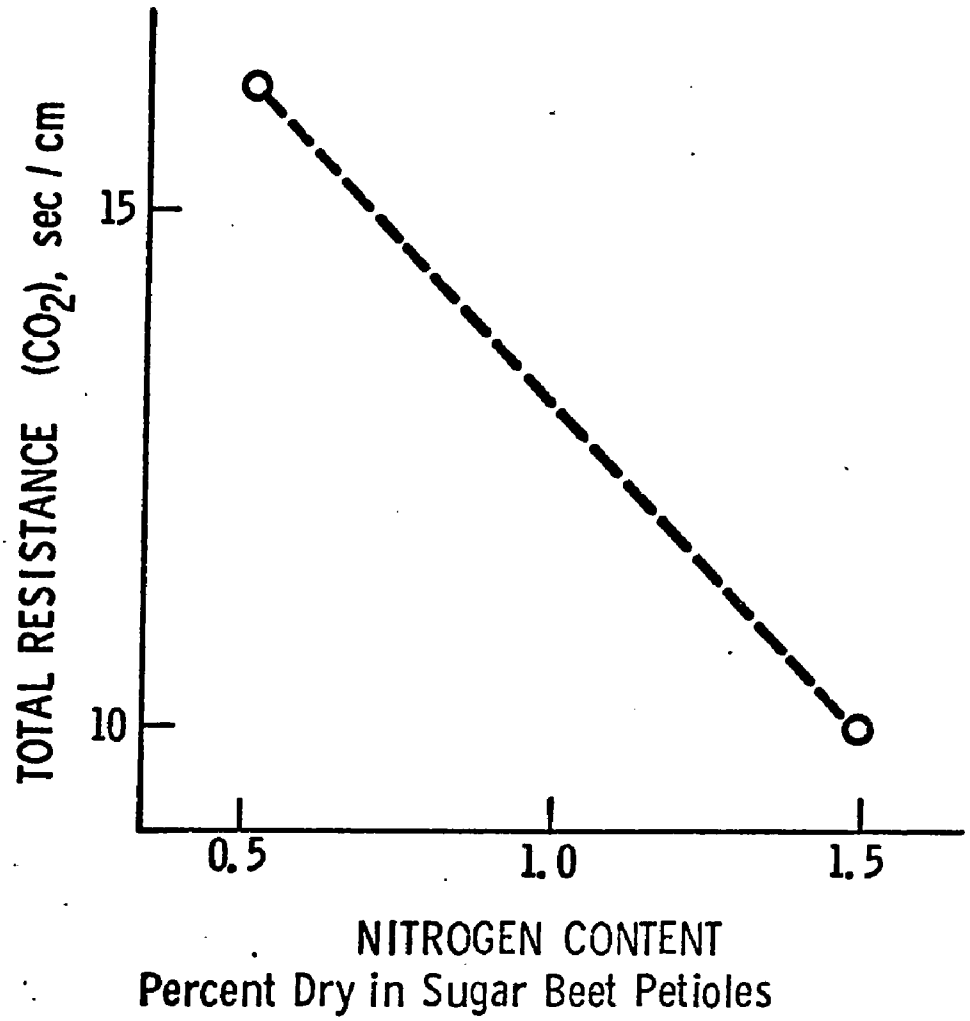



Figure 7. Leaf resistance to $CO_2$ diffusion as a function of leaf nitrogen content (After Nevins and Loomis 1970).

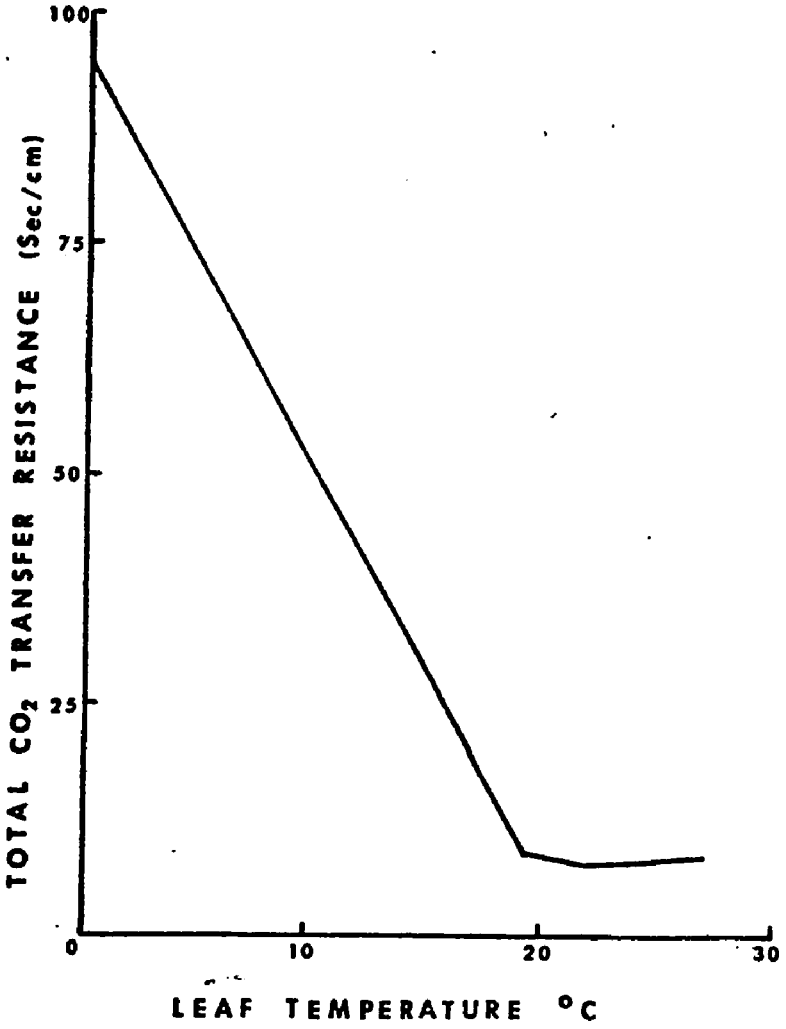



Figure 8. Leaf resistance response due to temperature (After Holmgren, et al. 1965).

photosynthetic response to light intensity for bog birch (Betula pumila) is shown in Figure 9 (Small 1972). The effect of light intensity on leaf resistance is described by Ehrler and van Bavel (1968) for several crop species and by Wuenscher and Kozlowski (1971) for several species of oak. A graph of mesophyll resistance response to light intensity for chestnut oak (Quercus macrocarpa) is shown in Figure 10.

Mesophyll and stomatal resistances are added together to obtain total leaf resistance. An algebraic expression for the resulting response is:

$$f6(z) = a/(1-\exp[b \cdot I(z)]) \qquad (2.10)$$

where: a = a constant

b = a constant

I(z) = light intensity at the point z in the canopy

The constant a is estimated from the graph and represents the minimum resistance value. The constant b which determines the slope of the curve is estimated by regressing ln (1-a/f6) on I. The maximum leaf resistance (pl) is factored out of the equation to obtain the response index. A regression of the response function on the data, to determine the fit of the equation, gives a value of .995 for the coefficient of determination. Since this function approaches infinity as light intensity approaches zero a lower bound is placed on light intensity.

It can be assumed that the light intensity follows the

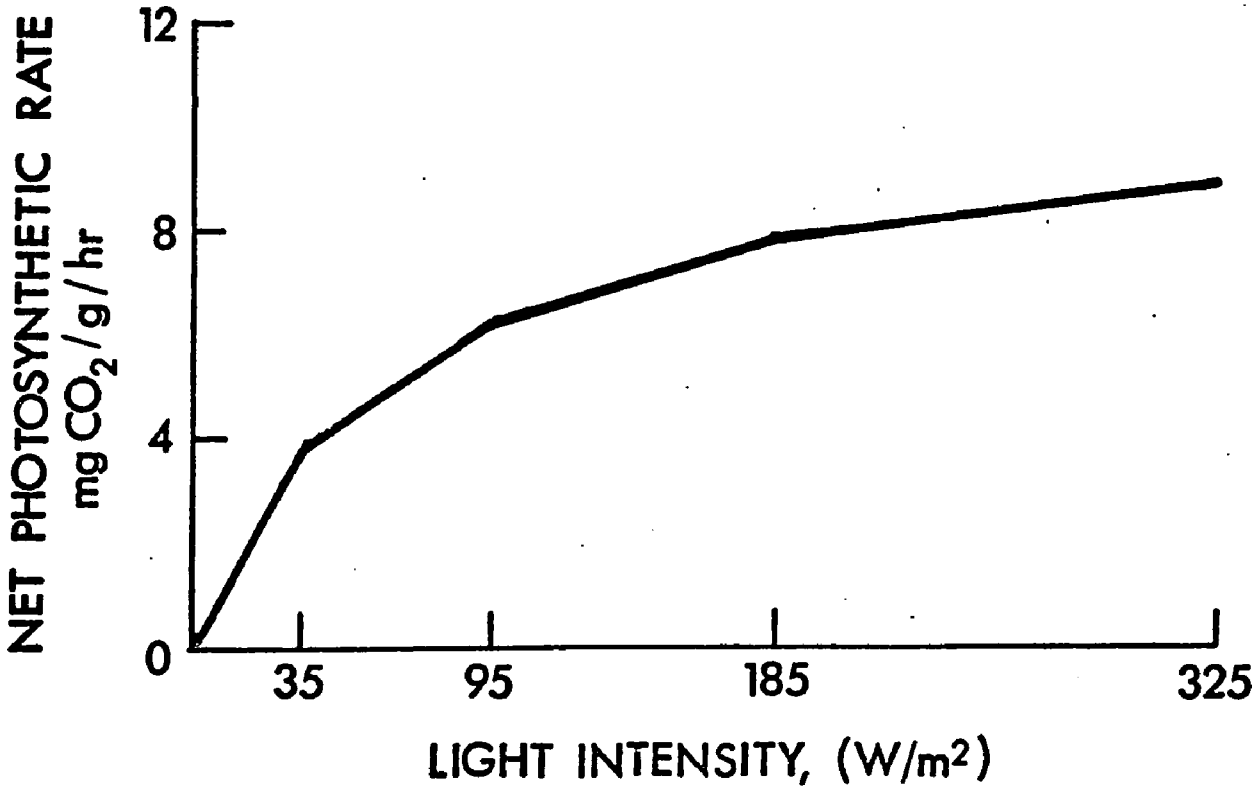



Figure 9. Photosynthetic response to light intensity in bog birch (After Small 1972).

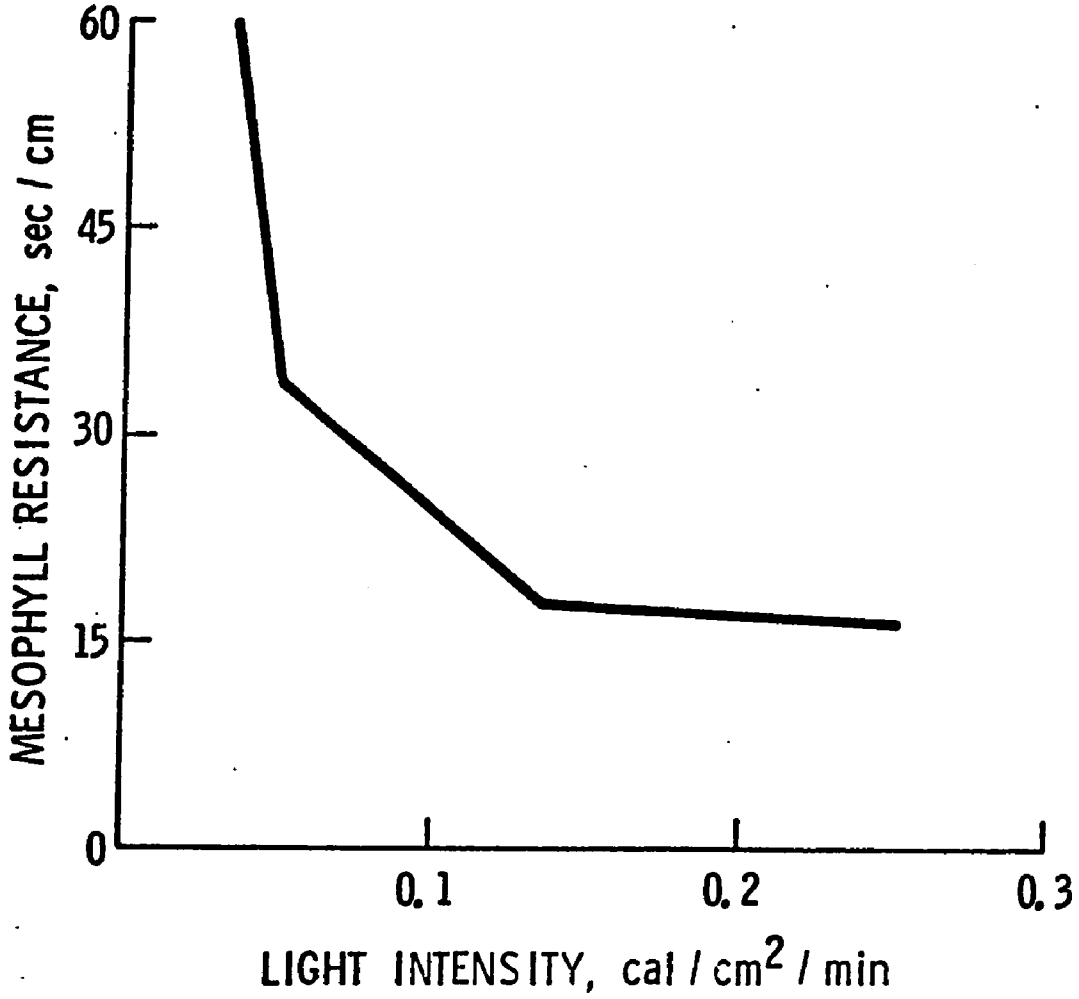



Figure 10. Mesophyll resistance response to light intensity in Quercus macrocarpa (After Wuenscher and Kozlowski 1971).

extinction law:

$$I(z) = I(0) \cdot \exp[-k\ f9(z)] \qquad (2.11)$$

where: $I(0)$ = light intensity at the top of the canopy ($z = 0$)

$k$ = extinction coefficient

$f9(z)$ = accumulated leaf biomass of all species from 0 to z (Monteith 1965)

The accumulated leaf biomass, f9(z), can be expressed in a general form by the integral

$$f9(z) = \int_0^z \lambda(\zeta)d\zeta \qquad (2.12)$$

where: $\lambda(\zeta)$ = the leaf biomass of all species at level $\zeta$ in the canopy

The function $\lambda(\zeta)$ can be assumed to follow a uniform vertical distribution within the canopy (Kira, et al. 1969; Sollins, et al. 1973) as a first approximation, and is given by:

$$\lambda(\zeta) = L/Z \qquad (2.13)$$

where: $L$ = total leaf biomass of plant species in the canopy

$Z$ = total canopy height

Baumgartner (1968) describes actual leaf area index distribution vertically within the canopy. The variable L is determined by summing the leaf biomass of each plant species:

$$L = \sum_{i=1}^{n} Xa_i \qquad (2.14)$$

where $Xa_i$ = the leaf biomass of plant unit i in the block.

In the same way, Xa(z), the leaf biomass of a species at height z is assumed to have a uniform vertical distribution, so that:

$$Xa(z) = \frac{Xa}{g} \qquad (2.15)$$

where: Xa = leaf biomass of this species

g = depth of leaf canopy for this species

For the total canopy to have a uniform distribution, associations of plant species must be one of two types. One is an assemblage of species of the same height, such as a grass-sedge type. The second type is where different species occupy different layers within the canopy, such as a birch-leatherleaf type, with birch being the dominant species, i.e., occupying the upper layers of the canopy.

The distribution of light intensity over the hours of daylight also must be considered. This distribution approximates a sinusoidal curve (Figure 11) (Lowry 1969:129). This curve can be represented by the equation (Monteith 1965):

$$I(0) = I^* \cdot \sin(\pi \cdot h/d) \qquad (2.16)$$

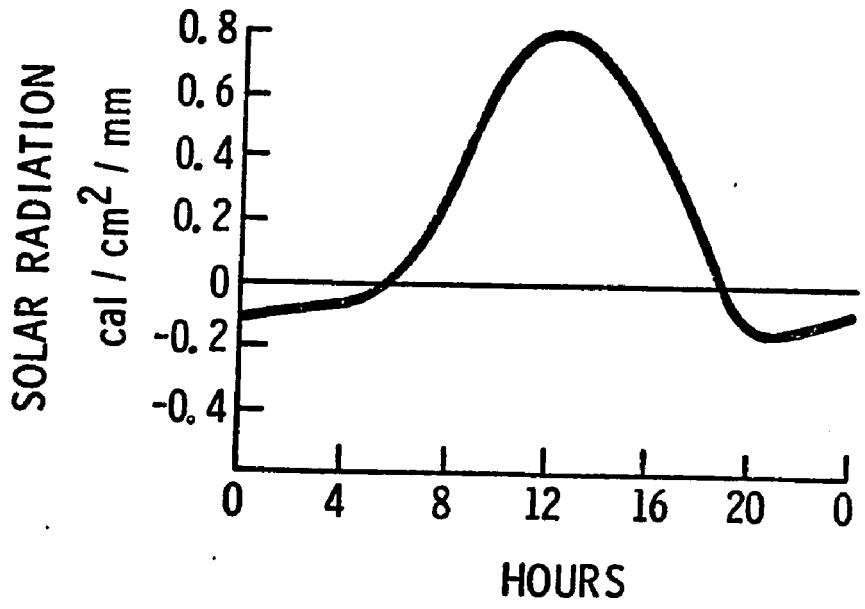



Figure 11. Diurnal net solar radiation (After Lowry 1969).

where: $I^*$ = maximum radiation

$d$ = duration of daylight

$h$ = time since sunrise

Using equations 2.2 through 2.16 and integrating over canopy height and daylength, the total net rate of growth ($r1'$) is determined:

$$r1' = \int_0^d \int_0^Z r1(z)\, d\zeta dy$$

$$= \frac{c1 \cdot Xa \cdot f10 \cdot c2 \cdot Z \cdot d}{p1 \cdot f5 \cdot f7 \cdot g \cdot a \cdot k \cdot L} \left\{ \frac{2bI^* (1-e^{-kLg/Z})}{\pi} - \right. \qquad (2.17)$$

$$\left. \frac{b^2 I^{*2} (1-e^{-2kLg/Z})}{2 \cdot 2 \cdot 2!} + \frac{4b^3 I^{*3} (1-e^{-3kLg/Z})}{3 \cdot 3 \cdot 3! \pi} - \ldots \right.$$

The series of equation (2.17) was shown to converge after five terms.

The vascular plant unit represents aboveground biomass only. However, the integral of $r1'$ in equation (2.17) gives the total photosynthate produced, which includes that apportioned to the roots. Therefore, a certain fraction of $r1'$ must be substracted to give photosynthate production in terms of aboveground biomass.

Nelson (1963:169) describes the translocation of assimilates from leaves to roots in eastern white pine (Pinus strobus):

> "The greatest translocation was in May before growth of new leader stem had begun and while the rate of photosynthesis was still low. Translocation stopped completely during June and July, slowly recovered in August, reached a new maximum in October, and declined again as winter set in."

A function which approximates this process is equation 2.18 (Figure 12).

$$f1 = \begin{cases} 0 & t<105 \\ .75 + .0055714\ (t-105) & 105 \leq t<140 \\ .27 - .0087096\ (t-140) & 140 \leq t<171 \\ 0 & 171 \leq t<206 \\ .0009756\ (t-206) & 206 \leq t<288 \\ .08 - .001568\ (t-288) & 339 \leq t \leq 365 \end{cases} \qquad (2.18)$$

This piece-wise linear function is estimated from Figure 8, page 119 of Nelson.

The rate of growth of aboveground biomass then becomes:

$$r1 = r1'(1-f1) \qquad (2.19)$$

Figure 13 gives the results of the simulated growth rate, r1, over one year for bog birch.

Stem mortality rate (r2). One important environmental factor contributing to plant mortality is winter cold (Peace 1962:20; Levitt 1956:5). Wetland vegetation, although normally adapted to saturated soil conditions, can be killed by unusually high water levels such as produced by wastewater disposal (Green 1947; Hall and Smith 1955; McDonald 1955; Peace 1962:71). The addition of excess water and nutrients may, in fact, increase a plant's susceptibility to cold temperatures by reducing its hardiness (Levitt 1956:51; Peace 1962:24; Rudolph, et al. 1957).

Although the mechanisms of cold injury are complex, it is assumed initially that stem mortality rate is a simple

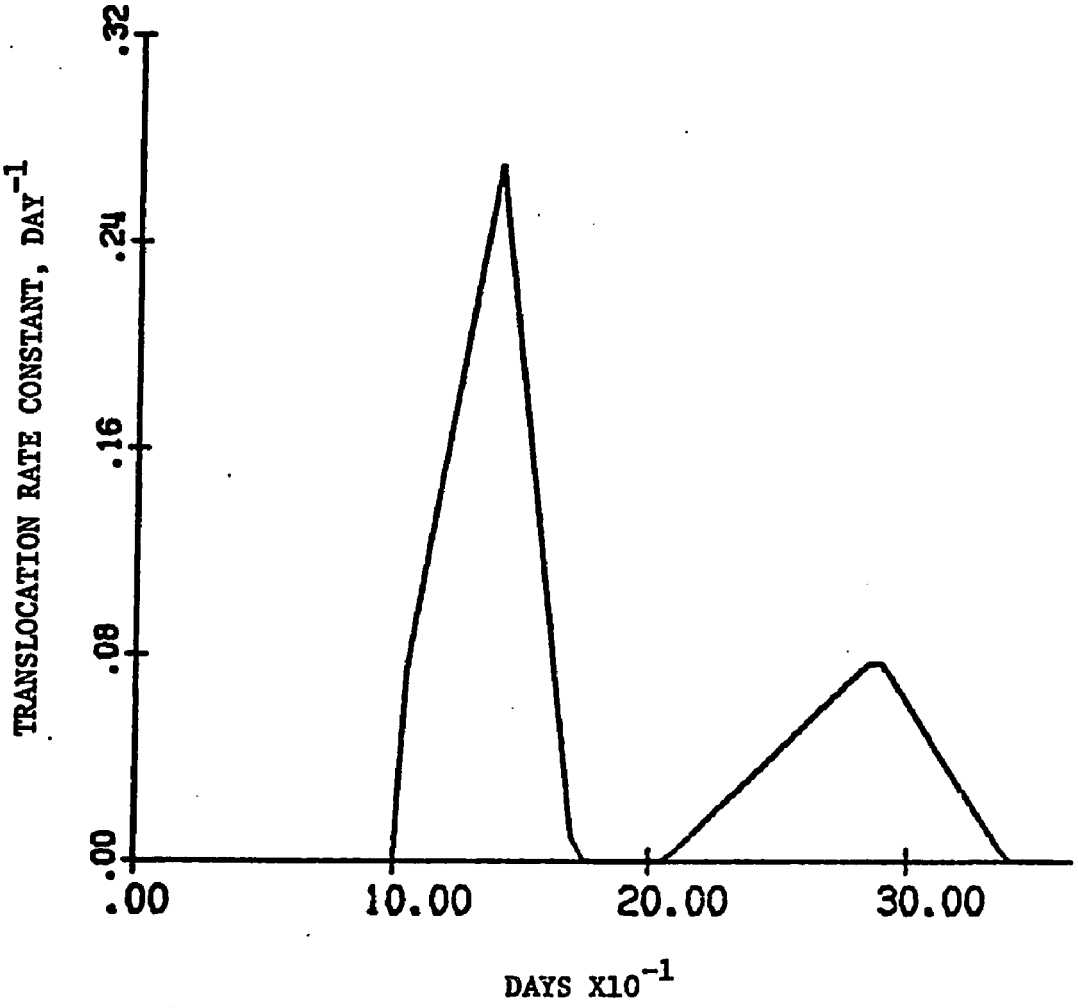



Figure 12. Translocation rate constant as a function of time (After Nelson 1963).

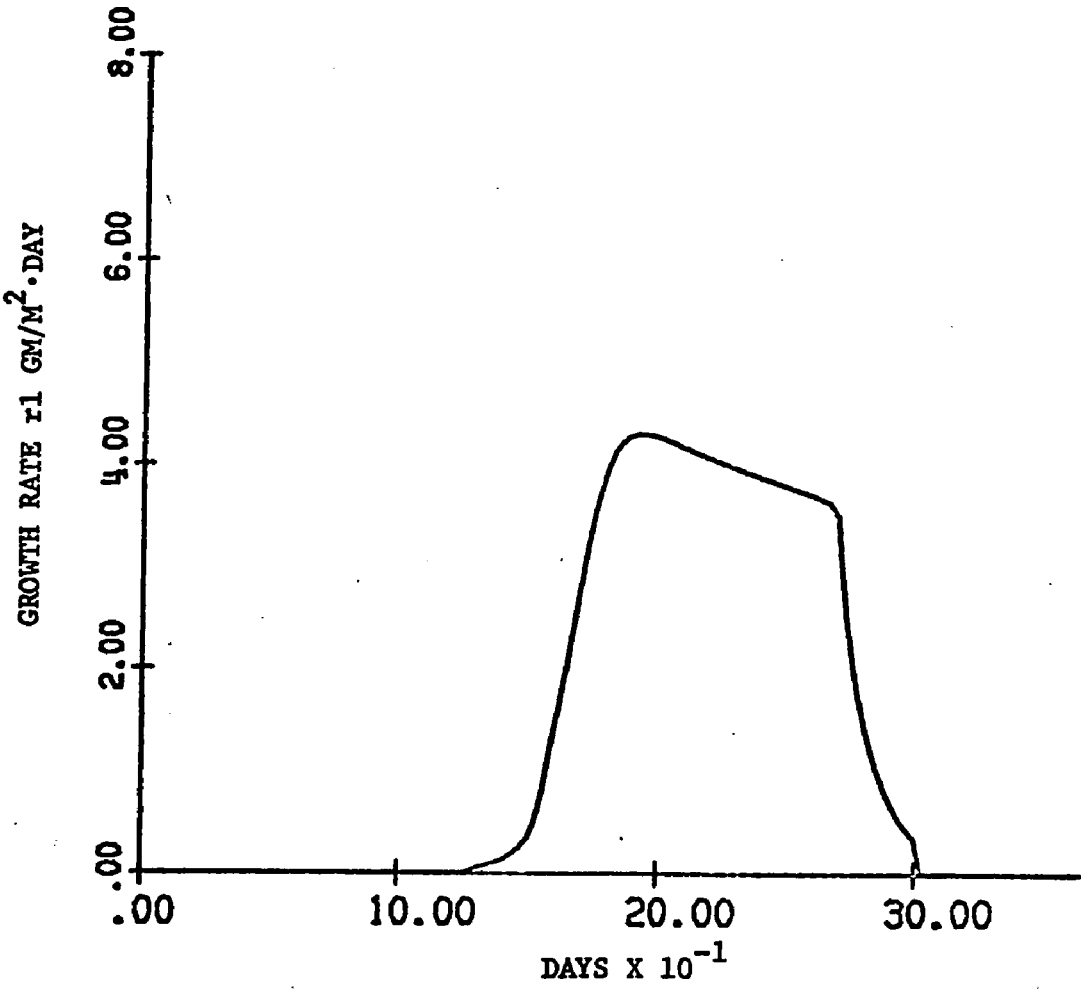



Figure 13. Results of growth rate, r1, simulation.

inverse function of the average daily temperature, Tavg. A function for the daily stem mortality rate coefficient, with units, $day^{-1}$, is expressed by equation (2.20):

$$f14 = p13 \cdot a/(Tavg + b) \qquad (2.20)$$

where: p13 = maximum daily stem mortality rate constant

Tavg = 24 hour average daily temperature

a and b = constants

The constants a and b are determined by setting f14 equal to 1.0 when Tavg was at the minimum and equal to 0.10 when Tavg was at the maximum, the solution of the two equations giving values of 2.895 and 9.284 for a and b respectively.

The parameter p13, for maximum daily mortality rate constant is estimated using data from Sollins, et al. (1973) on understory stem mortality. The estimate of standing crop (771 $gm/m^2$) and transfer to the standing dead compartment (52 $gm/m^2/yr$) give a value of .063 for an annual rate constant:

$$\frac{52}{771 + 52} = .063$$

Both sides of equation (2.20) are integrated over a period of one year, the left hand side is set equal to .063, and the resulting equation is solved for p13 giving a value of .00074. The rate of stem mortality, r2, then is determined

by multiplying the function f14 by stem biomass:

$$r2 = f14 \cdot Xb \qquad (2.21)$$

where: f14 = stem mortality rate coefficient

Xb = stem biomass

The curve showing stem mortality rate, as predicted in the model simulation, is shown in Figure 14.

Leaf mortality rate (r3). Mortality or leaf fall for several hardwood species has been reported, including birch (Betula pendula, B. pubescens) and alder (Alnus glutinosa) (Sykes and Bunce 1970; Hughes 1971). The leaf fall rates can be estimated from additional data of Hughes (1971) (see Table 3). From the data on number of leaves per square meter at sequential sampling dates (Table 3, columns 1 and 3), the number of leaves falling in a given interval can be calculated (column 4). These values multiplied by the respective leaf weight data (column 5) give estimates of leaf fall biomass (column 6). These values are added to the leaf biomass figures at the beginning of the interval (column 7) to give total standing crop estimates (column 8). The leaf fall biomass then is divided by the corresponding standing crop values to give the leaf fall rate coefficients for each interval (column 9). The resulting leaf fall rate function for birch is shown in Figure 15. Equation (2.22) is used to model this function:

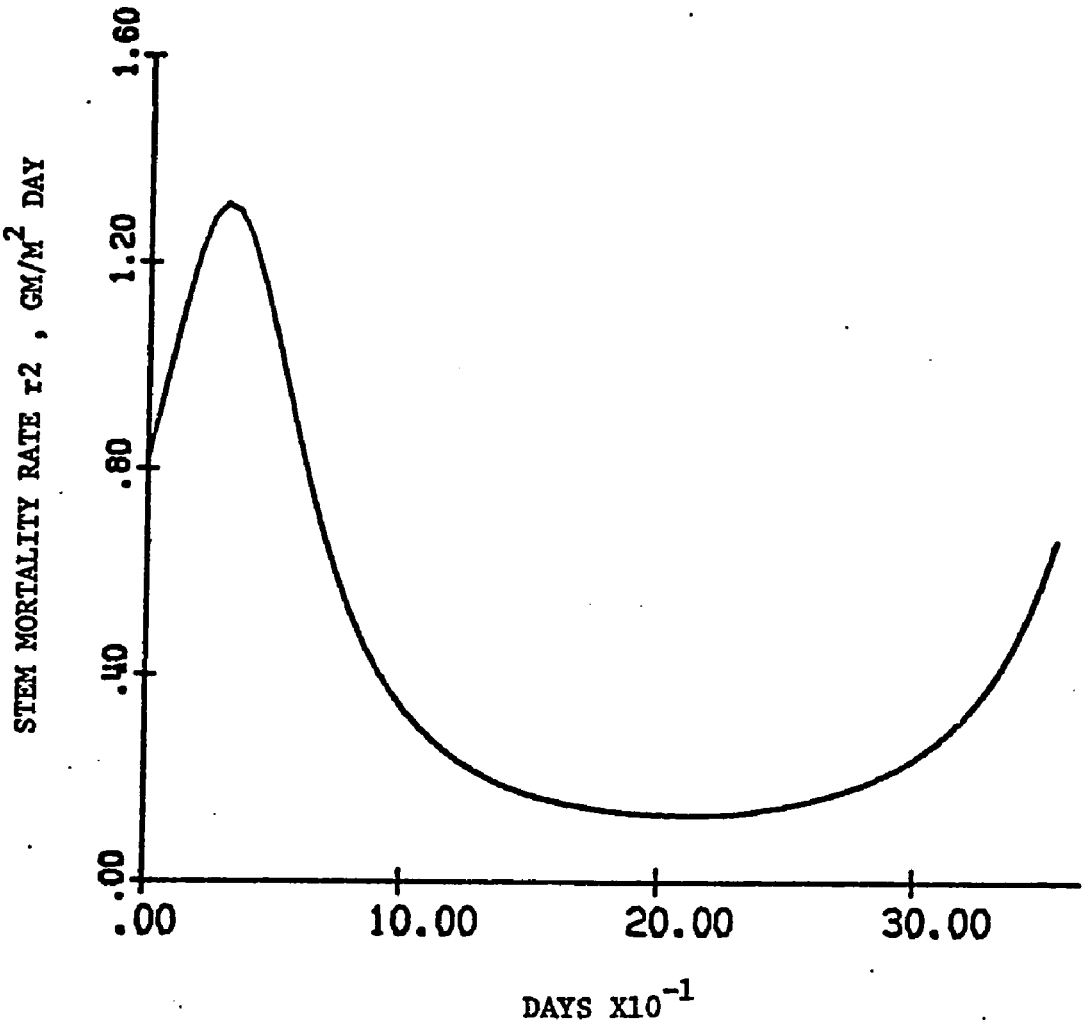



Figure 14. Stem mortality rate, r2, as estimated in model simulation.

Table 3. Calculation of leaf fall rate coefficient (Data from Hughes, 1971).

| Sampling date | Days between sampling dates | No. leaves in canopy/$m^2$ | No. leaves falling between sampling dates/$m^2$ | Leaf weight, gm | Leaf fall, $gm/m^2$ per interval (4) x (5) | Leaf biomass, $gm/m^2$ | Total leaf biomass for interval, $gm/m^2$ (6) + (7) | Leaf fall rate coefficient $(day^{-1})$ (6) ÷ (8) x (2) |
|---|---|---|---|---|---|---|---|---|
| (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) |
| 128 | | 3147 | | .0120 | | 37.7 | | |
| | 7 | | 0 | | 0 | | 37.7 | 0 |
| 135 | | 3147 | | .0136 | | 42.8 | | |
| | 14 | | 0 | | 0 | | 42.8 | 0 |
| 149 | | 3147 | | .0210 | | 66.2 | | |
| | 7 | | 15 | | .315 | | 66.510 | $6.77 \times 10^{-4}$ |
| 156 | | 3132 | | .0211 | | 66.0 | | |
| | 12 | | 0 | | 0 | | 66.000 | 0 |
| 168 | | 3132 | | .0215 | | 67.0 | | |
| | 12 | | 170 | | 3.605 | | 70.655 | $4.311 \times 10^{-3}$ |
| 180 | | 2962 | | .0216 | | 64.1 | | |
| | 11 | | 90 | | 1.944 | | 66.044 | $2.676 \times 10^{-3}$ |
| 191 | | 2872 | | .0213 | | 61.3 | | |
| | 21 | | 107 | | 2.279 | | 63.579 | $1.707 \times 10^{-3}$ |
| 212 | | 2765 | | (.0241)+ | | (66.6)* | | |
| | 18 | | 65 | | 1.566 | | 68.166 | $1.276 \times 10^{-3}$ |
| 230 | | 2700 | | .0258 | | 69.8 | | |
| | 19 | | 263 | | 6.785 | | 76.585 | $4.663 \times 10^{-3}$ |
| 249 | | 2437 | | (.0254)+ | | (62.0)* | | |
| | 19 | | 370 | | 9.398 | | 71.398 | $6.928 \times 10^{-3}$ |
| 268 | | 2067 | | (.0247)+ | | (51.0)* | | |
| | 16 | | 371 | | 9.164 | | 60.164 | $9.520 \times 10^{-3}$ |
| 284 | | 1696 | | .0225 | | 39.9 | | |
| | 15 | | 1100 | | 25.580 | | 65.750 | $26.621 \times 10^{-3}$ |
| 299 | | 596 | | .0219 | | 17.2 | | |
| | 19 | | 546 | | 11.957 | | 29.157 | $21.158 \times 10^{-3}$ |
| 318 | | 50 | | (.0199)+ | | (1.448)* | | |
| | 13 | | 50 | | .995 | | 2.438 | $31.139 \times 10^{-3}$ |
| 331 | | 0 | | - | | - | | |

*Interpolated using no. of leaves.
+Column (7) divided by column (3).

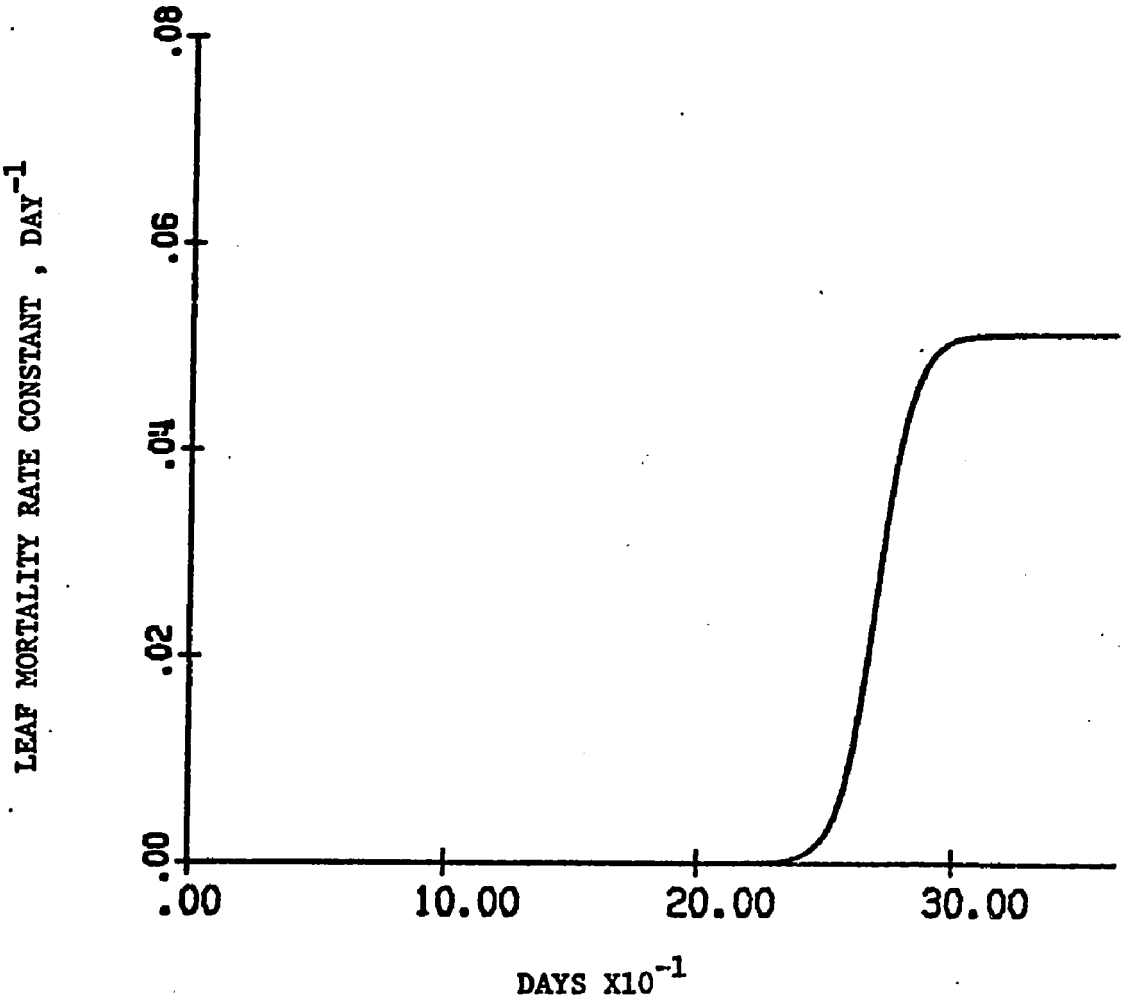



Figure 15. Leaf mortality rate constant (Data from Hughes 1971).

$$f15 = \frac{p14 \cdot \exp\{2.2(t-t1-t2)/t3\}}{1 + \exp\{2.2(t-t1-t2)/t3\}} \qquad (2.22)$$

where: p14 = maximum daily leaf fall rate constant

t = time in days

t1 = time of initial leaf fall

t2 = time between initial leaf fall and point of inflection on curve

t3 = number of days between 50 and 90 percent of maximum leaf fall rate

This is an empirical function which produces a sigmoid curve (Reeves 1971). It has the advantage over other functions which produce the same shaped curve of having only one parameter, p14, which is relatively easy to measure. The constants with units in days are readily determined from a plot of leaf fall rate over time.

The leaf mortality rate, r3, is determined by multiplying the leaf mortality rate function f15 by Xa:

$$r3 = f15 \cdot Xa \qquad (2.23)$$

where: f15 = leaf fall rate function

Xa = leaf biomass

The model simulation produces a curve of leaf fall rate as shown in Figure 16.

Dark respiration rate (r4). The factor which ordinarily has the greatest effect on dark respiration is temperature

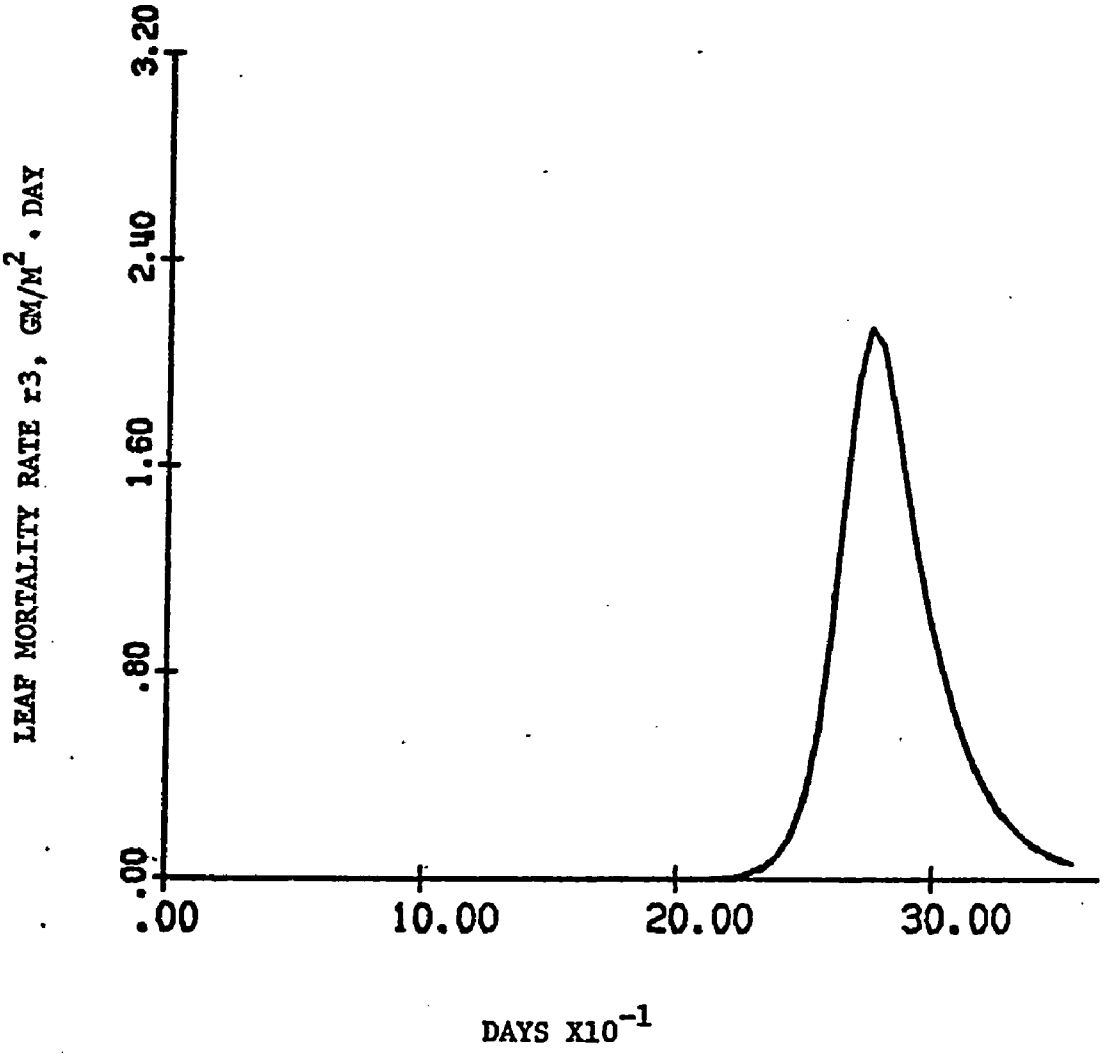



Figure 16. Leaf mortality rate, r3, as estimated in model simulation.

(Zelitch 1971:141). Assuming other factors are not limiting, the rate of dark respiration can be written as a function of average nightly temperature, Tnite. The effect of temperature on respiration of potato leaves has been studied by Lundegardh (1924) as shown in Figure 17.

The curve in Figure 17 can be represented by a straight line over the range of temperatures measured in the marsh. Dark respiration rate is assumed to be zero at temperatures $0^{o}C$ and below. The temperature index is determined by inverting the maximum nightly temperature, $13.55^{o}C$:

$$1/13.55 = 0.0738$$

The rate of dark respiration then can be expressed by the following equation:

$$r4 = p15 \cdot f10 \cdot Xa \cdot (8.64 \times 10^{4} - d) \cdot 0.0738 \cdot Tnite \qquad (2.24)$$

where: r4 = dark respiration rate

p15 = maximum respiration rate constant

f10 = empirical function to convert leaf area to leaf biomass

Xa = leaf biomass

d = duration of daylight, sec,

Tnite= average nightly temperature

The parameter for maximum respiration rate, p15, is calculated from data presented by Lake (1967) using a value of

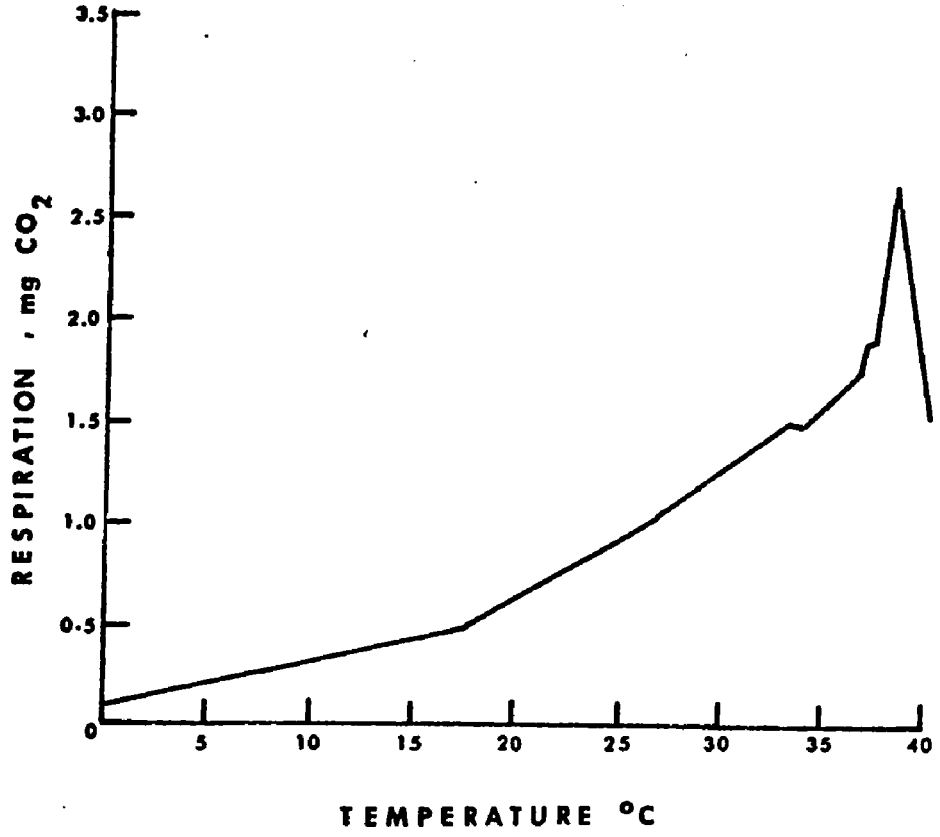



Figure 17. Respiration of potato leaves as a function of temperature.

2.28 mg·$CO_2$·$dm^{-2}$·hr for Betula verrucosa at 22°C. This is equivalent to a value for p15 of 2.528 x $10^{-9}$ gm·carbohydrate $cm^{-2}$ $sec^{-1}$.

The results of this model in the simulation is shown in Figure 18. This model is for respiration of leaves only. For the present, respiration of other plant parts is assumed not to be significant and is not included in the model.

Translocation rate (r10). At the end of the growing season, a fraction of leaf biomass is broken down into simple sugars and translocated to stems. This translocation is reflected in the data of Hughes (1971) which show an exponential decline in weight per leaf. A translocation rate function, r10, is written as a function of leaf biomass:

$$r10 = \begin{cases} .0321 \cdot Xa & 230 \text{ t } 300 \\ 0 & \text{otherwise} \end{cases} \qquad (2.25)$$

Vascular plant unit simulation. Numerical solutions to equations (2.1) for total aboveground biomass and stem biomass are shown in Figure 19. The difference between the two curves is leaf biomass which is presented in Figure 20.

At the first of the year, before growth begins, total biomass consists of stem biomass only. As growth starts, leaf biomass increases at a faster rate than stem biomass. As growth rate decreases and stem and leaf mortality (Figures 19 and 20) increase, total biomass decreases. In this simulation there is a net increase in total aboveground

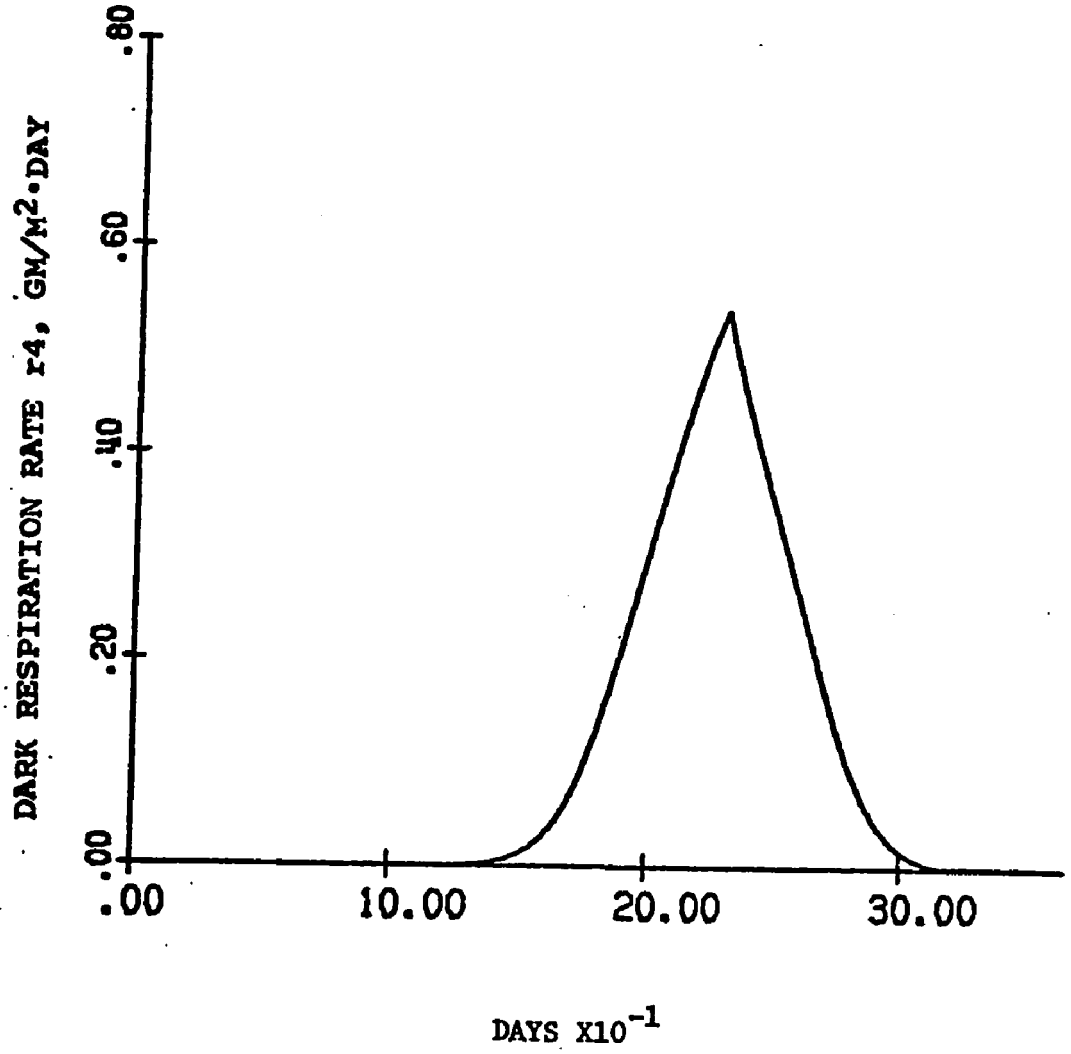



Figure 18. Dark respiration rate, r4, as estimated in model simulation.

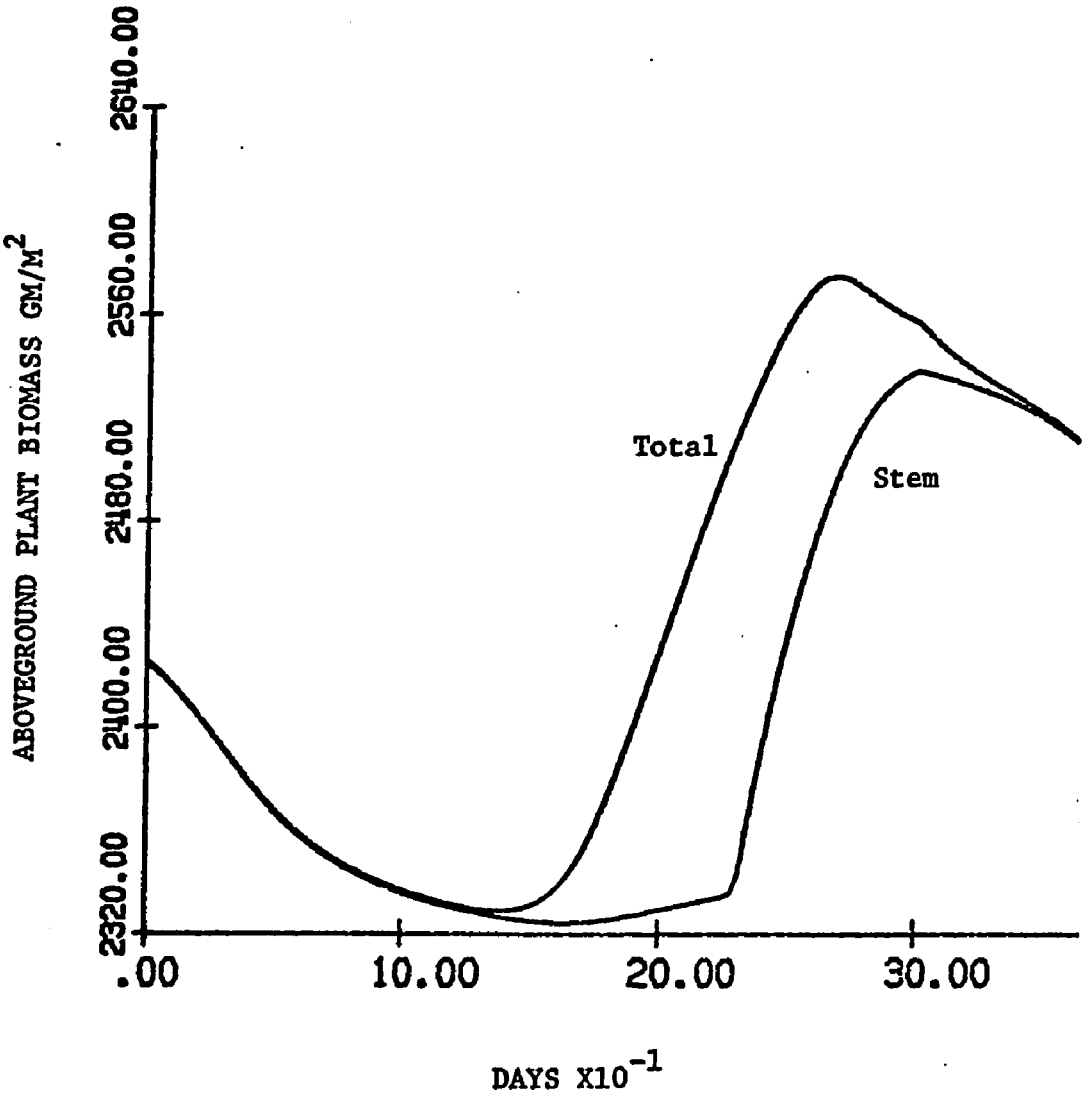



Figure 19. Total aboveground plant biomass, X1, and stem biomass, X1b, as estimated in model simulation.

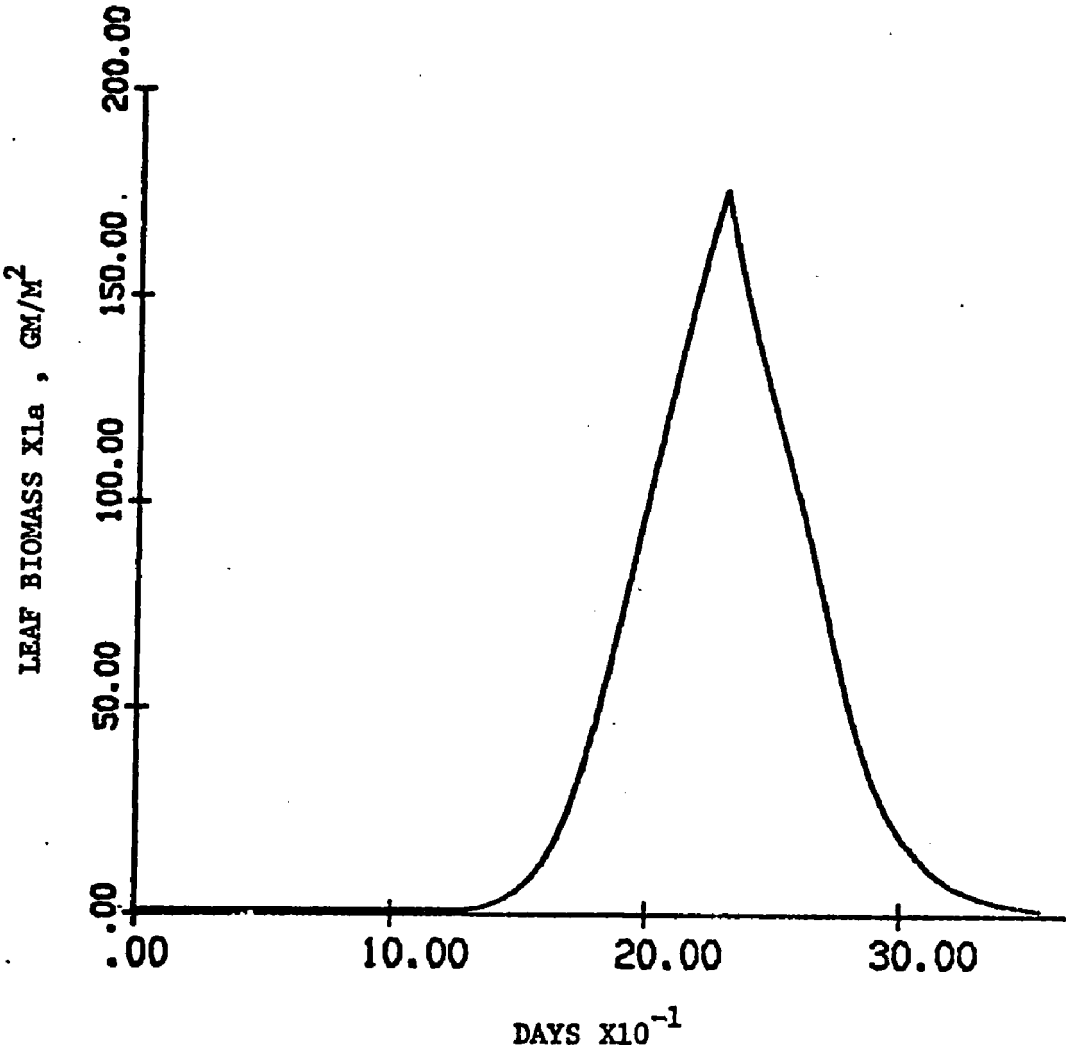



Figure 20. Leaf biomass, X1a, as estimated in model simulation.

biomass of 88.4 gm/$m^2$.

3. Standing Dead Unit (X = X14)

The woody stems and twigs which have died but have not fallen to the litter layer comprise the standing dead unit, X14. The input into the unit is the sum of the stem mortality rates, $r2_i$, of all vascular plant units. The output from the unit is the rate at which the dead stems fall into the litter unit. Equation (3.1) describes the mass balance for X14, the standing dead unit variable:

$$\dot{X} = \sum_{i=1}^{n} r2_i - r5 \qquad (3.1)$$

where: $r2_i$ = stem mortality rate of the $i^{th}$ plant group

$r5$ = stem litter production rate

A stem mortality rate equation was presented in the vascular plant unit model and is considered representative of the several woody plant species in the marsh study area. A description of the stem litter production rate, r5, for birch follows (see Table 1 for initial condition).

In two studies (Hughes 1971; Sykes and Bunce 1970), woody stem and branch fall was found to be sporadic with no tendency to fall in any particular month. Sykes and Bunce (1970) attribute the fall rate to infrequent storms or periods of high wind speed. The rate of stem litter

production, r5, is written as a function of rainfall, using the RFALL function described by Parker (1974):

$$r5 = p16 \cdot RFALL \cdot X \qquad (3.2)$$

where: p16 = stoichiometric coefficient relating rainfall to stem litter production

RFALL = rainfall function

X = biomass of standing dead unit

Assuming standing dead biomass to be in a steady-state, $\int r5/X = 0.063$, the annual stem mortality rate constant (page 40). The parameter, p16, can be estimated now by dividing equation (3.2) by X, the standing dead biomass and integrating both sides of the equation over a year:

$$\int \frac{r5}{X} = p16 \int RFALL \qquad (3.3)$$

Substituting an annual value of .063 for the left integral and 59.8 cm of annual rainfall for the right integral gives a solution for p16 of .001107 $cm^{-1}$.

The numerical solution to equation (3.1) as determined in the simulation is shown in Figure 21. Standing dead biomass increases initially in response to increasing stem mortality. After reaching a peak biomass descreases in response to the constant stem litter production rate, r5, until stem mortality again increases at the end of the year.

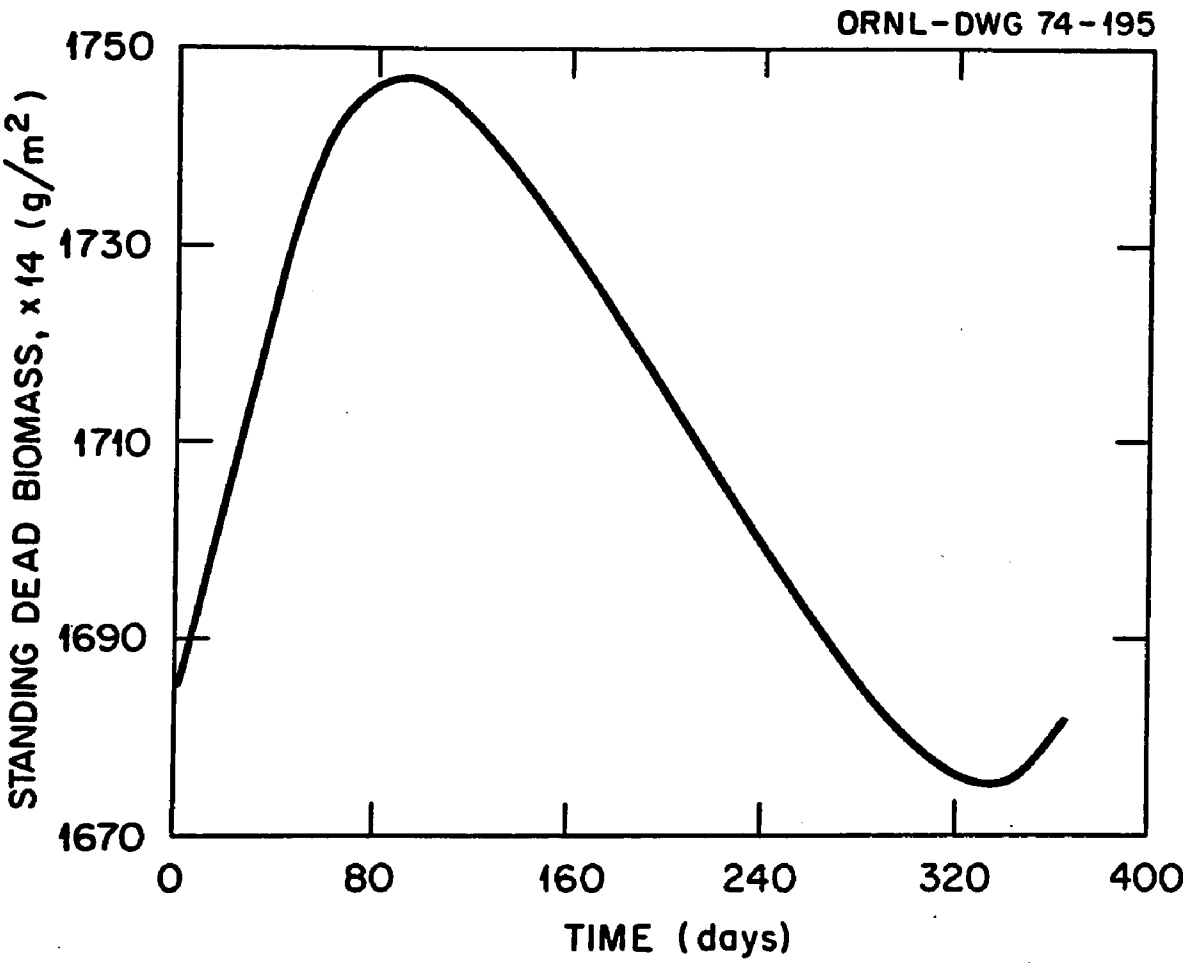



Figure 21. Standing dead biomass, X14, as estimated in model simulation.

## 4. Litter Unit Model (X = X11)

The litter unit, X11, consists of two sub-units: one of leaf litter, X11b; the other of stem and branch litter, X11a. The litter unit model is expressed by the following set of equations:

$$X = \int \dot{X}a + \int \dot{X}b \qquad (4.1)$$

$$\dot{X}a = \sum_i r5_i - r6 \qquad (4.1a)$$

$$\dot{X}b = \sum_i r3_i - r7 \qquad (4.1b)$$

where: X = biomass of total litter

Xa = biomass of stem litter

Xb = biomass of leaf litter

r3 = leaf mortality rate

r5 = stem litter production rate

r6 = stem litter decomposition rate

r7 = leaf litter decomposition rate

It is necessary to divide the litter unit into two sub-units since the rate of stem litter decomposition is usually much lower than that of leaf litter due to the greater proportion of refractory materials, such as lignin, cellulose, and hemicelluloses in woody material (Waksman and Stevens 1929b). Examples of these data are given in Table 4.

Table 4. Percentage values of refractory materials in leaves and stems of three hardwood species (Data from Mikola 1954; Nikitin 1966).

| Species | Betula pubescens | | Populus tremula | | Alnus glutinosa | |
|---|---|---|---|---|---|---|
| Material | leaves | stems | leaves | stems | leaves | stems |
| lignin | 29.2 | 20.3 | 16.4 | 21.3 | 10.1 | 22.5 |
| cellulose | 14.1 | 45.8 | 16.1 | 52.1 | 10.4 | 48.3 |
| hemicelluloses | 12.5 | 42.0 | 13.6 | - | 9.7 | 30.8 |

Models for leaf mortality rate, r3, and stem litter production rate, r5, were presented earlier in this chapter; the decomposition rate terms now will be covered.

Leaf litter decomposition rate (r7). Abiotic variables which have the greatest effect on litter decomposition rates are temperature and moisture, especially saturated or anaerobic conditions (Waksman and Gerretsen 1931; Witkamp 1966; Witkamp and van der Drift 1961). Experiments on litter decomposition which included birch (Betula verrucosa and B. pubescens) were conducted by Mikola (1954, 1960) and Nykvist (1961). The addition of nutrients also has been reported to have a stimulating influence on decomposition rates of oat straw (Waksman and Gerretsen 1931) and birch and alder leaf litter (Mikola 1954). After an initial increase in straw decomposition with added nitrogen, Pauli (1970) found the rate dropped below that of controls. These variables are combined in an equation for leaf litter decomposition of the form:

$$r7 = p10 \cdot f21 \cdot f22 \cdot f23 \cdot Xb \qquad (4.2)$$

where: p10 = maximum rate constant of leaf litter decomposition

f21 = a function describing the response of decomposition rate to temperature

f22 = a function relating the decomposition rate to the watertable

f23 = a function describing the response of decomposition rate to nutrient supply

Xb = biomass of leaf litter

The effect of temperature on decomposition rates is greatest and probably best documented. Witkamp (1966) found a highly significant correlation between respiration rate during litter decomposition and litter temperature. In their study of organic matter decomposition in a half-bog in the Arctic, Douglas and Tedrow (1959) also found a highly significant correlation with temperature. Studies of decomposition rates of tree litter, including birch (Betula papyrifera), by Daubenmire and Prusso (1963) showed a 45 percent increase between 10 and 25°C. A linear regression analysis of decomposition rate of oat straw against temperature (Waksman and Gerretsen 1931) gives a coefficient of determiniation ($r^2$) of 0.87 for temperatures between 7 and 37°C.

Using the regression of the data for Waksman and Gerretsen, a maximum rate constant, p10, of .003868, and a maximum temperature of 27°C, a response function for f21 can be written as:

$$f21 = .3313 + .02477\ Tavg \qquad (4.3)$$

The effect of moisture on litter decomposition rates has been studied extensively, but no standard method of defining litter moisture has been established. Witkamp

(1966) found a highly significant correlation between microbial respiration and leaf litter moisture as expressed by (grams moist weight/grams dry weight)$^{\frac{1}{2}}$. Anaerobic conditions in litter, caused by excessive moisture, greatly retard decomposition (Mikola 1954; Tenney and Waksman 1929, 1930; Waksman and Gerretsen 1931; Waksman, et al. 1928). In studies of birch litter decomposition Nykvist (1961) found aerobic decomposition was about twice as large as anaerobic after 43 days. Mikola (1954) and Mattson and Koutler-Andersson (1941) found similar results for a second birch species (Betula pubescens). Decomposition rates, calculated using $k = -\ln\left(\frac{W}{WO}\right) / t$, for these and other data are presented in Table 5. An equation is written for the decomposition rate response to the watertable, f22, using the values of Nykvist (1961). It is assumed that anerobic conditions exist for the entire litter layer when the watertable is higher than the litter layer, i.e., HS > p11, and aerobic conditions exist when HS < 0. Also, it is assumed that oxygen available for decomposition varies linearly between HS = 0 and HS = p11. Then f22 is written as:

$$f22 = \begin{cases} 1 & HS < 0 \\ 1 - \frac{0.5672HS}{p11} & 0 < HS < p11 \\ 0.4328 & HS > p11 \end{cases} \qquad (4.4)$$

where: HS = height of watertable relative to ground surface, cm

pll = height of litter layer in block, cm

The constant pll is the total height of litter relative to level ground. This height includes micro-relief of hummock areas. If litter height is greater than the micro-relief, it will be a function of litter biomass and pll will be redefined.

The effects of nutrient additions to litter on decomposition rates are not well documented and reports are conflicting. It has been suggested (Witkamp 1966) that nutrients released from litter during periods of drying and rewetting increase microbial activity. If this is true, it should be possible for the addition of nutrients to increase the litter decomposition rate provided other conditions are optimal and the microbial population is not at a self-limiting level.

Some laboratory studies have shown a positive effect of nutrient additions. Mikola (1954) found increases of 21 and 69 percent in the decomposition of birch (Betula pubescens) litter with added nutrients. Smaller increases have been reported over longer periods on other litter materials (see Table 5) by Tenney and Waksman (1929) and Waksman and Gerretsen (1931). Using Tenney's and Waksman's data and adjusting decomposition rates at different nutrient concentrations on the basis of a single litter type, a linear relationship was found between decomposition rate constant k

Table 5. Decomposition rate constants for various litter materials under aerobic and anaerobic conditions.

| Material | Daily decomposition rate constants, k* aerobic | anaerobic | Source |
|---|---|---|---|
| Betula pubescens | .003322 | .002144 | Mikola 1954 |
| Betula pubescens | .002011 | .000716 | Mattson and Koutler-Andersson 1941 |
| Betula verrucosa | .003868 | .001674 | Nykvist 1961 |
| rye straw | .001399 | .000847 | Tenney and Waksman 1929, 1930 |
| Oak leaves | .001329 | .000394 | Tenney and Waksman 1929, 1930 |
| sphagnum | .000647 | .000173 | Tenney and Waksman 1929, 1930 |

*Maximum values of k yield estimates of p10, the maximum decomposition rate constant.

and nutrient concentration in milligrams per liter. The parameter for maximum litter decomposition rate constant, p10, is measured in the absence of added nutrients so that the functional response to nutrients, f23, takes effect only at nutrient concentrations sufficient to increase k above its normal maximum. The response then is written as:

$$f23 = 1.306 \times 10^{-3} \cdot N \qquad (4.5)$$

where N = nitrogen concentration in soil solution. This linear response isdetermined by the data which ranges between 765.8 and 1045 ppm total nitrogen. It is reasonable to assume that the response will approach some limit determined by the microbial population itself as nutrient concentrations increase significantly. Should soil nitrogen concentrations reach such high levels, a non-linear function will be needed.

Stem litter decomposition rate (r6). As stated above, the rate of decomposition of stems or other woody material is ordinarily lower than that of leafy material due to the lower percentage of refractory substances in the latter. It is known that the same factors affect the decomposition of woody material as affect leafy material (Allison, et al. 1963; Campbell 1952:1066; Allison and Murphy 1962; Waksman and Stevens 1929b). It is assumed that the same functional responses, f21, f22, and f23 hold for stem litter decomposition, the difference being the maximum decomposition rate constant. Cromack (1971) gives an annual rate of stem and branch litter decomposition of 0.35 or a daily maximum rate of

.000959. The equation for the rate of stem litter decomposition then is:

$$r6 = p9 \cdot f21 \cdot f22 \cdot f23 \cdot Xa \qquad (4.6)$$

where: p9 = maximum rate constant of stem litter decomposition

f21 = a function describing the response of decomposition rate to temperature

f22 = a function relating the decomposition rate to the watertable

f23 = a function describing the response of decomposition rate to nutrient supply

Xa = biomass of stem litter

Litter unit simulation. Equations (4.1) for total litter, stem, and leaf litter are simulated with the results shown in Figure 22. In these simulations, watertable height was held constant at HS = 0 and nitrogen concentration was held constant at N = 765.8 ppm total nitrogen, while temperature was allowed to vary.

Stem litter biomass, X11a, increases from 109.0 to 205.4 $gm/m^2$ for a net increase of 96.4 $gm/m^2$. However, leaf litter biomass, X11b, decreases at an increasing rate until leaf mortality increases sharply in the fall. Due to the heavy buildup of stem litter and leaf fall, ther is a corresponding net increase in total litter biomass of 123.6 $gm/m^2$.

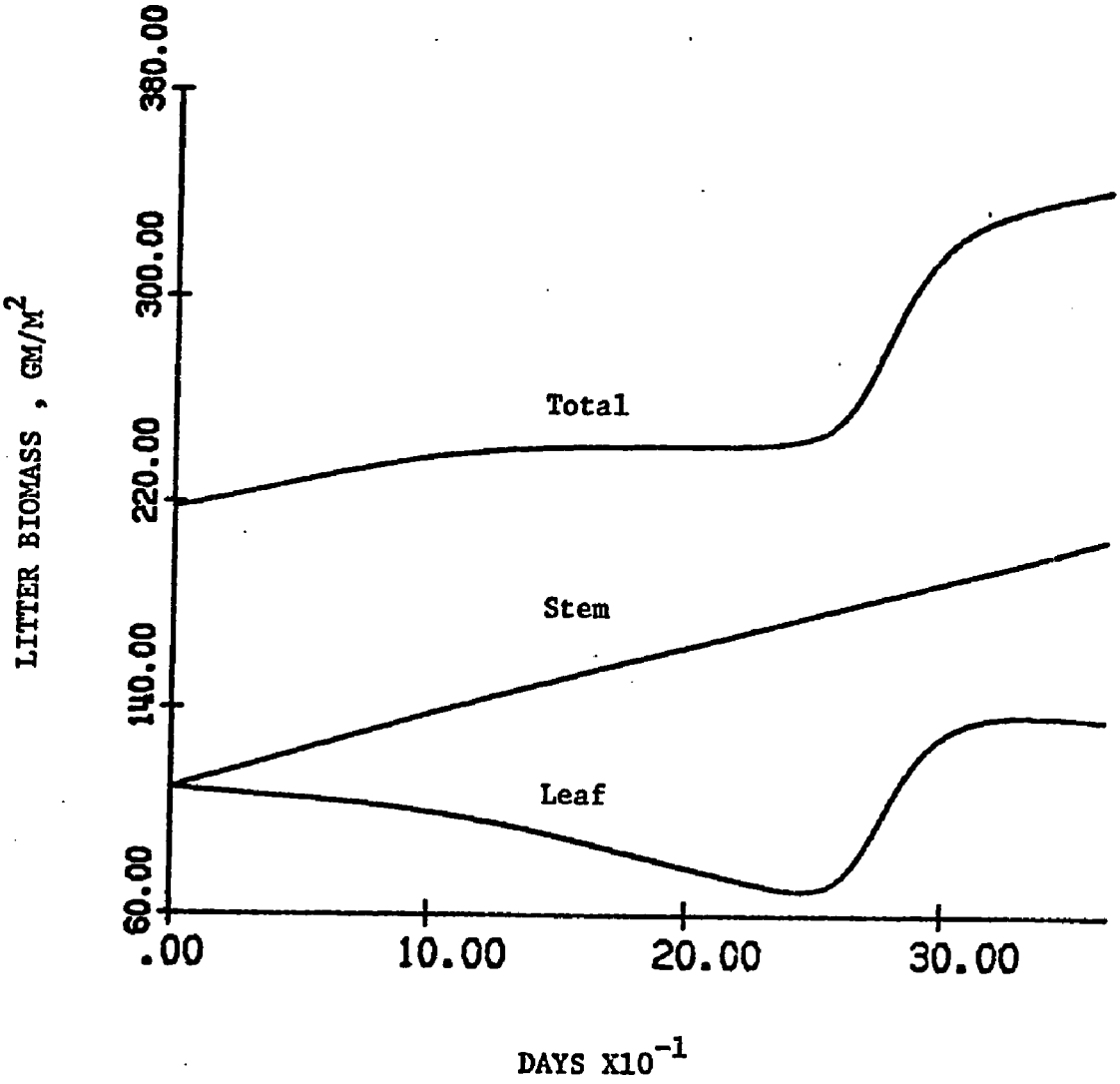



Figure 22. Total litter, X11, stem litter, X11a, and leaf litter, X11b, biomass as esimated in model simulation.

5. Soil Unit Model (X = X12)

The organic soil in wetland ecosystems, having accumulation and decomposition rates, is treated as the other unit variables in the model. Inputs into the soil unit come from the litter unit, X11. The output from the unit is due to decomposition but does not enter any other unit of the system. It is lost to the groundwater in soluble form or to the atmosphere as gases such as methane, hydrogen sulfide, and nitrogen. The biomass balance equation for the soil unit is:

$$\dot{X} = r8 - r9 \qquad (5.1)$$

where: r8 = rate of input from the litter unit

r9 = decomposition rate of peat soil

Peat accumulation rate (r8). The rate of input of material to the peat, r8, is a fraction of the decomposition rates of both woody and non-woody litter material:

$$r8 = p4 \cdot r6 \cdot + p5 \cdot r7 \qquad (5.2)$$

where: p4 = stoichiometric coefficient

p5 = stoichiometric coefficient

r6 = rate of decomposition of woody material

r7 = rate of decomposition of non-woody material

The parameters in equation (5.2) for fractions of

litter decomposition are based on the proportions of woody and non-woody material which is non-readily hydrolyzable. These fractions have been determined for various types of plant material (Polisini and Boyd 1972; Boyd and Blackburn 1970), non-woody litter (Tenney and Waksman 1929, 1930), woody litter (Waksman and Stevens 1929b), and peat (Kurbatov 1968; Rakovskii, et al. 1968).

Peat decomposition rate (r9). The decomposition rate, r9, is expressed as a function of temperature (Douglas and Tedrow 1959) and water level (Waksman and Stevens 1929a; Lähde 1969). There is considerable evidence that nutrient supply has little effect on decomposition rates of peat (Turk 1939; Stotzky and Mortensen 1957; Salonius 1972). Therefore, nutrient supply is not used as a variable in determining the decomposition rate term.

Douglas and Tedrow (1959) found a linear relationship between decomposition rate and soil temperature. Transforming their regression equation by substituting an optimum moisture of 500 percent and converting to biomass units ($gm/m^3 \cdot day$) by multiplying 1.8 times carbon evolved as $CO_2$, yields an expression, f24, for decomposition rate response to temperature:

$$f24 = 3.5958 + 2.7330\ Tsoil \qquad (5.3)$$

where Tsoil = soil temperature.

Soil temperature is estimated as a constant fraction of average daily temperature, Tavg.

To obtain the daily decomposition rate constant equation (5.3) is divided by biomass in $gm/m^3$:

$$f27 = 7.1916 \times 10^{-6} + 5.466 \times 10^{-6} \text{ Tsoil} \qquad (5.4)$$

Equation (5.4) is divided by p17, the optimal decomposition rate constant with a value of $2.944 \times 10^{-4}$ (see page 70), to give a temperature response index:

$$f31 = 0.024436 + 0.01873 \text{ Tsoil} \qquad (5.5)$$

The effect of soil moisture content on decomposition rate is significant but the lack of standardization in measurement and technique makes the determination of a generalized response difficult. It is assumed that the active microbial layer of the soil is confined to the top 20 cm surface layer. Lähde (1969), in studies of three different peat soils, found that below 16 cm, the loss of dry weight of cellulose was less than 5 percent. Heikurainen, et al. (1964), used the top 20 cm of the peat profile to measure moisture content. Their equation for weight of wet soil sample in kilograms as a function of watertable depth is:

$$y = 10.94 - 0.053 x \qquad (5.6)$$

where: y = weight of sample in kg

x = groundwater table from surface, cm

Equation (5.6) is rewritten in terms of moisture content

expressed as water weight/oven dried peat weight. Assuming that the total sample weight of equation (5.6) consists of oven-dry peat weight and water weight, the oven-dry peat weight can be approximated by subtracting the weight of water in their sample volume of 9817.5 $cm^3$ from the total sample weight. Now water weight is substracted from equation (5.6), which then is divided by oven-dry peat weight giving the following function:

$$f25 = \begin{cases} 8.746 + 0.0472\ HS & HS<0 \\ 8.746 & HS\geq 0 \end{cases} \qquad (5.7)$$

where HS = groundwater table from surface, cm.

The influence of moisture on decomposition rates of peat has been studied by Waksman and Stevens (1929a) and Waksman and Purvis (1932). The studies by Waksman and Stevens (1929a) showed a linearly decreasing decomposition rate with increasing moisture content. The range of moisture values, expressed as water weight/air-dry peat weight, was 0.67 to 4.5. The transformed data of Heikurainen gives a comparable value of 4.37 at saturation. Air-dried samples have been shown to have moisture holding capacities different from undisturbed samples (Waksman and Stevens 1929a; Boelter 1964). In this model, Waksman's and Steven's data are used, expressing moisture content in terms of water weight/oven-dry peat weight. Oven-dry weight is calculated by multiplying air-dry weight by an estimate of the ratio of oven-dry to air-dry weight. A linear regression of the transformed data

yields the following equation for decomposition rate constant, f26, with the intercept at the optimum moisture content:

$$f26 = 2.944 \times 10^{-4} - 1.722 \times 10^{-5} \cdot f25 \qquad (5.8)$$

where f25 = peat moisture content.

Assuming the decomposition rate constant at the optimum moisture content to be the rate constant, p17, a moisture response index is found by dividing equation (5.8) by p17 = $2.944 \times 10^{-4}$;

$$f32 = 1 - 0.0585 \cdot f25 \qquad (5.9)$$

The equation for peat decomposition rate, r9, is written as the rate constant, p17, the temperature and moisture indices and the unit variable X:

$$r9 = p17 \cdot f31 \cdot f32 \cdot X \qquad (5.10)$$

where: p17 = decomposition rate constant of peat

f31 = rate index as a function of temperature

f32 = rate index as a function of groundtable level

X = peat biomass

Soil unit simulation. The soil unit model, as represented by equation (5.1) is simulated with the results shown in Figure 23.

In the peat soil unit, X12, there is a net loss over one year of 67.5 gm/$.2m^3$ or assuming a constant peat density, a loss in soil depth of .043 cm. This loss can be corrected by

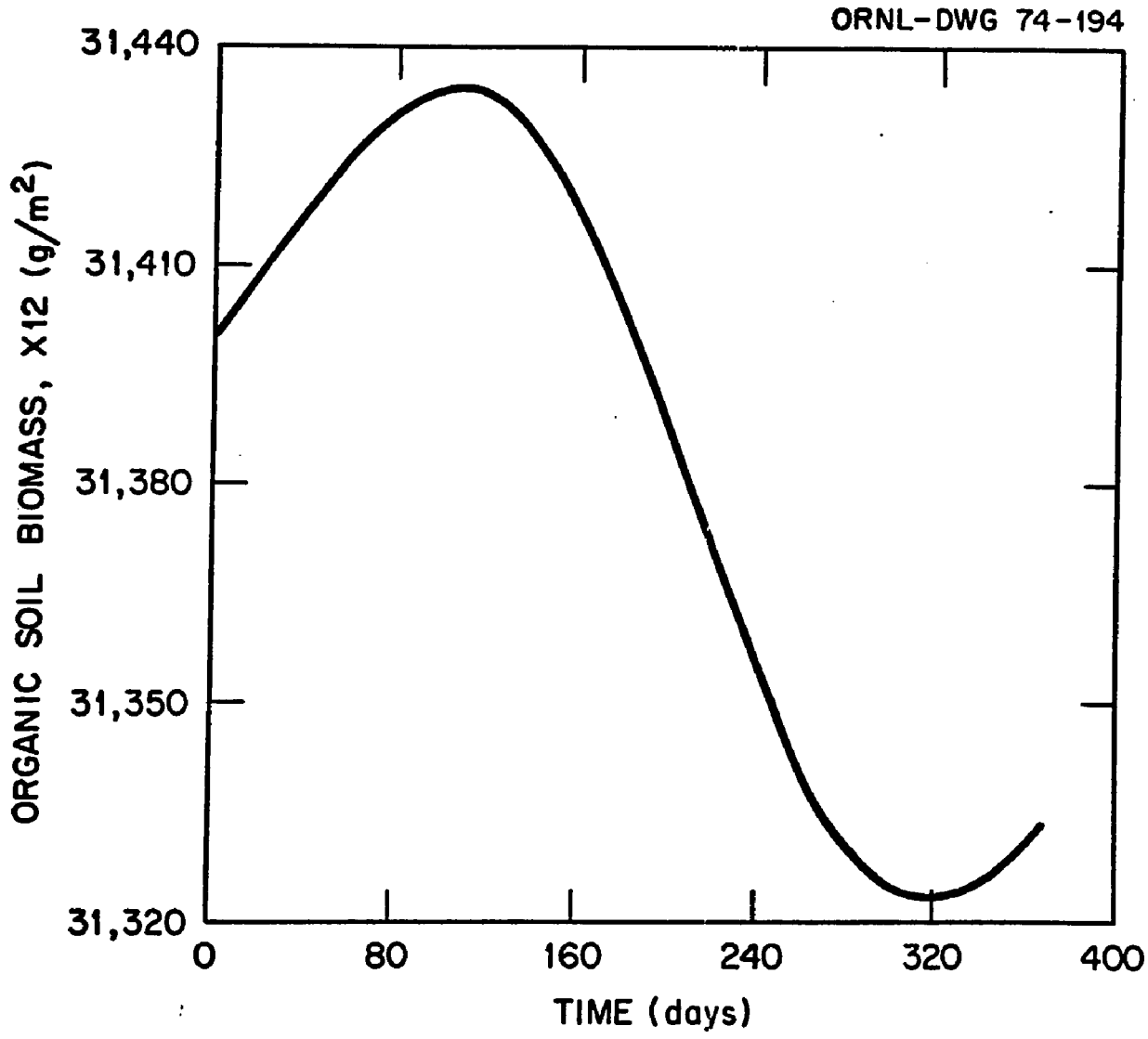



Figure 23. Organic soil biomass, X12, as estimated in model simulation.

adjusting the peat decomposition rate constant, p17, downwards.

# CHAPTER III

# MODEL ANALYSIS AND DISCUSSION

## Validity

Once an ecosystem model, or any model of an ecosystem process is developed, its validity must be examined. Since the marsh model is intended for use as an aid in making decisions concerning sewage wastewater disposal, the validity of its predictions will depend on how accurately it represents the system being modeled. Evidence of validity comes from a history of making satisfactory predictions. For a "first-time" model, such evidence is not available. A test of a model's credibility--the only kind of validity we have for a first-time model--requires a detailed examination of the internal structure of the model and of the data used for estimated parameters (Emshoff and Sisson 1970).

The examination of the model structure includes a determination of its internal validity and its stability and sensitivity to parameter variability. The internal validity concerns the model's sensitivity to internal processes, such as numerical integration methods, when simulations are replicated with all exogenous inputs held constant. No significant differences in similations were found using different integration methods both with CSMP and the dynamic simulator (Parker, personal communication).

Sensitivity analysis describes the change in quantitative responses of the model to a perturbation in relevant

parameters. Those parameters to which the model is most sensitive should, in general, be estimated most accurately.

If X is a state variable of the model, and p is a relevant parameter, then X can be expressed as a function of the parameter:

$$X = X(p)$$

The perturbation is the difference between solutions obtained when the parameter is perturbed and when it has its nominal value:

$$\Delta X = X(po + \Delta p) - X(po),$$

where po is the nominal value of the parameter and $\Delta p$ is the parameter perturbation (Mankin and Brooks 1973). Sensitivity now can be defined by:

$$s(t) = c(t)\,\Delta X(t)$$

where c(t) is a weighting function. To express sensitivity as a percentage change,

$$c(t) = \frac{100}{X(po)}$$

Results of the sensitivity analysis for the state variables vascular plants (X1), standing dead (X14), litter (X11), and organic soil (X12) are shown in Figures 24, 25, 26, and 27, respectively. In each figure, the sensitivity is the percentage change in the state variable

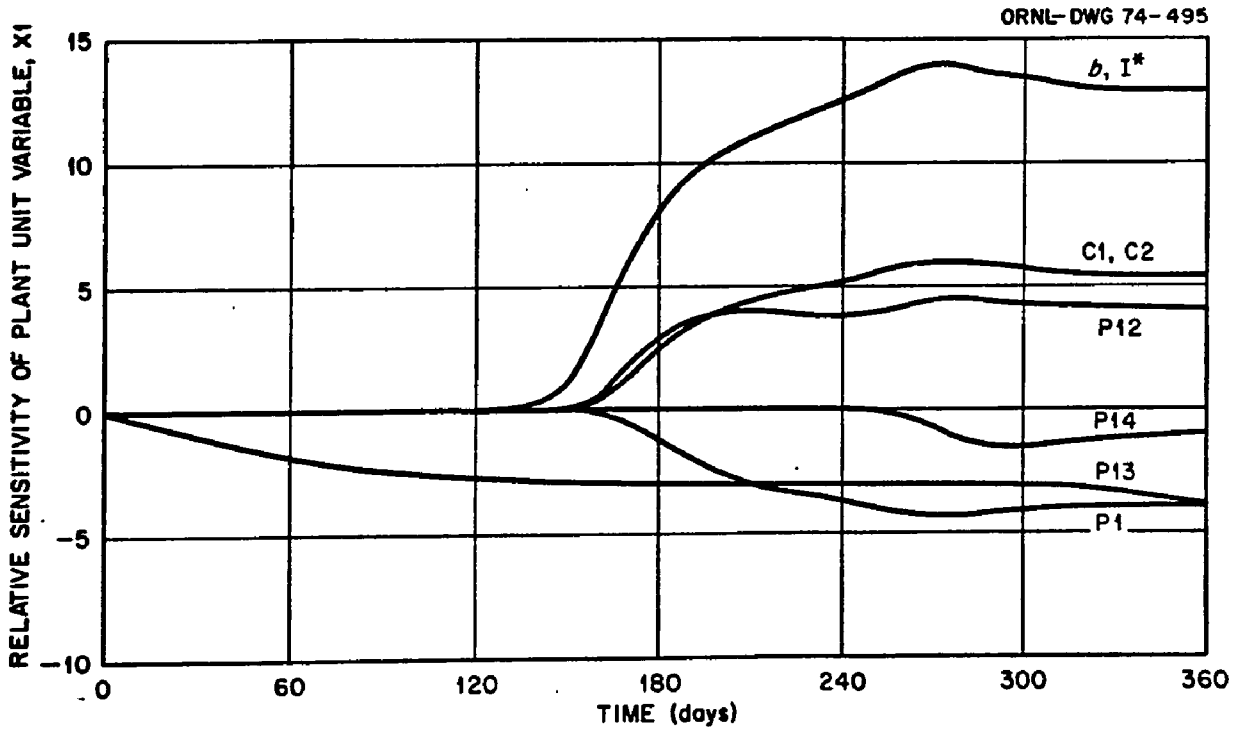



Figure 24. Relative sensitivity of vascular plant unit variable, X1. Each curve represents the percentage change in X1 due to a 50 percent increase in the indicated parameters. b = leaf resistance to light constant, $I^*$ = midday radiation, c1 = $CO_2$ concentration, c2 = coefficient to convert $CO_2$ to photosynthate, p12 = max. leaf area, p14 = max. daily leaf fall rate constant, p13 = max. daily stem mortality rate constant, p1 = max. leaf resistance.

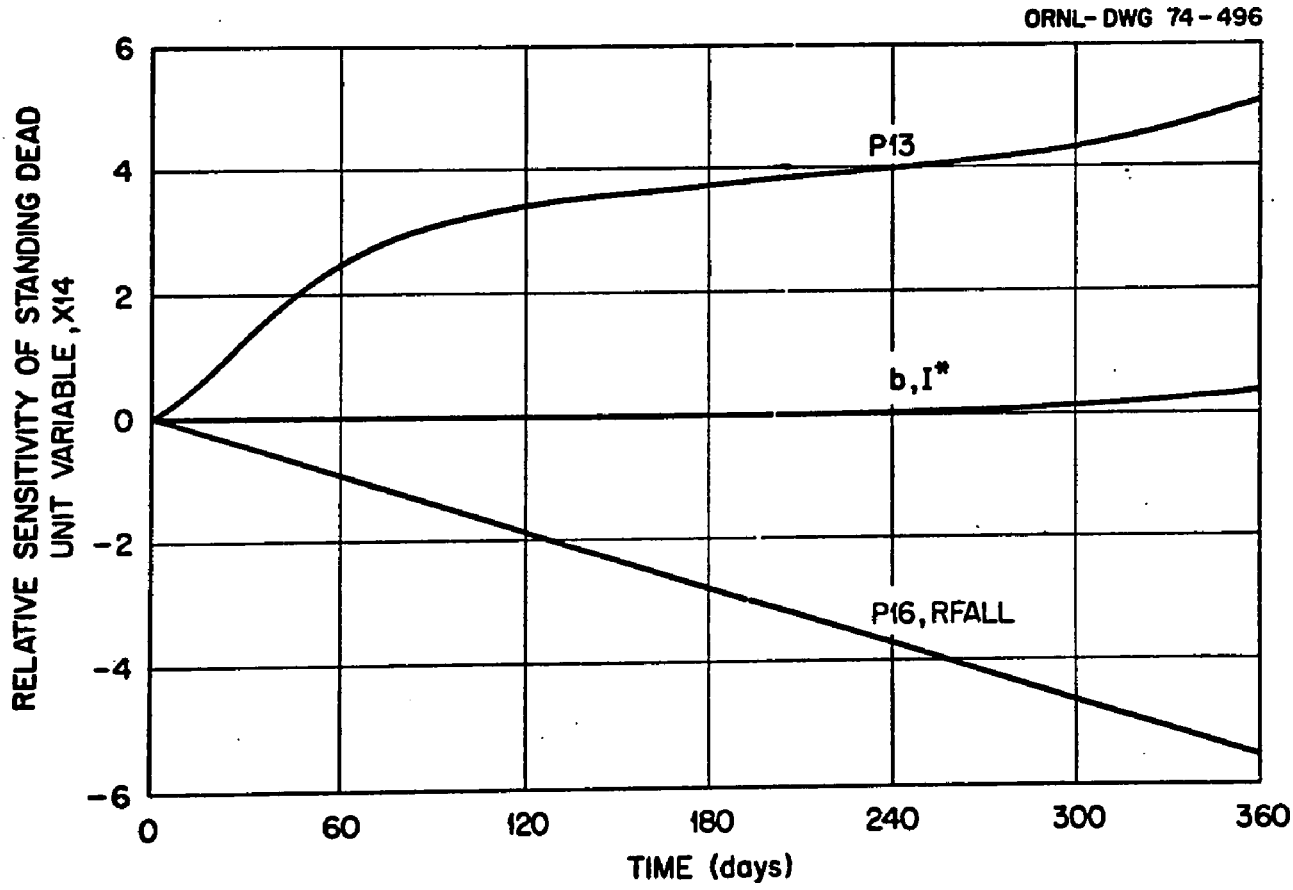



Figure 25. Relative sensitivity of standing dead unit variable, X14. Each curve represents the percentage change of X14 due to a 50 percent increase in the indicated parameter. p13 = max. daily stem mortality rate constant, $b_*$ = leaf resistance response to light constant, $I^*$ = max. midday radiation, p16 = max. stem litter production rate constant, RFALL = daily rainfall constant.

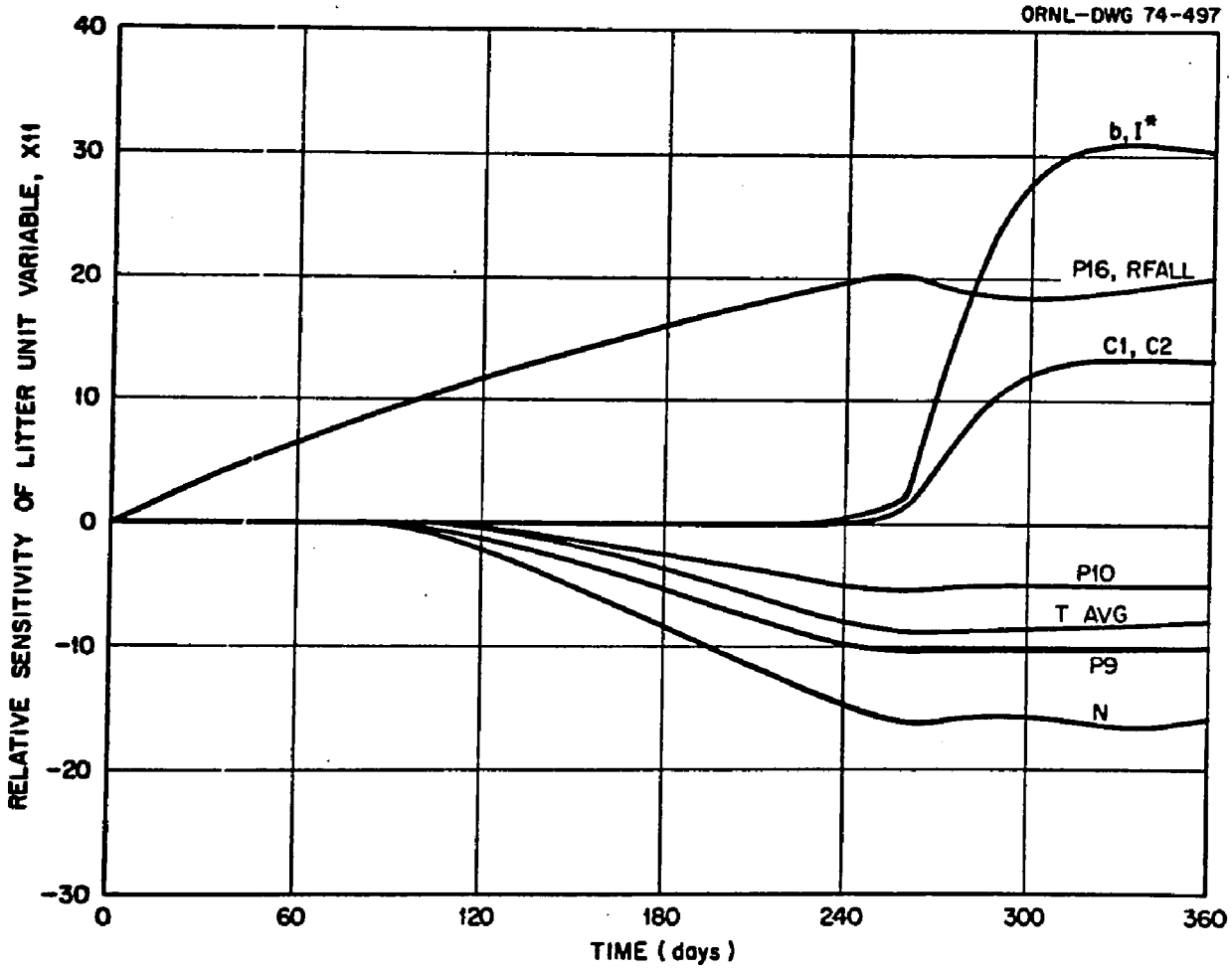



Figure 26. Relative sensitivity of litter unit variable, X11. Each curve represents the percentage change in X11 due to a 50 percent increase in the indicated parameter. b = leaf resistance response to light constant, $I^*$ = max. midday radiation, p16 = max. stem litter production rate constant, RFALL = daily rainfall constant, c1 = $CO_2$ concentration, c2 = coefficient to convert $CO_2$ to photosynthate, p10 = max. leaf litter decomposition rate constant, Tavg - avg. 24 hour temperature, p9 - max. stem litter decomposition rate constant, N = soil nitrogen concentration.

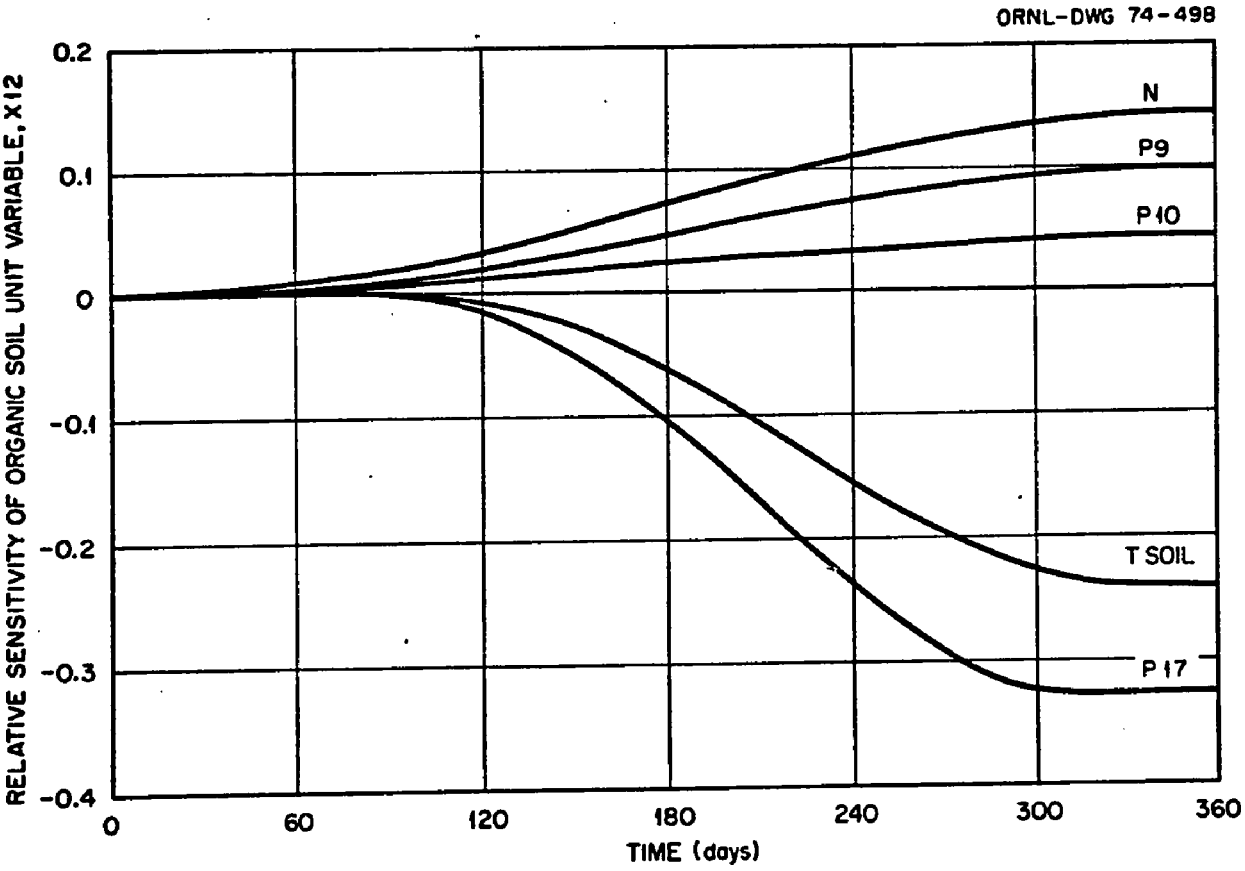



Figure 27. Relative sensitivity of organic soil unit variable, X12. Each curve represents the percentage change in X12 due to a 50 percent increase in the indicated parameter. N = soil nitrogen concentration, p9 = max. stem litter decomposition rate constant, p10 = max. leaf litter decomposition rate constant, Tsoil = soil temperature, p17 = peat decomposition rate constant.

corresponding to a 50 percent increase in each parameter. Also, those parameters shown are those with the greatest effect on the sensitivity during a one-year simulation.

Evident from Figures 24 through 27 is the damping effect of the model. A 50 percent positive perturbation in any parameter has less than a 50 percent perturbation on the system over a period of one year. Greater perturbations are likely over longer range simulations. The parameters which have the greatest effect on the vascular plant unit model (Figure 24) are those included in the growth rate equation (2.17). Maximum midday radiation (I*) and leaf resistance light response constant (b) have the greatest effect on the plant model. The next greatest positive factors are $CO_2$ concentration (c1) and the coefficient to convert $CO_2$ to photosynthate (c2), followed by p12, the maximum leaf area per leaf. The factors having the greatest negative effect are, in decreasing order, maximum leaf resistance, (p1), stem mortality rate constant (p13), and leaf fall rate constant (p14).

One use of sensitivity analysis can be pointed out here. If a parameter, assumed to have a constant value, has a significant effect on the model's sensitivity, it may have to be written as a variable function; carbon dioxide concentration may vary within the canopy, the constant c2 may vary with temperature, and p12 may be a function of leaf nitrogen concentration.

The sensitivity analysis of the standing dead unit model (Figure 25) shows that the stem mortality rate constant has the greatest positive effect. The factors which have the

next greatest positive effect are the light parameters $I^*$ and b of the growth rate equation. A 50 percent increase in these parameters, which have the greatest effect on the plant unit model, causes an increase in primary production and thereby an increase in standing dead material. The factors with the greatest negative effect are the stem litter production rate constant (p16) and the amount of rainfall (RFALL). This analysis shows the importance of increasing the realism of the parameter, RFALL, in the macromodel (see page 15).

The sensitivity analysis of the litter unit model (Figure 26) shows that several parameters have a significant effect. The importance of the input from the standing dead unit is evident by the sensitivity to the parameter p16 and RFALL. During the growing season, the light parameters $I^*$ and b have a dominant effect, with an added effect due to the constants c1 and c2. The decomposition rate constants p9 and p10 have a significant negative effect with a greater sensitivity to the stem decomposition rate constant, p9, than to the leaf decomposition rate constant, p10. This analysis shows the relative effect of those factors which affect decomposition rates, with soil nitrogen concentration (N) having a relatively greater effect than temperature (Tavg). An equal positive perturbation in watertable height has a relatively lesser effect on the litter unit model sensitivity. Watertable height, if included in the stem mortality rate

function, could have a more significant effect on the litter unit model.

The dominant output parameters of the litter unit model are also the dominant input parameters of the soil unit model--in the same order but at a lower sensitivity (Figure 27). The soil decomposition rate constant (p17) has the greatest negative effect on this model, with temperature being the factor having the greatest effect on decomposition.

The sensitivity analysis is of simulations over a period of one year, which shows the effect of relevant parameters during seasonal changes in the model. The long-range stability of the model is examined by simulations which run for a period of several years. The ten-year simulation in Figure 28 shows the relative stability of the unit variables of vascular plants, standing dead, litter, and soil. Vascular plants and standing dead material, as forecast by the simulation, are quite stable over the ten years while there is a buildup in the litter unit and, after an initial decline, an accumulation in the organic soil unit also.

The increase in the litter unit could be due to any of the following:

1) The assumption of a steady-state in the standing dead unit is not valid, i.e., there is an accumulation of standing dead material, reducing the input into the woody litter unit.
2) The rates of decomposition for woody and non-woody litter are too low.

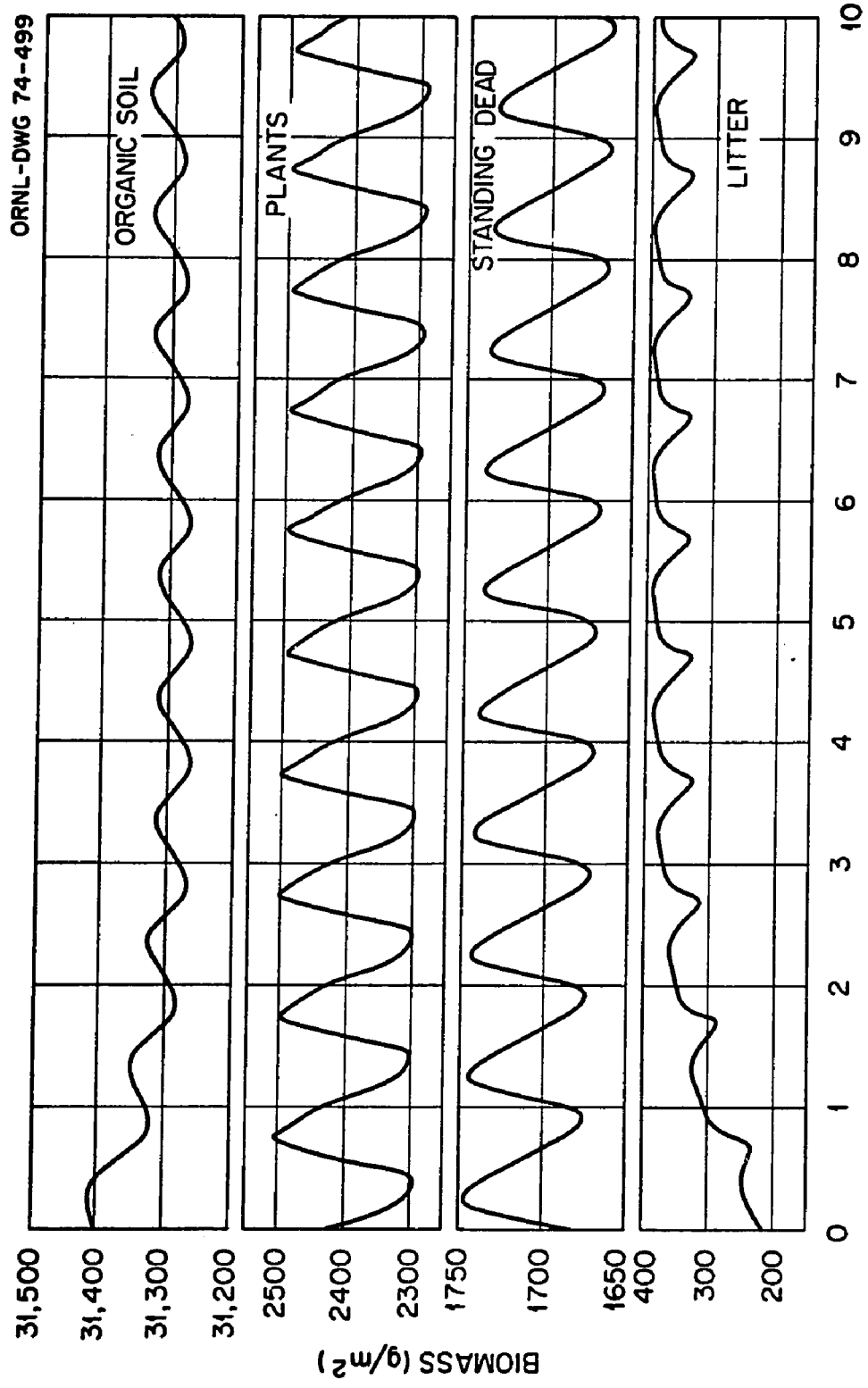



**Figure 28.** Ten-year simulation of unit variables vascular plants (X1), standing dead (X14), litter (X11), and organic soil (X12).

3) Sources of biomass loss are not accounted for in the vascular plant and standing dead units which provide the inputs into the litter unit. Two possible such terms would be herbivore consumption in the plant unit and decomposition in the standing dead unit.

Such interpretation of the results of model simulation is helpful in pointing out areas which may need further study in the laboratory and in the field.

The results of the sensitivity analysis and long-range simulation suggest that the model is sufficiently valid to be used for further development and use in the macromodel as an aid in decision making.

Preliminary Model Predictions

Although this model is a first-time model, to be updated using data from the marsh study, certain preliminary manipulations can be instructive. These should be considered as general indications and not predictions of actual ecosystem behavior. Since the ultimate objective of the model is to predict the effects of sewage effluent on a wetland ecosystem, the variables of primary interest are added water and nutrients.

A series of simulation exercises was run varying nitrogen and water parameters to determine the effect on the biomass balances of vascular plants, standing dead, litter, and soil. In the vascular plant model nitrogen affects $CO_2$ assimilation as described in equation (2.8) (page 28). Increased nitrogen

availability also may increase leaf area (pages 79, 93). The parameter for maximum leaf area, p12, is increased in those simulations representing high nitrogen levels. Nitrogen concentration in the soil solution, N, affects litter decomposition rate as described in equation (4.5) (page 63 ). Added water, as expressed by watertable height, HS, affects the decomposition rate of both litter and organic soil. Increases in water level also may increase stem mortality rate (page 37). This effect is approximated by increasing the maximum stem mortality rate parameter, p13. The set of parameter values for each simulation exercise is presented in Table 6. The four runs represent conditions of low watertable level, natural conditions with the watertable at the soil surface, and added water and nutrients at two levels.

The results of the simulations for the unit variables--vascular plants, standing dead, litter, and peat soil--are shown in Figures 29 through 32, respectively.

Figure 29 shows the effects on vascular plants, specifically bog birch. Runs one and two are identical, the difference being in water level only. Run three shows a marked increase in biomass due to increased leaf nitrogen content and leaf area, even though stem mortality was increased 50 percent. When stem mortality is doubled (Run four), however, plant biomass shows a lower final value than under natural conditions. In either case input into the standing dead and litter compartments is increased (Figures 30 and 31). The question posed by these preliminary simulations

Table 6. Parameter values for simulation runs. (See text for description of parameters.)

| Parameter | run 1 low water level | run 2 natural | run 3 med. water & nitrogen | run 4 high water & nitrogen |
|---|---|---|---|---|
| HS | -5.0 | 0.0 | 1.5 | 3.0 |
| c3 | 1.81 | 1.81 | 2.715 | 2.715 |
| N | 765.8 | 765.8 | 1045.0 | 1045.0 |
| p12 | 1.8 | 1.8 | 2.7 | 2.7 |
| p13 | $5.5 \times 10^{-4}$ | $5.5 \times 10^{-4}$ | $8.2 \times 10^{-4}$ | $1.1 \times 10^{-3}$ |

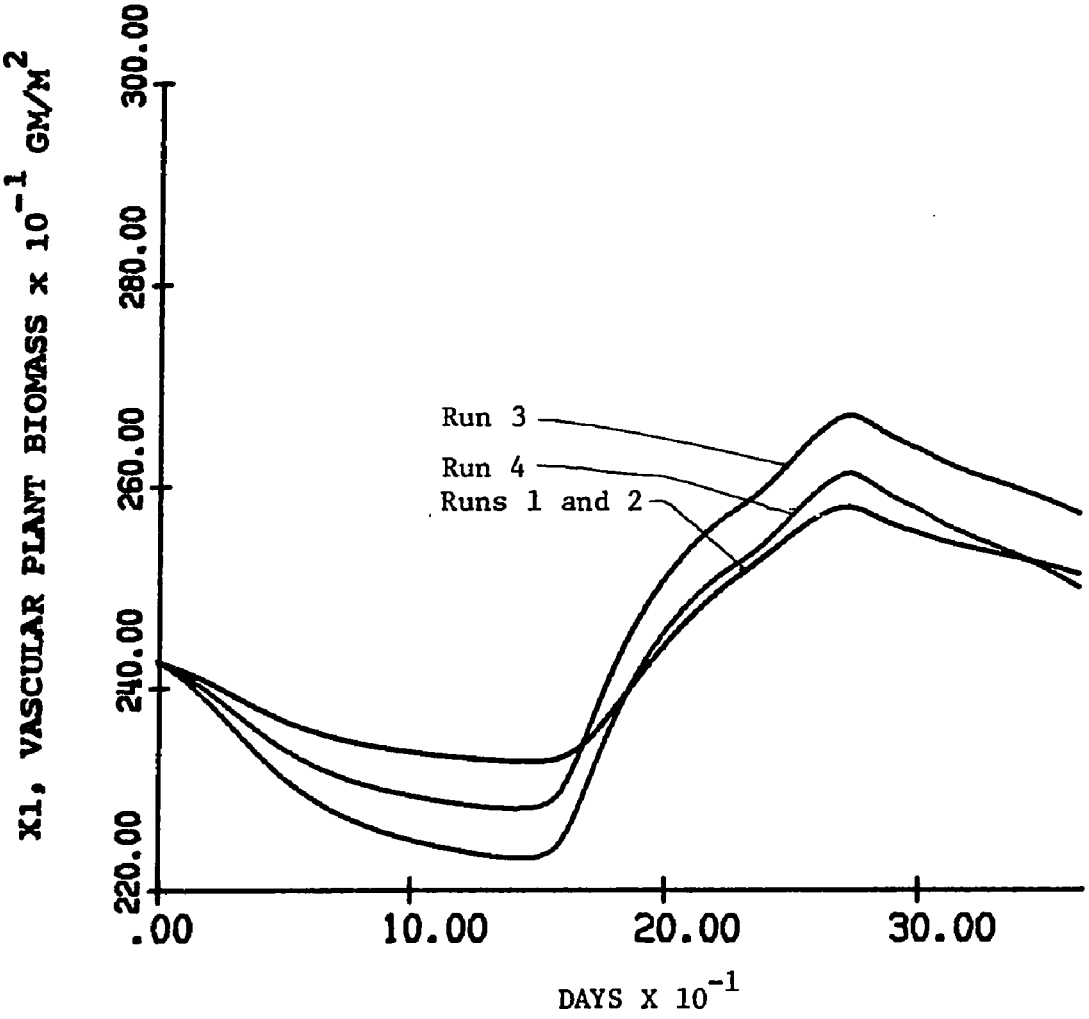



Figure 29. Simulated effect of added water and nutrient on vascular plant unit variable.

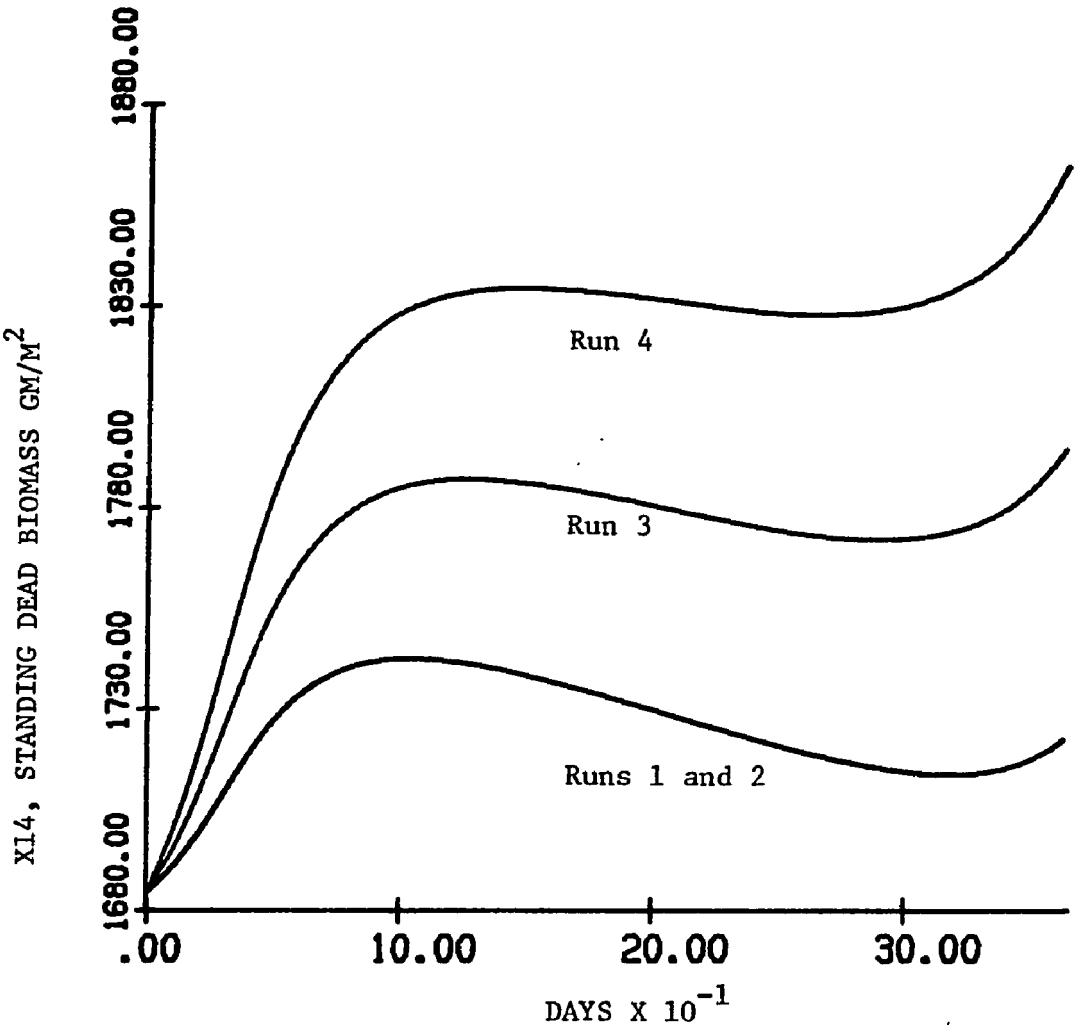



**Figure 30.** Simulated effect of added water and nutrient on standing dead unit variable.

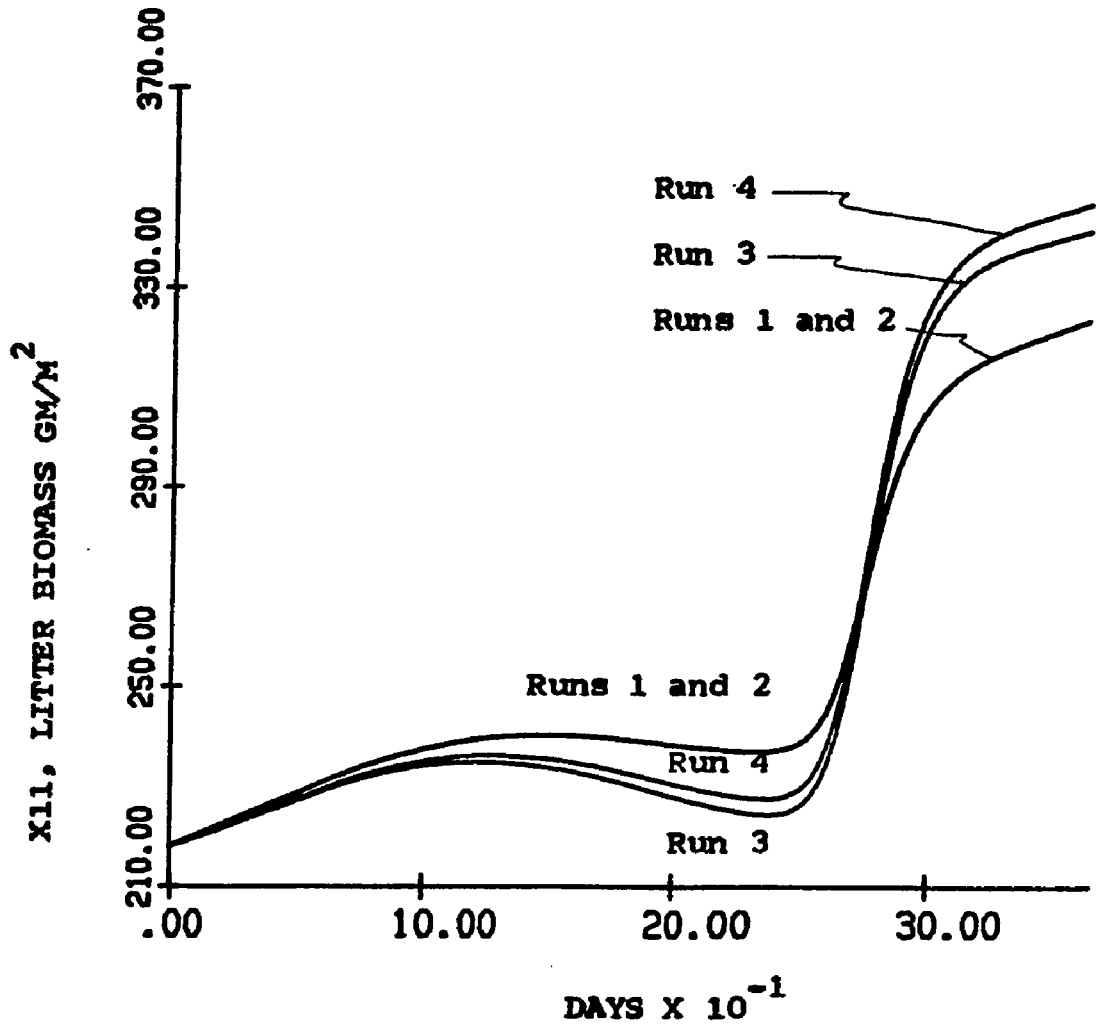



Figure 31. Simulated effect of added water and nutrient on litter unit variable.

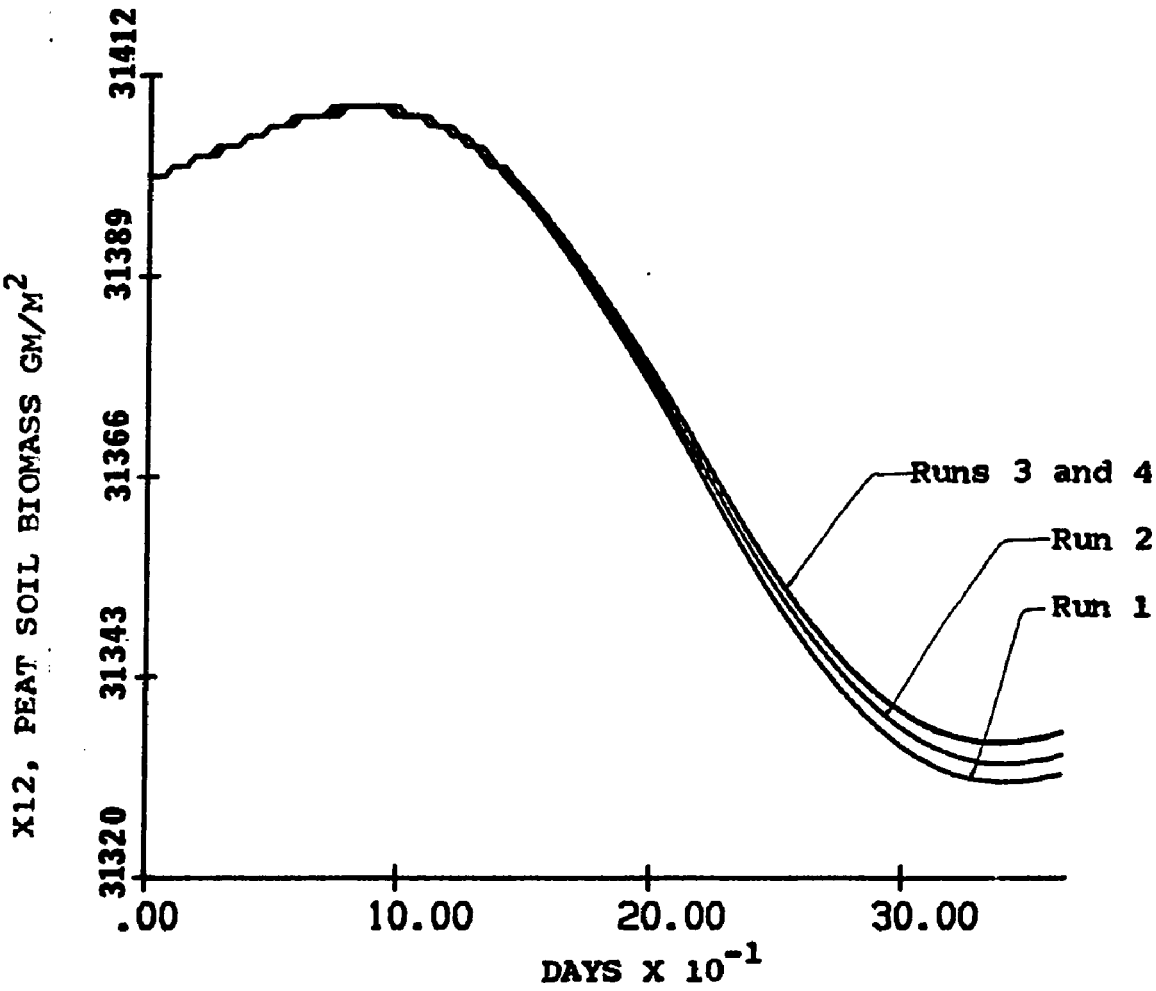



Figure 32. Simulated effect of added water and nutrient on organic soil unit variable.

concerns the net effect of increased primary production due to increased nitrogen and increased stem mortality as a result of increased water level.

The effects on standing dead are shown in Figure 30. The indication here is that high water levels cause a definite increase in standing dead biomass levels.

There is no effect of low water on litter decomposition due to the assumption that the water level does not drop enough to reduce moisture levels below optimum (Figure 31). In run three, soil nitrogen dominates water level initially, increasing decomposition and decreasing litter biomass. As leaf fall occurs, the litter layer builds up due to increased primary production which results from increased leaf nitrogen and leaf area. The effect of increased water level is seen in run four where decomposition rates are decreased and litter biomass increases. The litter unit appears particularly sensitive to changes in water level and nutrients as both inputs and outputs are affected. The net effect of added nutrients and water should be significant and the responses to them accurately estimated.

The peat soil unit is less affected by added water and nutrients (Figure 32). In run one decomposition rate is increased since water level is below the surface. Nitrogen has no direct effect on soil decomposition under the assumptions of equation (5.9). The only significant effect is a low watertable. To prevent a gradual accumulation of peat soil, it appears that the watertable should not be maintained

constantly above the surface by wastewater disposal.

It should be reemphasized that these preliminary simulations are intended to give an indication of the relative effects of added water and nutrients and not a prediction of actual results. These exercises and the sensitivity analysis suggest that the accumulation of biomass in most units is a likely possibility. The results of the simulations can be helpful in further model development but actual predictions should await the complete updating and validation of the model.

Updating the Model

It is anticipated that the present model will be updated as additional data are collected as part of the marsh study. This information can be used to revise existing parts of the model or to develop additional parts where information is lacking. In general, such revision can be described by the following five actions listed in order of decreasing effect:

1) addition or deletion of unit equations;
2) addition or deletion of rate equations;
3) redefine response functions;
4) write parameter as function of variable(s); and
5) change of parameter values.

Addition or deletion of unit equations. It has been mentioned that additional unit variable models, including water and nutrients, will be used in the macromodel simulation. In some ecosystem models secondary producers and microbial populations are included as state variables. Initially these

are not included in this model. Secondary producers consume the vegetation, but it was felt that changes in herbivore biomass would not be great enough to change normal consumption rates. Microbial population models are not included due to the difficulty in obtaining accurate estimates of microbe numbers. Instead, microbial processes are defined directly as functions of extrinsic variables.

Addition or deletion of rate equations. As stated above, herbivore consumption may have a significant effect on some plant species. Therefore, an herbivore consumption rate term may be added to the plant model. A standing dead decomposition term may be needed in that unit model (see page 83). If preliminary simulation indicates that conditions become unfavorable for some existing plant species and favorable for others, a rate of invasion term also may have to be added to the vascular plant model.

Redefine response functions. The response functions in the growth model are based on relatively precise data with substantive background information on growth or leaf resistance responses. In the case of leaf resistance response to temperature, the response had to be extrapolated out of the range of temperatures measured (equation 2.9). When this response is defined for the marsh plants it is anticipated that a continuous hyperbolic function will be written.

The stem mortality rate function (equation 2.20) is written as a function of temperature. In addition, a mortality response to high water levels is needed if the

amount of effluent disposal is sufficient to increase water levels significantly above normal levels. At present this effect can be approximated by arbitrarily increasing the maximum stem mortality rate, p13.

Perhaps the processes which need the greatest definition are the decomposition rate responses of litter and soil to nutrient, temperature, and moisture. In particular, information is needed on the effect of watertable level on decomposition through its effect on moisture content or aerobic conditions. The most accurate model likely would result from defining decomposition as a function of moisture content or percent oxygen available for microbial respiration and then defining those conditions for a given soil depth as a function of watertable height. This function then could be integrated over the depth of soil profile desired. As discussed above (page 63), a non-linear response for litter decomposition as a function of nutrient supply may be needed.

Write parameter as function of variable(s). When a parameter is determined to show a significant response to a variable in the system, it is written as a function of that variable. For example, if studies show a significant increase in leaf area with increased leaf nitrogen content, the parameter p12 for maximum leaf area may be written as a function of leaf nitrogen, c3. The constant c3 also likely will be rewritten as a function of soil nitrogen concentration. As indicated by the sensitivity analysis, the constants c1 and

c2 may have to be written as functions.

Change of parameter values. Parameter values are changed continually as information is collected from the marsh study area and from laboratory experiments. It should be pointed out, however, that changing a parameter value alone may not improve the predictive ability of the model since the responses have been determined from other studies under other conditions. These responses should be verified before the parameters are changed.

Throughout the development of the model, the major consideration has been to define the component or process models at the level of resolution which balances desired precision of measurement and feasibility of data collection. In some unit variable models a higher level of resolution is used than in others. In the vascular plant model the processes are described in relatively great detail. This is possible due to the advanced methodology of photosynthesis studies. The less developed methodology and lack of standardization in microbial studies has made it necessary to use a lower level of resolution in the decomposition processes of the litter and soil unit variable models. In these decomposition models changes in biomass are measured directly. Laboratory studies can determine the decomposition responses to key variables while field studies can provide the data for validation.

The level of resolution used is appropriate for models

of large ecosystems. The vascular plant model, which was developed from a model of photosynthesis for a single leaf is not detailed enough, for most cases, to be considered a true mechanistic model. However, the particular form used in equations (2.2) and (2.7) can be increased in its detail and used for analysis of photosynthetic mechanisms. In general, a truly mechanistic model will not be suitable as an ecosystem model even when integrated over time and space.

The model is general enough to be used for most wetland ecosystems. It may be used for terrestrial ecosystems also, if the assumptions in the model are met.

This model has some distinct advantages over other ecosystem models. The equations have variable coefficients which respond to extrinsic variables providing for seasonal variation in the inputs to the model and its solution. The model has a fairly simple structure and, although not truly mechanistic, has parameters with biological counterparts which can be estimated with little difficulty.

# CHAPTER IV

## SUMMARY

A mathematical model of the organic matter components of a wetland ecosystem is developed, primarily from data in the published literature. Components of the ecosystem included in the model are vascular plants, standing dead biomass, stem and leaf litter, and soil. The objective of the model is to be able to forecast the effects of sewage wastewater disposal on the ecosystem. This requires that the variables of water and nutrients be included in the models of the several processes which may be affected by the wastewater disposal.

The model consists of a set of ordinary first-order, nonlinear differential equations representing the mass balance of the biomass components of the system. The vascular plant growth model is based on a $CO_2$ diffusion model for photosynthesis of a single leaf. The model then is expanded in scale of time and space to represent plant growth for an entire vegetative canopy. Models of other ecosystem processes, such as litter decomposition, are necessarily of lower resolution due to the fact that less is known of the functioning of these processes. A sensitivity analysis of each unit variable was made where sensitivity was defined as the percentage change in the unit variable due to a 50 percent change in a parameter during a one-year simulation. The results of the sensitivity analysis of the vascular plant unit variable showed that the maximum midday light intensity has the greatest effect on

plant growth. Other analyses showed that the factor having the greatest effect on decomposition is temperature. Of the factors related to wastewater disposal, the analysis showed nutrients have a greater effect on litter decomposition than the amount of water covering the litter.

The long-range stability of the model was determined by making simulations for periods of several years. A ten-year simulation showed the model to be quite stable although an accumulation of litter was indicated. Litter accumulation as predicted in the model, may be due to the lack of terms for such processes as standing dead decomposition in the standing dead unit model and herbivore consumption in the vascular plant unit model. These are areas which need further study before models of these processes can be developed.

The analyses show the model to be a credible first-time model which can be used as an aid in making decisions about the feasibility of using a wetland ecosystem for wastewater disposal.

Some preliminary investigations of the effect of wastewater on the marsh are made by varying the parameters related to added water and nutrients. The results of these simulations indicate that an accumulation of biomass is likely in most of the ecosystem components. Further updating of the model is likely when more data are collected from the marsh study area. Ways of updating the model are discussed ranging from changing parameter values to the addition of unit models.

The biomass models developed in this thesis will be

combined with models for nutrients and water for making actual forecasts of the effects of sewage wastewater disposal on the marsh ecosystem.

## APPENDIX

### GLOSSARY OF VARIABLES AND PARAMETERS

| Algebraic symbol | Description | Units |
|---|---|---|
| | **Extrinsic Variables** | |
| R | Daily solar radiation | $kcal \cdot cm^{-2} \cdot day^{-1}$ |
| d | Duration of daylight | sec |
| $I^*$ | Maximum midday radiation | $kcal \cdot cm^{-2} \cdot sec^{-1}$ |
| T | Temperature | $^oC$ |
| RFALL | Rainfall | cm |
| Tday | Average daytime temperature | $^oC$ |
| Tnite | Average nighttime temperature | $^oC$ |
| Tavg | Average 24 hour temperature | $^oC$ |
| | **Vascular Plant Unit** | |
| X1 | Aboveground vascular plant biomass | $gm \cdot m^{-2}$ |
| X1a | Leaf biomass | $gm \cdot m^{-2}$ |
| X1a(z) | Leaf biomass at height z | $gm \cdot m^{-2} \cdot cm^{-1}$ |
| X1b | Stem biomass | $gm \cdot m^{-2}$ |
| r1 | Growth rate | $gm \cdot m^{-2} \cdot day^{-1}$ |
| r2 | Stem mortality rate | $gm \cdot m^{-2} \cdot day^{-1}$ |
| r3 | Leaf mortality rate | $gm \cdot m^{-2} \cdot day^{-1}$ |
| r4 | Dark respiration rate | $gm \cdot m^{-2} \cdot day^{-1}$ |
| r10 | Translocation rate | $gm \cdot m^{-2} \cdot day^{-1}$ |
| r1(z)′ | Net photosynthate production rate at height z in the canopy per unit of ground area | $gm \cdot m^{-2} \cdot sec^{-1} \cdot cm^{-1}$ |

APPENDIX--Continued

| Algebraic symbol | Description | Units |
|---|---|---|
| | Vascular Plant Unit | |
| f1 | Fraction of total growth translocated to roots | - |
| f3(z) | $CO_2$ uptake rate per unit leaf area at height z | $cm^3 \cdot cm^{-3} \cdot sec^{-1}$ |
| f4(z) | Leaf resistance at depth z | sec |
| f5 | Leaf resistance response index for nitrogen content of leaves | - |
| f6(z) | Leaf resistance response index for sunlight | - |
| f7 | Leaf resistance response index for temperature | - |
| f9(z) | Accumulated leaf biomass of all species from 0 to z | $gm \cdot cm^{-2}$ |
| f10 | Empirical function to convert leaf area to leaf biomass | $cm^2 \cdot gm^{-1}$ |
| f11 | Leaf area function | $cm^2$ |
| f12 | Leaf weight function | gm |
| f14 | Stem mortality rate function | $day^{-1}$ |
| f15 | Leaf mortality rate function | $day^{-1}$ |
| p1 | Maximum leaf resistance | $sec \cdot cm^{-1}$ |
| p3 | Fraction of growth apportioned to leaves | - |
| p12 | Maximum leaf area | $cm^2$ |
| p13 | Maximum daily stem mortality rate constant | $^oC \cdot day^{-1}$ |

APPENDIX--Continued

| Algebraic symbol | Description | Units |
|---|---|---|
| | **Vascular Plant Unit** | |
| p14 | Maximum daily leaf fall rate constant | $day^{-1}$ |
| p15 | Maximum respiration rate | $gm \cdot cm^{-2} \cdot sec^{-1}$ |
| c1 | $CO_2$ concentration within the plant canopy, assumed constant | ppm |
| c2 | Stoichiometric coefficents to convert $CO_2$ uptake in cm3 to biomass in grams | $gm \cdot cm^{-3}$ |
| c3 | Percent leaf nitrogen | $gm \cdot gm^{-1} \cdot 100$ |
| I(0) | Light intensity at the top of the canopy(z=0) | $kcal \cdot cm^{-2} \cdot sec^{-1}$ |
| $I^*$ | Maximum midday radiation | $kcal \cdot cm^{-2} \cdot sec^{-1}$ |
| I(z) | Light intensity at the point z in the canopy | $kcal \cdot cm^{-2} \cdot sec^{-1}$ |
| a | Constant | - |
| b | Constant | $cm^2 \cdot sec \cdot kcal^{-1}$ |
| k | Light extinction coefficient | $m^2 \cdot gm^{-1}$ |
| $\lambda(\zeta)$ | The leaf biomass of all species at level $\zeta$ in the canopy | $gm \cdot m^{-2} \cdot cm^{-1}$ |
| L | Total leaf biomass of plant species in the canopy | $gm \cdot m^{-2}$ |
| Z | Total canopy height | cm |
| z | Depth into canopy, measured downward | cm |
| h | Time since sunrise | sec |

APPENDIX--Continued

| Algebraic symbol | Description | Units |
|---|---|---|
| | **Vascular Plant Unit** | |
| g | Depth of leaf canopy for this species | cm |
| d | Duration of daylight | sec |
| | **Standing Dead Unit** | |
| X14 | Standing dead biomass | $gm \cdot m^{-2}$ |
| r5 | Stem litter production rate | $gm \cdot m^{-2} \cdot day^{-1}$ |
| p16 | Stoichiometric coefficient relating rainfall to stem litter production | $cm^{-1}$ |
| RFALL | Rainfall function | $cm \cdot day^{-1}$ |
| | **Litter Unit** | |
| X11 | Biomass of total litter | $gm \cdot m^{-2}$ |
| X11a | Biomass of stem litter | $gm \cdot m^{-2}$ |
| X11b | Biomass of leaf litter | $gm \cdot m^{-2}$ |
| r5 | Stem litter production rate | $gm \cdot m^{-2} \cdot day^{-1}$ |
| r6 | Stem litter decomposition rate | $gm \cdot m^{-2} \cdot day^{-1}$ |
| f21 | A function describing the response of decomposition rate to temperature | - |
| f22 | A function relating the decomposition rate to the watertable | - |
| f23 | A function describing the response of decomposition to nutrient supply | - |

APPENDIX--Continued

| Algebraic symbol | Description | Units |
|---|---|---|
| | **Litter Unit** | |
| p9 | Maximum rate constant of stem litter decomposition | $day^{-1}$ |
| p10 | Maximum rate constant of leaf litter decomposition | $day^{-1}$ |
| p11 | Height of litter layer in block | cm |
| HS | Height of watertable relative to ground surface | cm |
| N | Nitrogen concentration in soil solution | ppm |
| | **Soil Unit** | |
| X12 | Peat soil biomass | $gm \cdot m^{-2}$ |
| r8 | Rate of input from the litter unit | $gm \cdot m^{-2} \cdot day^{-1}$ |
| r9 | Peat decomposition rate | $gm \cdot .2m^{-3} \cdot day^{-1}$ |
| f24 | Decomposition rate response to temperature | $gm \cdot m^{-3} \cdot day^{-1}$ |
| f25 | Peat moisture content | $gm \cdot gm^{-1}$ |
| f26 | Decomposition rate constant | $day^{-1}$ |
| f27 | Decomposition rate constant | $day^{-1}$ |
| f31 | Rate index as a function of temperature | - |
| f32 | Rate index as a function of groundwater level | - |
| p4 | Stoichiometric coefficient | - |

APPENDIX--Continued

| Algebraic symbol | Description | Units |
|---|---|---|
| | Soil Unit | |
| p5 | Stoichiometric coefficient | - |
| p17 | Decomposition rate constant of peat | $day^{-1}$ |
| Tsoil | Soil temperature | $^{o}C$ |

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