Technical Report A-96-8
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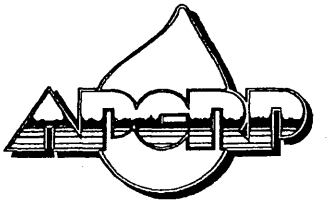
US Army Corps of Engineers
Waterways Experiment Station

Aquatic Plant Control Research Program

A Simulation Model for Growth of the Submersed Aquatic Macrophyte Hydrilla (*Hydrilla verticillata* (L.F.) Royle)

by Elly P. H. Best, AScI Corporation
William A. Boyd, WES



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Final report

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Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP), Work Unit 32440. The APCRP is sponsored by the Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of Army Appropriation Number 96X3122, Construction General. The APCRP is managed under the Environmental Resources Research and Assistance Programs (ERRAP), Mr. J. L. Decell, Manager. Mr. Robert C. Gunkel, Jr., was Assistant Manager, ERRAP, for the APCRP. Program Monitor during this study was Ms. Denise White, HQUSACE.

Principal Investigator for work under APCRP Work Unit 32440 was Mr. R. M. Stewart, Ecosystem Processes and Effects Branch (EPEB), Environmental Processes and Effects Division (EPED), EL, WES. The work described herein was performed under contract DACW39-90-D-0001 by Dr. Elly P. H. Best, AScI Corporation, with technical assistance from Mr. William A. Boyd, EPEB. Dr. Best and Mr. Boyd prepared this report. Drs. J. E. Titus, Binghamton University, Binghamton, NY, and M. A. Scheffer, Institute for Inland Water Management and Waste Management, Lelystad, The Netherlands, provided external technical reviews. Particularly, the comments and suggestions of Dr. Titus are greatly acknowledged. The report was reviewed internally by Drs. John Madsen and Robert Kennedy, EPEB.

This investigation was performed under the general supervision of Dr. Richard E. Price, Acting Chief, EPEB, Mr. Donald L. Robey, Chief, EPED, and Dr. John W. Keeley, Director, EL.

At the time of publication of this report, Director of WES was Dr. Robert W. Whalin. Commander was COL Bruce K. Howard, EN.

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1 Introduction

General

The degree to which aquatic macrophytes influence the ecosystem is proportional to plant mass and depends on plant species and physico-chemical factors. Therefore, predictions of the environmental impact of management measures concerning the aquatic community should be based on accurate estimates of (a) plant species, mass, and its pertinent physiological properties, (b) the plants' contribution to the various food chains, and (c) the contribution of the plants' decay to biogeochemical cycling and oxygen regime. A simulation model for metabolism and growth of aquatic community types may serve as a useful tool in this respect. A relatively small number of simulation models for growth of monotypic, submersed macrophytic communities has been published (e.g., Titus et al. 1975; Best 1981; Collins, Park, and Boylen 1985; Best and Jacobs 1990; Hootsmans 1991; Scheffer, Bakema, Wortelboer 1993). The present model has been developed because none of the models mentioned were suitable to simulate the behavior of a monotypic *Hydrilla* community under various environmental and climatological conditions. In its present form, the model is calibrated for dioecious *Hydrilla*.

Hydrilla: Biotypes and Their Distribution Within the United States

The submersed, rooted aquatic macrophyte *Hydrilla verticillata* (L.f.) Royle belongs to the family Hydrocharitaceae. It has the ability to survive unfavorable environmental conditions and has been demonstrated to outcompete most other submersed aquatic plant species in temperate, subtropical, and tropical areas. Consequently, this species has a very large distributional area (Robson 1976).

Hydrilla was introduced into the United States in 1960 in Florida (Blackburn et al. 1969). Originally, only the dioecious biotype (plants producing only pistillate flowers) occurred. *Hydrilla* has rapidly spread to other southern states (i.e., Georgia, Alabama, South Carolina, North Carolina, Louisiana, and Texas) into California, moving up the eastern seaboard. A

monoecious biotype was first sighted in the Potomac River in 1982 and began spreading rapidly to Virginia, Maryland, Washington DC, and Delaware (Steward et al. 1984). Both *Hydrilla* biotypes propagate largely vegetatively, despite the production of seeds in the monoecious biotype, and they are composed by several strains (Mitra 1960; Scannel and Webb 1976; Verkleij et al. 1983).

Hydrilla is considered a nuisance aquatic plant in parts of the United States, since it may interfere with human utilization of freshwater resources, become aesthetically displeasing, or displace desirable indigenous community. From a shoreline perspective, the biomass in a dense "mat" of submerged weeds appears to be enormous. However, data on total biomass and productivity indicate that they are small compared with those of several terrestrial plant communities (Spencer and Bowes 1990). This apparent anomaly may be largely due to the uneven distribution of biomass over the water column, with typically >60 percent concentrated in the upper water layers (only dioecious *Hydrilla*).

The simulation model developed in this study concerns the dioecious *Hydrilla* biotype. The following appendixes are included in this report: Model Listing as Appendix A, Variable Listing as Appendix B, and Manipulation of Literature Data Used for the Model Equations as Appendix C.

2 HYDRIL: Description of Model

Modeling Concepts

The HYDRIL (Version 1.0) model simulates growth of dioecious *Hydrilla* community, i.e., its dry matter accumulation including subterranean tuber formation under ample supply of nitrogen and phosphorus in a pest-, disease-, and competitor-free environment under the prevailing weather conditions. The rate of dry matter accumulation is a function of irradiance, temperature, CO_2 availability, and plant characteristics. The rate of CO_2 assimilation (photosynthesis) of the plant community depends on the radiant energy absorbed by the canopy, which is a function of incoming radiation, reflection at the water surface and attenuation by the water column, attenuation by the plant material, and leaf area of the community. From the absorbed radiation, the photosynthetic characteristics of individual shoot tips and the pH-determined CO_2 availability, the daily rate of gross CO_2 assimilation of the community, is calculated. These calculations are executed in a set of subroutines added to the model.

Part of the carbohydrates produced is used to maintain the existing biomass. The remaining carbohydrates are converted into structural dry matter (plant organs). In the process of conversion, part of the weight is lost in respiration. The dry matter produced is partitioned among the various plant organs using partitioning factors defined as a function of the phenological cycle of the community. The dry weights of the plant organs are obtained by integration of their growth rates over time. The plant winters through tubers in the sediment without or with aboveground plant biomass present. All calculations are performed on a square meter basis.

Turion and seed formation are not included in the model because their role in maintaining an existing *Hydrilla* community is minimal. Dispersal and colonization of new habitats by turions and plant fragments are recognized, important characteristics of *Hydrilla*. The latter processes, however, are better described using other modeling approaches (based on logistic regression or on descriptions of population dynamics varying in time and in space), as discussed by Scheffer (1991).

HYDRIL requires as input physiological properties of the plant community (in this case dioecious *Hydrilla*) and the actual environmental and weather conditions at the site, characterized by its geographical latitude and longitude, i.e., water temperatures (optional), alkalinity, pH, and daily maximum and minimum temperatures and irradiance for each day of the year. It can be run for periods of 1 to 5 years.

Modeling Approach

HYDRIL is a mechanistic model that explains plant growth on the basis of the underlying processes, such as CO_2 assimilation and respiration, as influenced by environmental conditions. This type of model follows the state-variable approach in that it is based on the assumption that the state of each system can be quantified at any moment and that changes in the state can be described by mathematical equations. In this type of model, state, rate, and driving variables are distinguished. State variables are quantities such as biomass and number of individuals of a population. Driving variables characterize the effect of environment on the system at its boundaries, such as climate and food supply. Each state variable is associated with rate variables that characterize its rate of change at a certain instant, as a result of specific processes. These variables represent flows of material between state variables, the values of which are calculated from the state and driving variables according to knowledge of the physical, chemical, and biological processes involved. After calculating the values of all rate variables, they are then used to calculate the state variables according to the scheme: state variable at time $t+\Delta t$ equals state variable at time t plus the rate at time t multiplied by Δt. This procedure, called numerical integration, gives the new values of the state variables, from which the calculation of rate variables is repeated. To avoid instabilities, the time interval Δ t must be small enough so that the rates do not change materially within this period. This is generally the case when the time interval of integration is smaller than one-tenth of the "time coefficient" or "response time." This characteristic time of a system is equal to the inverse of the fastest relative rate of change of one of its state variables. The smaller the time coefficient, the smaller the time interval of integration (Rabbinge and De Wit 1989).

The predictive ability of mechanistic models does not always live up to expectations. It should be realized, however, that each parameter estimate and process formulation has its own inaccuracy, and that errors may accumulate in the prediction of the final yield. The primary aim of this model is to increase insight in the system studied by quantitatively integrating the present knowledge in a dynamic simulation model. By studying the behavior of the model, better insight in the real system is gained.

Model Language and Structure

The HYDRIL model is written in FORTRAN77. Model approach and organization are similar to those used for agricultural crops (SUCROS1; Goudriaan, Van Keulen, and Van Laar 1992). Several features from an earlier HYDRIL version (Lips 1985) and from a general growth model for submersed angiosperms, SUBANG (Best and Jacobs 1990), have been used.

HYDRIL runs within a FORTRAN SIMULATION ENVIRONMENT (FSE) shell, Version 2.1, to enable easy handling of input and output files and rapid visualization of the simulation results (Van Kraalingen 1995). It can be executed on IBM PC-AT's and compatibles as a stand-alone version. Because of its language and simple structure, it will generally be compatible with ecosystem models that accept FORTRAN.

The organization of the model and its subroutines in combination with the FSE shell is illustrated in Figure 1.

Model Features

Features of HYDRIL are as follows:

a. Phenology is tied indirectly to air temperature through development rate and is, therefore, independent of day of year; thus, the model can be used under climatological conditions ranging from temperate to tropical.

b. Plant growth starts from the tuber bank in the sediment and/or from rooted plants.

c. Photosynthetic response is to instantaneous irradiance.

d. Removal of biomass through harvesting can be calculated if desired.

e. Air and/or water temperatures can be used to run the model.

f. The model can be used for community at various water depths, ranging from 0.1 to 2.5 m.

g. Plant parameter values and climatological variables can be easily changed.

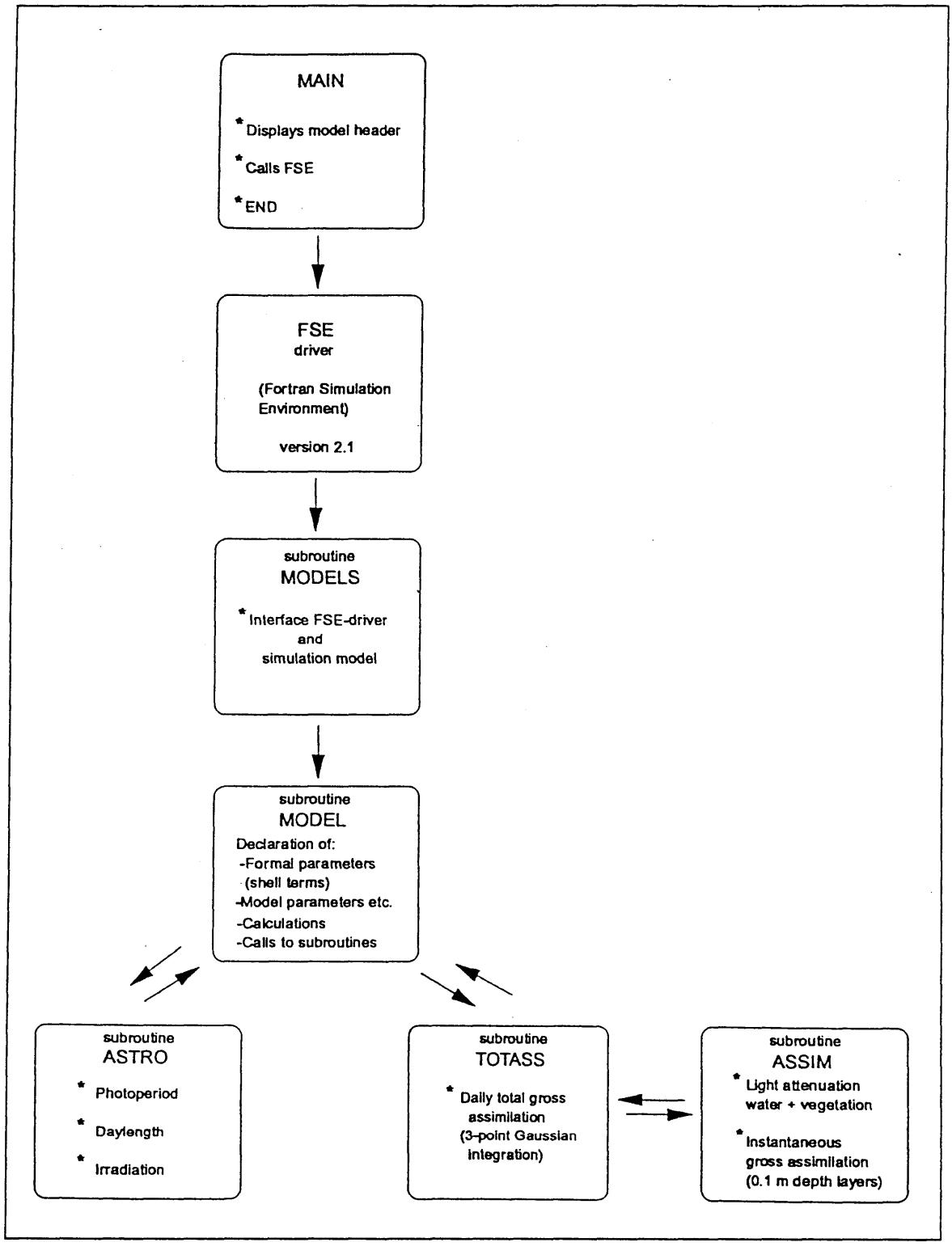

Figure 1. Relational diagram illustrating the organization of the model HYDRIL and its subroutines in combination with the FSE shell

3 Model Processes

Morphology, Development, and Phenological Cycle

Morphology

The dioecious *Hydrilla* biotype is anchored to the hydrosoil by long, white, adventitious roots. In summer the plant has tall stems, which branch close to the water surface. The leaves are whorled. The dioecious biotype can propagate only vegetatively in the United States, since only plants producing pistillate flowers occur. It is unclear whether crossings between and/or within biotypes occur. The most important means of vegetative propagation is the formation of tubers. Tubers are small, dormant organs that develop on the rhizomes in the sediment under special daylength and temperature conditions, usually in autumn (Mitra 1964). They are composed of a small amount of dividing tissue surrounded by several fleshy leaf whorls. Other vegetative reproduction mechanisms are (a) stem fragmentation, (b) horizontal shoot formation in the sediment, and (c) turion formation on the shoots.

Development and phenological cycle

The phenology of a plant community, for which development phase can be used as a measure, quantifies physiological age and is related to its morphological appearance. Development phase cannot be expressed simply as chronological age, because several environmental factors such as temperature and stress (e.g., nutrients and grazing) can speed up or reduce the rate of phenological development. Contrary to what is suggested by intuition, the rate of plant growth per se has no effect on phenological development, as long as the growth rate is not very low (Penning de Vries et al. 1989, and citations therein). The concept of development phase is used to characterize the whole plant community; it is not appropriate for individual organs.

The response of developmental rate to temperature in the present model is in accordance with the degree-day hypothesis (Thornley and Johnson 1990). The idea is as follows. The mean temperature T_i for each day i is measured, and a sum h is formed according to

$$h = \sum_{i=1}^{j} (\bar{T}_i - T_c)$$

which includes only those terms where $\bar{T}_i$ is above some threshold value T_c. When h reaches a particular value, this signifies that a phase in development is complete, and this is generally associated with a biological event that occurs over a short period of time and is readily observed. The day-degree sum h essentially integrates some underlying temperature-dependent processes. For *Hydrilla*, for example, there are various phases in the development of the plant, and the temperature sum is found to have a certain value for the successful completion of each. The temperature threshold T_c may be different for each of these phases. The approach is based on the notion of a developmental rate whose response to temperature is approximately linear over a restricted temperature range. Comparison with actual temperature responses suggests that this is not unreasonable, and the method works well in practice. It is implicitly assumed that the organ possesses a developmental clock that is proceeding at the rate k_d. In general, it is to be expected that the development rate k_d may depend on a number of quantities. This can be represented by

$$k_d = f(V, P, E)$$

in which f represents some function of the state variables V, parameters P, and environmental quantities E. The temperature-sum rule works because the most important environmental variable is temperature, and the response to temperature is approximately linear.

The phenological cycle is described using *Hydrilla* in Lake Orange, Florida, in 1977 as an example (Bowes, Holaday, and Haller 1979). Plant data of this year were chosen after verifying that climatological conditions did not deviate from the usual at that site.

Development phase (DVS) is a state variable in HYDRIL. In the model, the temperature that affects development of *Hydrilla* can be chosen as equal to the daily average air temperature at the height of the shoots' growing point, with a lag period of 1 week to correct for changes in temperature in the water body in which the aquatic community grows. It is more accurate to use water temperatures for this purpose; but since water temperatures are not always available for the site for which the user wants to run the model, HYDRIL can be run using either one.

The rate of phenological development can be affected by temperature differently in the vegetative phase than in the reproductive phase. These differences indicate that the physiological process of development may not be the same before and after anthesis. Since the timing of anthesis has not been described in detail, the period of anthesis could only be inferred from literature and thus distinction between preanthesis and postanthesis development

rate could not be made. For *Hydrilla* a development rate of 0.012.day^{-1} at a reference temperature of 30 °C and a temperature threshold of 3 °C was derived from the Lake Orange field data (Bowes, Holaday, and Haller 1979). The development rate of *Hydrilla* cannot be compared with that of other submersed plants since the latter have not been published so far. It is, however, higher than the development rate of sweet potatoes (DVR 0.006.day^{-1}, reference temperature 27 °C), a terrestrial tuber-forming species.

The development phase has the value 0.0 when the simulation starts at the first Julian daynumber. The simulation starts using an observed tuber density, with maximum individual tuber weight, as an initial value. The quantities of leaves, stems, and roots are set equal to 0. If simulation of the community at another site is desired, the simulation can start also with wintering plants present; first, however, initial quantities of plant organs must be calculated. The sprouting of the tubers occurs at DVS 0.326. Sprouts develop through remobilization of carbohydrates from the tubers. The sprouts elongate rapidly to the water surface and form a canopy in the upper water layers from DVS 0.360 onwards. Anthesis is initiated at DVS 1.000 and finishes at DVS 1.999, just before tuber induction is initiated. Tuber formation lags behind tuber induction. Senescence sets in at DVS 2.200 and continues until the end of the year. The development phase is dimensionless, and its value increases gradually. The development rate has the dimension d^{-1}. The multiple of rate and time period yields an increment in phase (Table 1; for more details, see Appendix C).

Table 1
Relationship Between Development Phase (DVS) of *Hydrilla*, Day of Year, and 3 °C Day-Degree Sum

Developmental Phase		Daynumber	3 °C Day-degree sum
Description	DVS Value		
First Julian daynumber-->tuber sprouting and initiation elongation	0->0.326	0->74	1->596
Tuber sprouting and initiation elongation-->leaf expansion	0.327->0.359	75->78	597->673
Leaf expansion-->floral initiation and anthesis	0.360->1.000	79->150	674->2063
Floral initiation and anthesis-->induction of tuber formantion	1.001->2.000	151->241	2064->4279
Induction tuber formation-->tuber formation and senescence	2.001->2.200	242->260	4280->4744
Tuber formation and senescence-->senesced	2.201->2.979	261->365	4745->6357
Scenesced	2.979	365	6357

Note: Calibration was on field data 1974-75 (Haller, Miller, and Garrard 1976) and climatological data 1980, Gainesville, FL.

Plant Density

Generally, biomass production of *Hydrilla* is far more constrained by plant-inherent factors, light- and space-availability, and temperature, than by plant density. For example, studies in outdoor pools have demonstrated that 1 *Hydrilla* plant produced the same amount of biomass as 16 plants that were cultivated under the same conditions (water volume and environmental conditions identical (Sutton, Littell, and Langeland 1980)). However, since initial plant density is required as an input variable into the model, a feasible plant density under field conditions had to be found.

A range of 34 to 53 plants.m^{-2} was "determined" for *Hydrilla* community in Lake Orange in August (1977; Bowes, Holaday, and Haller 1979), using a typical plant weight range of 3.08 to 4.76 g DW.$plant^{-1}$ (average values laboratory experiment at 97 percent and full sunlight; Barko and Smart 1981). Since individual plant weight is expected to be higher under natural conditions with higher light intensities and usually more water movement than in the laboratory, natural densities are expected to be on the low side within the range determined, i.e., in the order of 35 plants.m^{-2}.

In HYDRIL plant density is set to 35 plants.m^{-2}. This implies that at the beginning of the growth season, plant density is always 35, irrespective of whether the plant has hibernated in the form of tubers with or without rooted plants present. The number of tubers sprouting in spring always equals 35.m^{-2}. In the presence of aboveground biomass in spring, biomass is redistributed over 35 plants.m^{-2}.

Wintering and Sprouting of Tuber Bank

The published tuber densities in the *Hydrilla* tuber banks vary over a large range (0 to $>1{,}000$.m^{-2}; Haller, Miller, and Garrard 1976; Bowes, Holaday, and Haller 1979), probably largely as a result of (a) the patchy spatial distribution of the community over the water body and (b) limited number of replicate samples taken. It is to be expected that most of these tubers, like seeds in seed banks, lie dormant if not disturbed (Van and Steward 1990), i.e., that maintenance processes proceed at a very low level of activity and that no active respiration occurs. Tuber density may decrease by tuber death and possibly grazing of water fowl and other organisms, by the sprouting of tubers, which transform into plants, and it may increase by the formation of new tubers.

Death rates of tubers have not been published so far. A death rate value has been inferred from recent observations on a tuber bank in the North New River Canal (South Florida) that became exhausted after a 3-year

prevention of tuber formation.[1] Assuming a tuber density of 500 tubers.m^{-2} (Lake Orange, Florida; Bowes, Holaday, and Haller 1979), a tentative relative death rate of 0.36.day^{-1} was calculated (tuber per tuber.day^{-1}; Figure 2). The latter value is surprisingly close to the relative death rate found for a potato crop in Florida, being 0.37.day^{-1} (Ingram and McCloud 1984). Effects

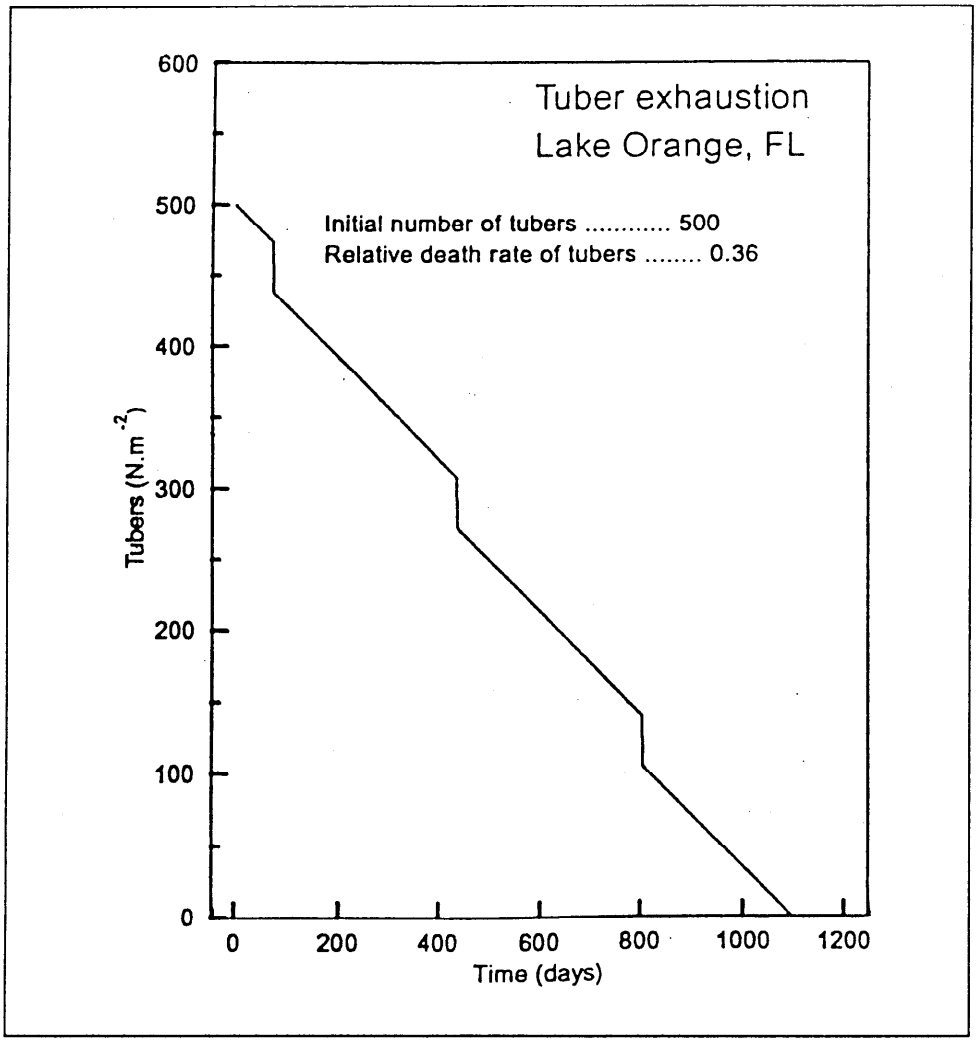

Figure 2. Simulation showing exhaustion of *Hydrilla* tuber bank in Lake Orange, Florida, under conditions at which tuber formation is prevented (Simulation was done to estimate relative tuber death rate. Initial values on tuber number extrapolated to Julian daynumber 1, 1977 (Bowes, Holaday, and Haller 1979). Initial plant biomass absent. Climatological data 1980, Gainesville, FL. Measured biomass data 1977 (Bowes, Holaday, and Haller 1979))

[1] Personal Communication, 1995, D. L. Sutton, Professor, University of Florida, IFAS, Fort Lauderdale Research and Education Center, Fort Lauderdale, FL.

of grazing on the *Hydrilla* tuber bank are unknown to us. That grazing, especially by waterfowl, can be substantial has been demonstrated in several European lakes (Jupp and Spence 1977; Scheffer, Bakema, and Wortelboer 1993).

The sprouting potential of tubers under experimental laboratory conditions is usually high (up to 100 percent; Bowes et al. 1977; Spencer and Anderson 1986; Steward and Van 1986; Sutton and Portier 1992). The tubers used for these experiments, however, have probably artificially lost their dormant state by removal from their natural environment (perhaps due to exposure to oxygen, desiccation). Actual sprouting frequency under natural conditions is unknown. Sprouting frequency in an established community is probably not important as long as the usual plant density of 35 plants.m^{-2} is somehow reached, since plant density tends to play a lesser role in biomass production compared with space availability (see plant density).

Daylength at which the tubers sprout is >13 hr, as for potatoes (Hahn and Hozyo 1983), but only within a temperature range >18 °C and <33 °C (Haller, Miller, and Garrard 1976). Sprouting may be triggered by a certain red-far red ratio in the light reaching the plants' photosensitive pigments (Spencer and Anderson 1986); however, the latter phenomenon can only play a role when wintering aboveground biomass is present. Phytochrome is not expected to trigger tuber sprouting during the spring for *Hydrilla* in Lake Orange, since it winters in the form of tubers in the sediment.

In HYDRIL, initial tuber density at the onset of the simulation is set at 500 tubers.m^{-2}, similar to the highest tuber density found in Lake Orange (1-m rooting depth, 1977; Bowes, Holaday, and Haller 1979). The relative tuber death rate is 0.36.day^{-1} (on number basis). Sprouting is set at 35 tubers.m^{-2}. Sprouting is a function of development phase; it occurs from DVS 0.326 onwards, provided that daylength >13 hr and temperature (of water, when water temperature data available; otherwise of daily average air, with a lag period of 7 days) >18 °C and <33 °C. A relational diagram illustrating the wintering and sprouting tubers in the tuber bank of *Hydrilla* is shown in Figure 3. For tuber chemistry, see Appendix C.

Growth of Sprouts to Water Surface

The sprouting tubers convert their carbohydrate reserves into sprout material, according to a fixed biomass allocation pattern (see next section). It is assumed that the sprouts can elongate up to the water surface by mere remobilization processes, not even requiring photosynthetic products (see Appendix C). A relative conversion rate of tubers into adolescent plants of 0.0025.hr^{-1} has been derived from published changes in light compensation points (LCP) during transformation of young sprouts into adolescent plants (Appendix C). After reaching the water surface, canopy formation takes place and photosynthesis proceeds.

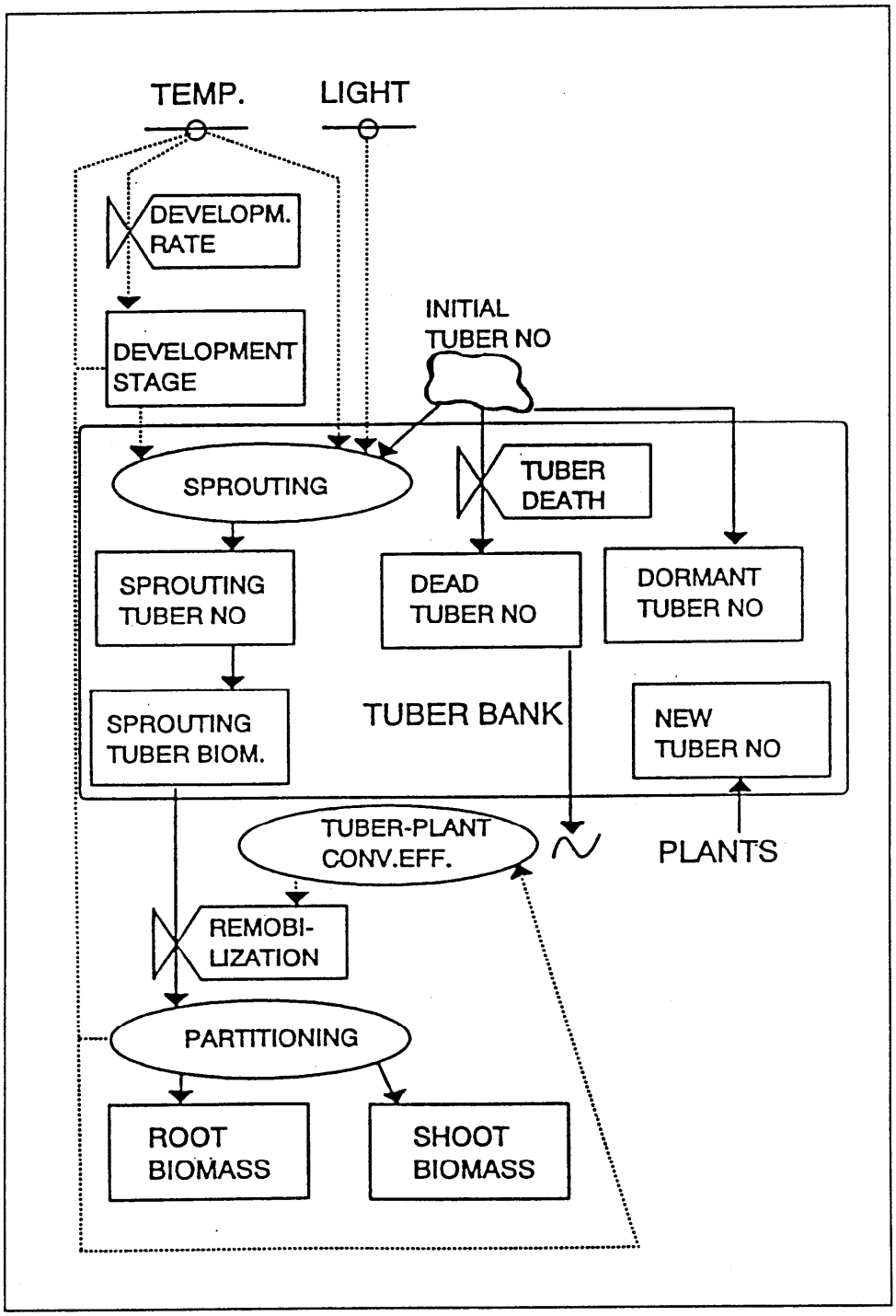

Figure 3. Relational diagram illustrating wintering and sprouting of tubers in tuber bank of *Hydrilla*

Light, Photosynthesis, Maintenance, Growth, and Assimilate Partitioning

Light

The measured daily total irradiance (wavelength 300 to 3,000 nm) is used as input for the model. Only half of the irradiance reaching the water surface is photosynthetically active and is therefore used to calculate CO_2 assimilation. Six percent of the irradiance is reflected by the water surface (Golterman 1975).

The subsurface irradiance is attenuated by color and particles within the water column with a site- and season-specific extinction coefficient. Moreover, the vertical profiles of the radiation within the community layers are characterized. The absorbed irradiance for each horizontal community layer is derived from these profiles. The community-specific extinction coefficient, K (m^2.g DW^{-1}), is assumed to be constant throughout the year.

The incoming irradiance is attenuated by the shoots, part of which is absorbed by the photosynthetic plant organs, i.e., the leaves.

$$IRZ_{i+1} = IRZ_i \cdot e^{(-0.1.L - K.SCi)}$$

$$IABS_i = (IRZ_i - IRZ_{i+1}) \cdot SCI_i \cdot K/(K.SCI_i + 0.1.L)$$

$$IABSL_i = IABS_i \cdot FL$$

where

IRZ = photosynthetic active part of irradiance ($J.m^{-2}.s^{-1}$)

L = light extinction coefficient of water (m^{-1})

K = plant-specific extinction coefficient (m^2.g DW^{-1})

SC = shoot matter (g DW per 0.1-m stratum of a square meter water column)

$IABS$ = shoot-absorbed part of irradiance

$IABSL$ = leaves-absorbed part of irradiance

FL = leaf fraction of shoot

The subscript i is 0.1-m depth layer.

Photosynthesis

The instantaneous rates of gross assimilation are calculated from the absorbed light energy and the photosynthesis light response of individual shoot apices, here used synonymously to leaves.

The photosynthesis light response of leaves is described by the exponential function

$$FGL = SC_i \cdot AMAX \cdot (1 - e^{-EE \cdot IABSL/ \cdot 3600AMAX \cdot SCi})$$

where

FGL = gross assimilation rate per depth layer (g CO_2. m^{-1}. h^{-1})

SC = shoot matter (g DW per 0.1-m stratum of a square meter water column)

$AMAX$ = actual CO_2 assimilation rate at light saturation for individual shoots (g CO_2.g DW^{-1}.hr^{-1})

EE = initial light use efficiency for shoot tips (g CO_2.J^{-1} absorbed)

Substituting the appropriate value for the absorbed photosynthetically active radiation yields the assimilation rate for each specific shoot layer. A decrease in gross assimilation rate at light saturation due to ageing is included into the model. However, since no data were yet available to calibrate this parameter in relation to developmental phase, this function has the value 1. A reduction factor REDAM corrects the AMX for daily changes in pH and oxygen concentrations (daily average pH Lake Orange pH 7.6) and a fitted function ETGF for the effect of daytime temperature (Appendix C).

The instantaneous rate of gross assimilation over the height of the community is calculated by relating the assimilation rate per layer to the community-specific biomass distribution and by subsequent integration of all community layers, each 0.1 m high.

The daily rate of gross assimilation is calculated by using the Gaussian integration method. This method specifies the discrete points at which the value of the function to be integrated has to be calculated and the weighting factors that must be applied to these values to attain minimum deviation from the analytical solution. A three-point method performs very well for calculating daily total assimilation (Goudriaan 1986; Spitters 1986).

The process of photosynthesis reduces CO_2 to carbohydrates (CH_2O) using the energy supplied by the absorbed light. For each g CO_2 absorbed, 0.68 g CH_2O is formed, the numerical values representing the molecular weights of CH_2O and CO_2, respectively.

Maintenance, growth, and assimilate partitioning

Some of the carbohydrates formed are respired to provide energy for maintaining the existing plant components. The maintenance costs increase with metabolic activity, probably due to higher enzyme turnover and higher transport costs (Penning de Vries 1975).

The maintenance cost can be estimated from the chemical composition of the plant. Typical maintenance coefficients for various plant organs have been derived, based on numerous chemical agricultural crops (Penning de Vries and Van Laar 1982b).

In the present model, these coefficients are used to calculate the maintenance requirement of the community:

$$MAINTS = 0.016.TWLVG + 0.010.TWSTG + 0.015.TWRTG + 0.010.TWSO$$

where

MAINTS = maintenance respiration rate at reference temperature (g $CH_2O.m^{-2}.day^{-1}$)

TWLVG = total dry weight of live leaves (g $DW.m^{-2}$)

TWSTG = total dry weight of live stems (g $DW.m^{-2}$)

TWRTG = total dry weight of roots (g $DW.m^{-2}$)

TWSO = total dry weight of storage organ (g $DW.m^{-2}$)

Higher temperatures expedite the turnover rates of plant tissues and increase maintenance costs. A temperature increase of 10 °C increases maintenance respiration by a factor of about 2 (reference temperature 30 °C; $Q_{10} = 2$; Penning de Vries and Van Laar 1982b).

The assimilates in excess of maintenance costs are available for conversion into structural plant material. In this conversion process of the glucose molecule, CO_2 and H_2O are released. The assimilates required to produce one unit weight of any particular plant organ can be calculated from its chemical composition and the assimilate requirements of the various chemical components. Typical values are 1.46 for leaves, 1.51 for stems, 1.44 for roots, and 1.41 g $CH_2O.g\ DW^{-1}$ for storage organs (including tubers; Penning de Vries and Van Laar 1982b).[1] At higher temperatures, the conversion processes are accelerated, but the pathways are identical.

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[1] Personal Communication, 1989, F. W. T. Penning de Vries, Professor, Centre for Agrobiological and Soil Fertility Research, Wageningen, The Netherlands.

Assimilate partitioning is the process by which assimilates available for growth are allocated to leaves, stems, roots, and storage organs. The distribution pattern is a function of physiological age.

In HYDRIL, the allocation pattern used for plants stays the same during the year since only summer values on biomass partitioning were available. The assimilate allocation is 0.34 of total to leaves, 0.60 to stems, and 0.06 to roots (Haller and Sutton 1975; Van, Haller, and Garrard 1978; Van der Zweerde 1981). At tuber formation, however, the assimilates are first translocated to fill the tubers that grow with a temperature-dependent growth rate, and only the remainder is allocated according to the abovementioned key. A relational diagram illustrating photosynthesis, respiration, and biomass formation of *Hydrilla* is shown in Figure 4.

Induction and Formation of Tubers

Tubers are formed under short day conditions (< 13 hr, but > 10 hr) and in a temperature range between 14 and 33 °C (Van, Haller, and Garrard 1978). Tuber formation is believed to be regulated by phytochrome and to be associated with increased levels of abscisic acid (ABA) (Van, Haller, and Bowes 1978; Klaine and Ward 1984). Although this process has scarcely been investigated in *Hydrilla*, tuber formation has been studied in terrestrial plants like potatoes. In the latter case, it involves changes in ABA and gibberellic acid (GA) content, with an increase in ABA during tuberization and a subsequent decline in GA levels (Kooman 1995). It is probably a critical ratio between these two hormonal levels that determines potential tuber formation. A similar mechanism regulating dormancy involving phytochrome, levels of ABA and GA, but also temperature, has been described to be in operation in the submersed *Ceratophyllum demersum* (Best 1982).

Environmental conditions favoring tuber induction occur in spring and in autumn in Lake Orange; but since *Hydrilla* plants winter there by tubers only, tuber induction is only feasible in autumn. However, at other sites with warmer climatological conditions, tubers may be induced also in spring. Tuber formation was observed in Lake Orange from October onwards, but formation could have happened earlier since the field observations were performed once a month (Haller, Miller, and Garrard 1976). The lag period between tuber induction and formation ranges, consequently, from 19 to 40 days. Water temperature in that period averaged 20 °C. The number of tubers concurrently formed per plant under (semi-)natural conditions ranged from 7 to 11 (Bowes, Holaday, and Haller 1979; see Appendix C). Tuber behavior in the model has been derived from the literature cited in this paragraph.

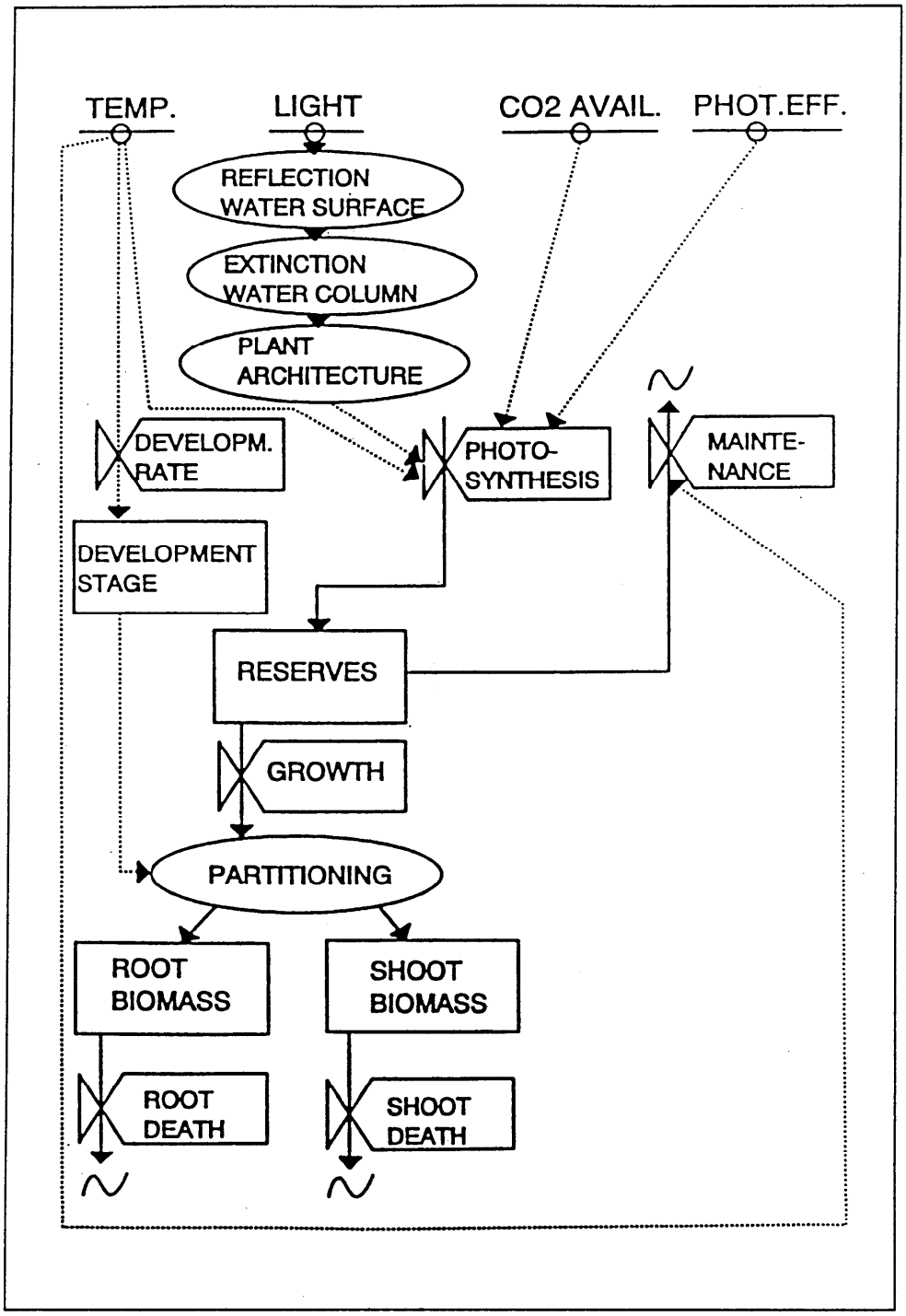

Figure 4. Relational diagram illustrating photosynthesis, respiration, and biomass formation of *Hydrilla*

In HYDRIL, induction of tuber formation occurs at development phase > 1.0, daylength < 13 hr and in a temperature range of 14 to 33 °C. Once initiated, a tuber class grows with a relative tuber growth rate of 0.4 g

DW.tuber^{-1}. day^{-1}(reference temperature 20 °C; calculated from a measured relative tuber growth rate of 0.006 g DW.tuber^{-1}.day^{-1} at ambient temperature) and is finished in 20 days when its maximum attainable weight of 0.1 g DW.tuber^{-1} has been reached. Temperature effects on tuber formation rate are accounted for using a Q_{10} relationship of 2. The number of tubers concurrently initiated is set at seven tubers.plant^{-1}. Once such a tuber class is finished, the plant starts forming the next class. The finished new tuber class serves no longer as a carbohydrate sink for the plant and is added to the tuber bank in the sediment. Tuber initiation continues as long as environmental conditions permit. At the end of the season, the last tuber class may not be finished because the available assimilates are not sufficient. This tuber class reaches a lower than maximum attainable size, but it is also added to the tuber bank as tuber number; its dry weight.m^{-2} is calculated before the class is added to the tuber bank, and it is added to the former weight of all tubers.

Senescence

Senescence refers to the loss of capacity to carry out essential physiological processes and to the loss of biomass. The fundamental processes involve physiological ageing and protein (enzyme) breakdown. These processes are difficult to quantify. It is known that hormones are important messengers in this context, but not how they precisely act. In addition, translocation of nutrients and assimilates to hibernating and/or storage organs occurs. High temperature usually accelerates senescence.

In HYDRIL, a mechanistic approach to senescence is chosen by setting the death rate of the plants to a certain fraction per day once the conditions for growth deteriorate. The timing and value of the relative death rate (RDR) have been derived from field observations on aboveground biomass in Lake Orange, Florida (initiation of senescence at DVS 2.2; RDR 0.033 g DW.g DW^{-1}.day^{-1} on dry weight basis; Bowes, Holaday, and Haller 1979). The quantity of assimilates translocated to the tubers is described as being sink-limited (similar to translocation in potatoes and cassava; Penning de Vries et al. 1989; Chapter 3 and references therein).

A relational diagram illustrating tuber formation and senescence is shown in Figure 5.

Choice of Parameter Values

A relatively simple simulation model like HYDRIL includes parameter values that can be defined with varying certainty. Most parameters have been calculated/estimated from published literature (Table 2). Only development rate in relation to 3 °C day-degree sum and base temperature have been calibrated by running the model. The choice of the parameter values has been detailed in the preceding sections of this chapter.

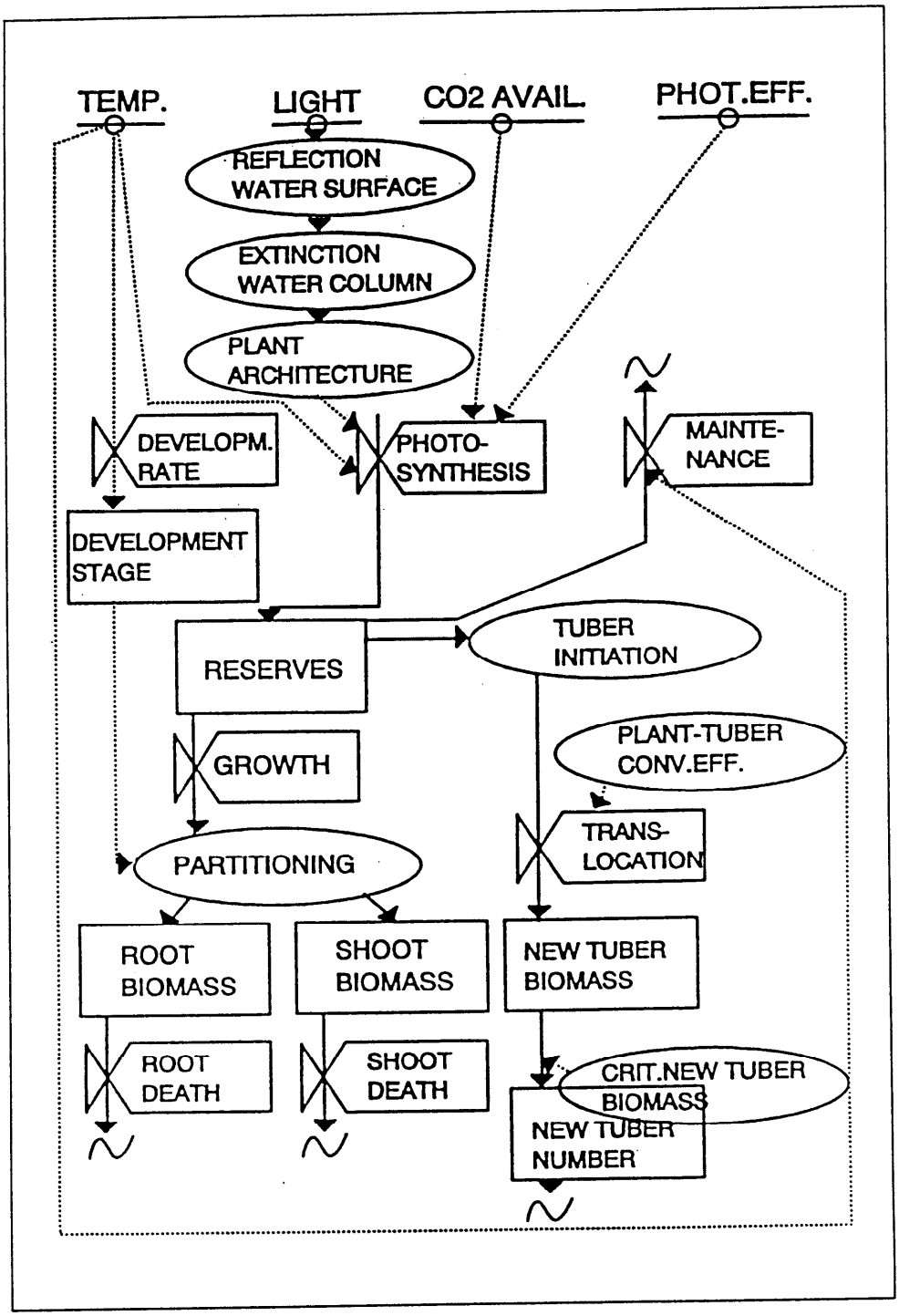

Figure 5. Relational diagram illustrating tuber formation and senescence of *Hydrilla*

Table 2
Parameter Values Used in HYDRIL

Parameter	Abbreviation	Value	Reference
Morphology, Development, and Phenological Cycle			
First Julian daynumber	DAYEM	1	
Base temperature for juvenile plant growth	TBASE	3 °C	calibrated
Development rate as function of temperature	DVRT*	0-0.012	calibrated
Fraction of total dry matter increase allocated to leaves	FLVT	0.34	7,15,16
Fraction of total dry matter increase allocated to stems	FSTT	0.60	7,15,16
Fraction of total dry matter increase allocated to roots	FRTT	0.06	7,15,16
Plant Density			
Plant density	NPL	$35.m^{-2}$	2,4
Wintering and Sprouting of Tuber Bank			
Initial tuber density	NT	$500.m^{-2}$	4
Relative death rate of tubers (on number basis)	RDTU	$0.36.day^{-1}$	10
Growth of Sprouts to Water Surface			
Relation coefficient tuber weight-stem length	RCSHST	12 m.g DW^{-1}	3,16
Relative conversion rate of tuber into plant material	ROC	0.0576 g CH_2O.g $DW^{-1}.day^{-1}$	3
Light, Photosynthesis, Maintenance, Growth, and Assimilate Partitioning			
Potential CO_2 assimilation rate at light saturation for shoot tips	AMX	0.0158 g CO_2.g $DW^{-1}.hr^{-1}$	4,14
Assimilate requirement for storage component production	ASRQSO	1.41 g CH_2O.g DW^{-1} stor.organ	9
Conversion factor for translocated dry matter into CH_2O	CVT	1.1	9

(Continued)

Notes: 1. Ambasht and Ram 1976; 2. Barko and Smart 1981; 3. Bowes et al 1977; 4. Bowes, Holaday, and Haller 1979; 5. Golterman 1975; 6. Haller, Miller, and Garrard 1976; 7. Haller and Sutton 1975; 8. Ikusima 1970; 9. Penning de Vries and Van Laar 1982a,b; 10. Sutton, pers.comm., 1995; 11. Titus et al. 1975; 12. Van, Haller, and Bowes 1976; 13. Van et al. 1977; 14. Van, Haller, and Bowes 1978; 15. Van, Haller, and Garrard 1978; 16. Van der Zweerde 1981.
*, Calibration function.

Table 2 (Concluded)

Parameter	Abbreviation	Value	Reference
Light, Photosynthesis, Maintenance, Growth, and Assimilate Partitioning (Continued)			
Water depth	DEPTH	1.0 m	user def.
Initial light use efficiency for shoot tips	EE	0.000011 g CO_2.J^{-1}	9
Reduction factor to relate AMX to water pH	REDAM	0.581	4,12
Thickness per plant layer	TL	0.1 m	11
Daytime temperature effect on AMX as function of DVS	AMTMPT*	0-1	12
Plant species specific light extinction coefficient	K	0.01m^2.g DW^{-1}	4,8
Water type specific light extinction coefficient	L	0.83.m^{-1}	4,7
Reduction factor for AMX to account for senescence plant parts over vertical vegetation axis	REDF	1.0	user def.
Dry matter allocation to each plant layer	DMPC*	0-1	1,4
Daily water temperature (field site)	WTMPT	-, °C	user def.
Total live dry weight measured (field site)	TGWMT	-, g DM.m^{-2}	user def.
Induction and Formation of Tubers			
Initial dry weight of a tuber	INTUB	0.1 g DW.$tuber^{-1}$	13
Tuber number concurrently initiated per plant	NINTUB	7.$plant^{-1}$	4
Maximum relative tuber growth rate at 20 °C	RTR	0.4.day^{-1}	6
Initial tuber density measured (field site)	NTMT	500.m^{-2}	default (3)
Senescence			
Relative death rate of leaves (on DW basis)	RDRT	0.033.day^{-1}	3
Relative death rate of stems and roots (on DW basis)	RDST	0.033.day^{-1}	3
Harvesting			
Harvesting	HAR	0 or 1	user def.
Harvesting day number	HARDAY	1-365	user def.
Harvesting depth (measured from water surface)	HARDEP	0.1m < DEPTH	user def.

4 Model Output

Simulated and Measured Behavior of *Hydrilla* Community in Lake Orange, Florida

The seasonal changes in the biomass of, respectively, plant organs and subterranean tubers as simulated by HYDRIL are shown in Figure 6A and of the simulated tuber number in Figure 6B. Generally, the simulated plant biomass compared well with the plant biomass found in the lake (Figure 6C). Peak biomass occurred somewhat earlier in the simulation than found in the lake; this may be an artifact, due to the rather low frequency of field observations (no measurements between September and November). Simulated tuber number was well within the tuber number range found in the lake.

Transport of carbohydrates is intensive in spring and autumn, when, respectively, carbohydrate remobilization from subterranean tubers supports growth of the sprouts, and carbohydrate translocation from plant organs supports the filling of subterranean tubers (Figure 7).

Running the model using air temperatures, with a time delay of 7 days, or measured water temperatures as forcing variables yields similar biomass values (Figure 8), both close to the field-measured biomass, illustrating that both temperature options in the model give similar results. Inclusion of this option in the model makes it relatively easy for the user to use the model, since not a full dataset of water temperatures of the water body for which the user desires to run the model is required.

Simulated and Measured Behavior of *Hydrilla* Community in Lake Trafford, Florida

To investigate whether the model was able to simulate the behavior of *Hydrilla* community at other sites, a run was made using initial values of another Florida lake more to the south, Lake Trafford. The results of this simulation are shown in Figure 9. Obviously, the simulated biomass compares well with the measured one. Comparison of the tuber behavior is

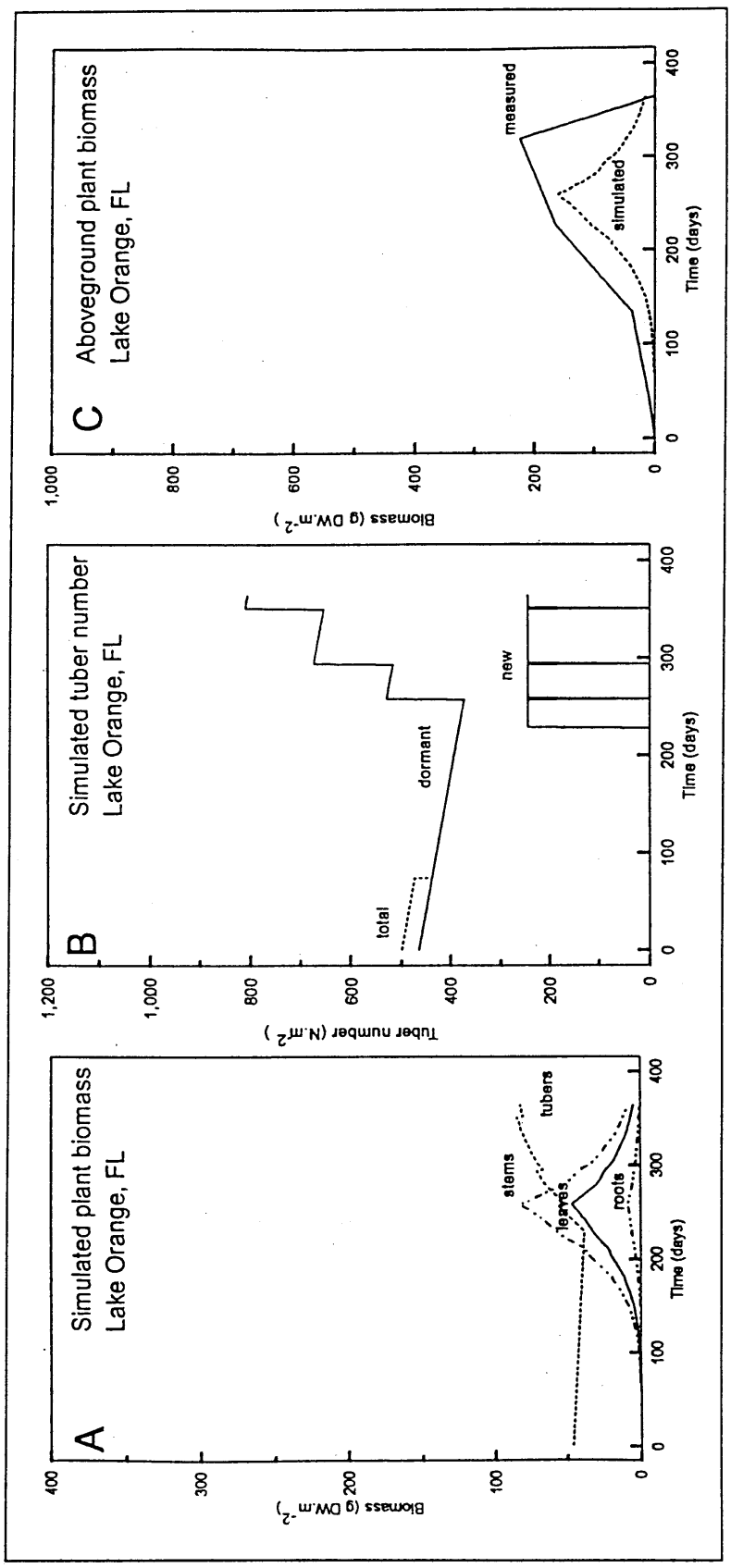

Figure 6. Simulated biomass of plant organs and tubers, simulated tuber numbers, and measured aboveground plant biomass of a *Hydrilla* community in Lake Orange, Florida (Initial values on aboveground plant biomass and tuber number extrapolated to Julian daynumber 1, 1977 (Bowes, Holaday, and Haller 1979). Climatological data 1980, Gainesville, FL (longitude 82° 22'W, latitude 29° 38'N). Measured biomass data 1977 (Bowes, Holaday, and Haller 1979))

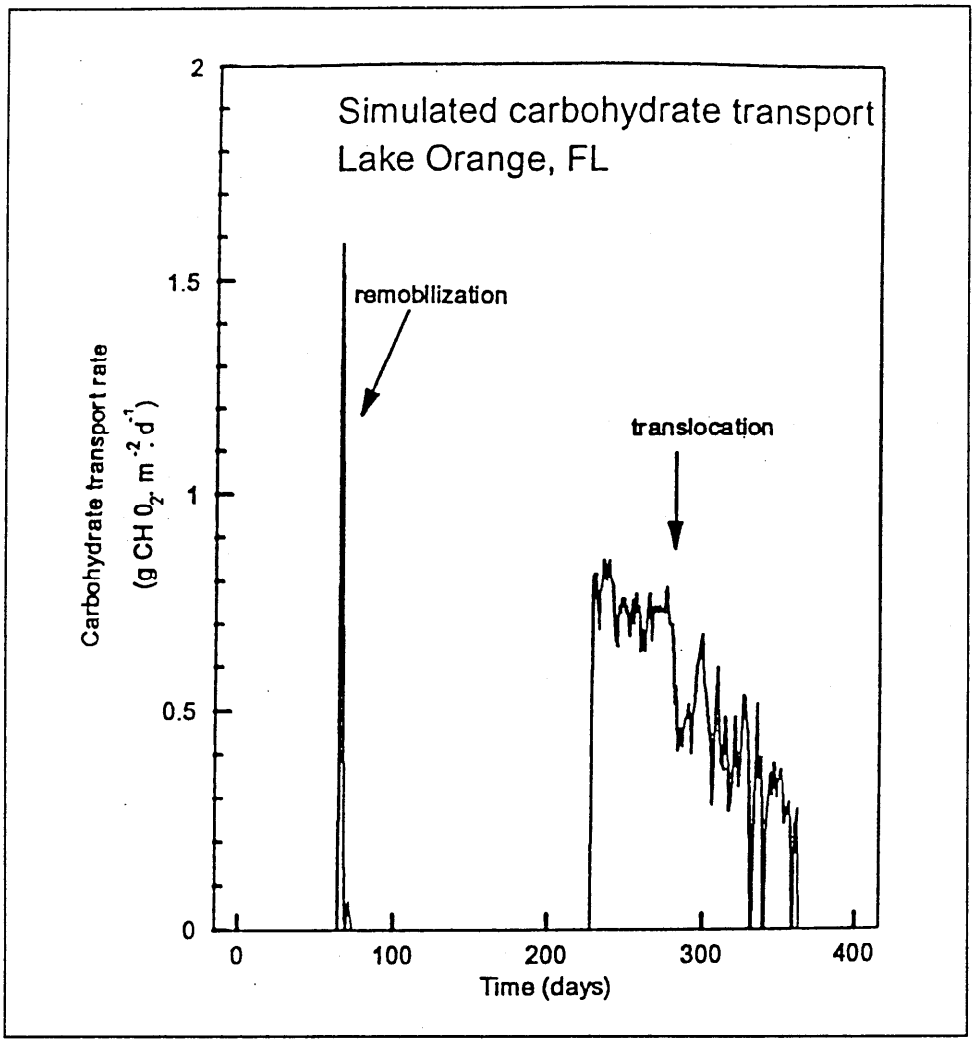

Figure 7. Simulated behavior of carbohydrates being remobilized in spring from subterranean tubers and translocated in autumn into tubers of *Hydrilla* (Initial values on aboveground plant biomass and tuber number extrapolated to Julian daynumber 1, 1977 (Bowes, Holaday, and Haller 1979). Climatological data 1980, Gainesville, FL)

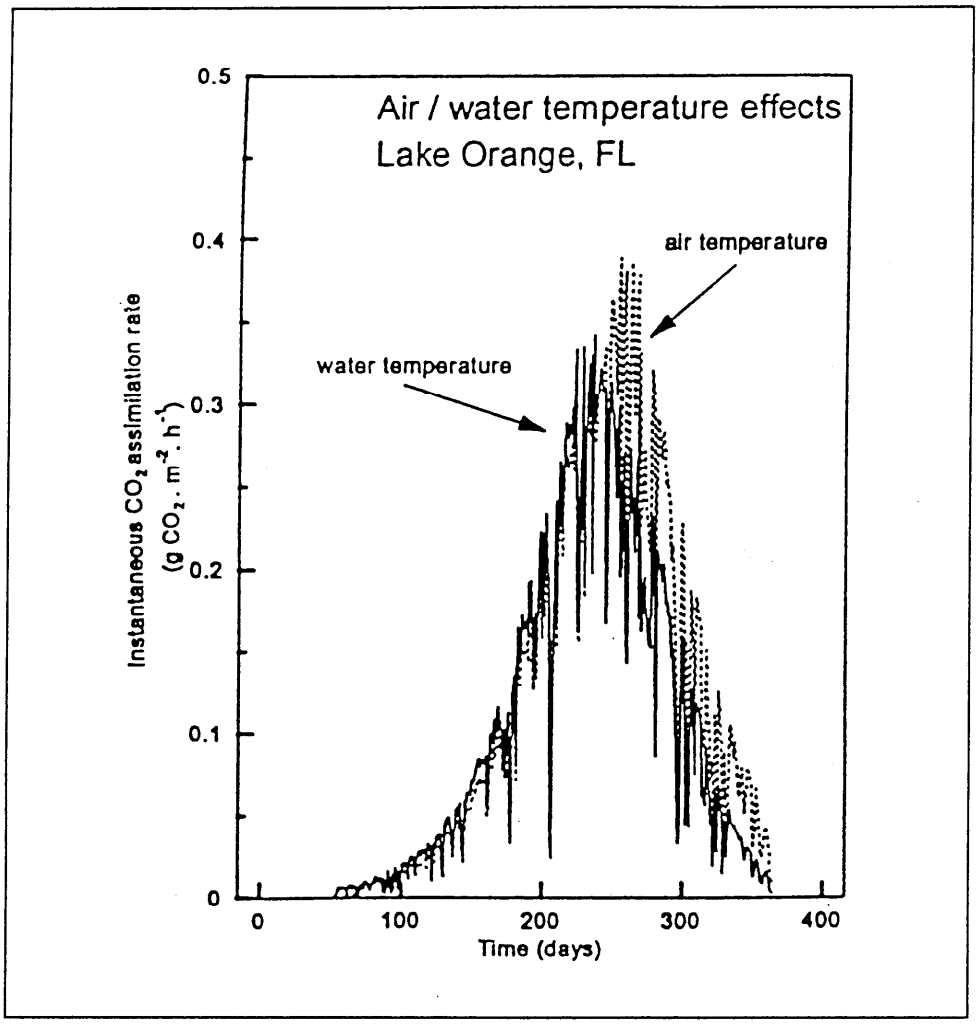

Figure 8. Simulated photosynthetic rate of a *Hydrilla* community in Lake Orange, Florida (Rates were calculated using, respectively, water and air temperatures in the model. Initial values on above-ground plant biomass and tuber number extrapolated to Julian daynumber 1, 1977 (Bowes, Holaday, and Haller 1979). Climatological data 1980, Gainesville, FL)

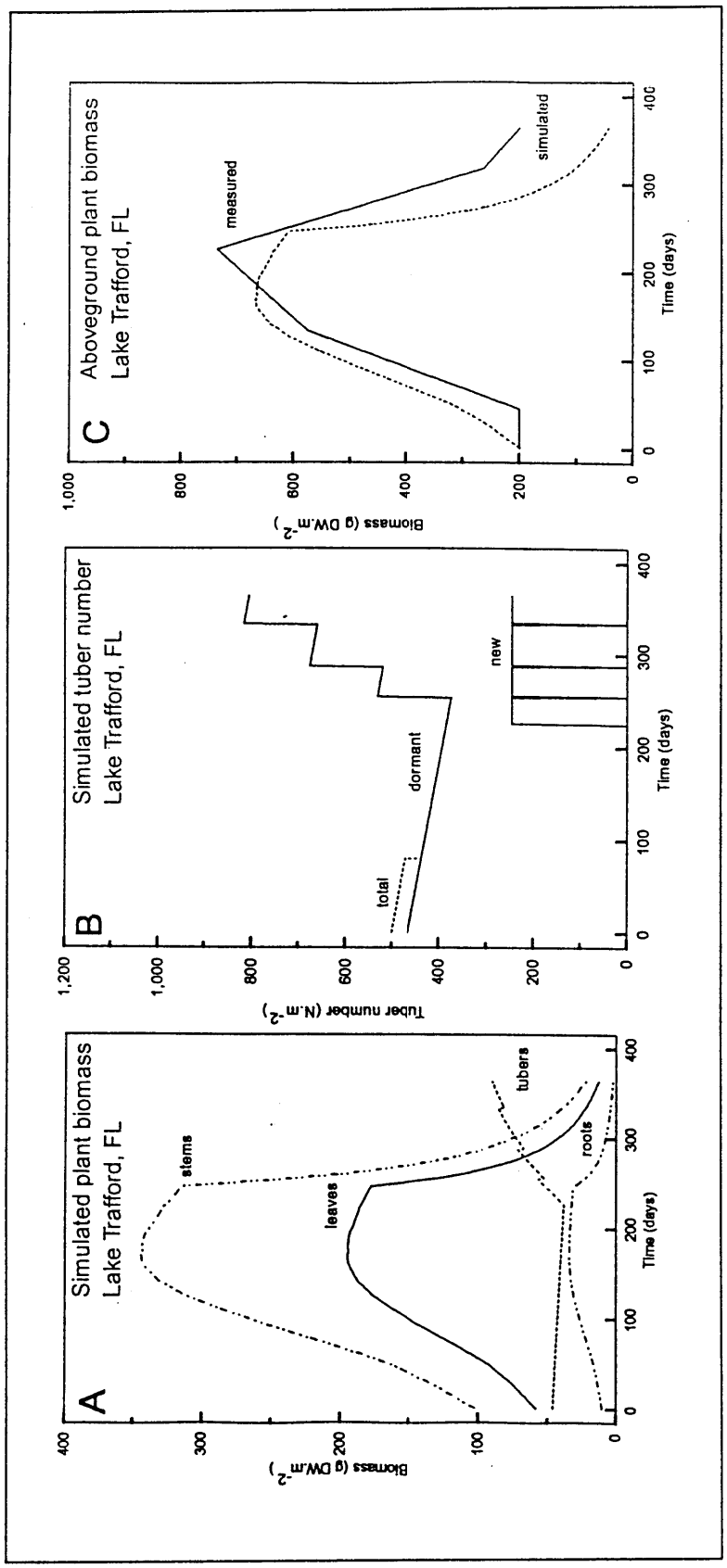

Figure 9. Simulated biomass of plant organs and tubers, simulated tuber numbers, and measured aboveground plant biomass of a *Hydrilla* community in Lake Trafford, Florida (Initial values on aboveground plant biomass and tuber number extrapolated to Julian daynumber 1, 1977 (Bowes, Holaday, and Haller 1979). Climatological data 1975-80, Tampa, FL. Measured biomass data 1977 (Bowes, Holaday, and Haller 1979))

not useful in this case since measured tuber data had such a wide scatter that no conclusions could be drawn.

Simulated and Measured Behavior of *Hydrilla* Community at Other Latitudes

Simulation of a *Hydrilla* community in Lake Ramgarh, India, demonstrated that usually lower peak biomass than in Florida is reached, when started merely from subterranean tubers. This is largely caused by the formation of more tubers and their inherent sink function for assimilates (Figure 10A, B). A simulation started from wintering plant biomass and from tubers generated a far higher peak biomass (Figure 10C). The latter simulation showed biomass curves that agreed well with the onsite measured biomass (Figure 10C).

Using the model calibrated on North-Florida to calculate the timing of phenological events in other climatological conditions indicated in the tropics earlier anthesis and extensive tuber formation in two periods of the year, but in temperate areas postponement of anthesis and reduced tuber formation in autumn only. Both of these model results are confirmed by literature data from, respectively, India and Ireland (data not shown; Sahai and Sinha 1973; Scannel and Webb 1976).

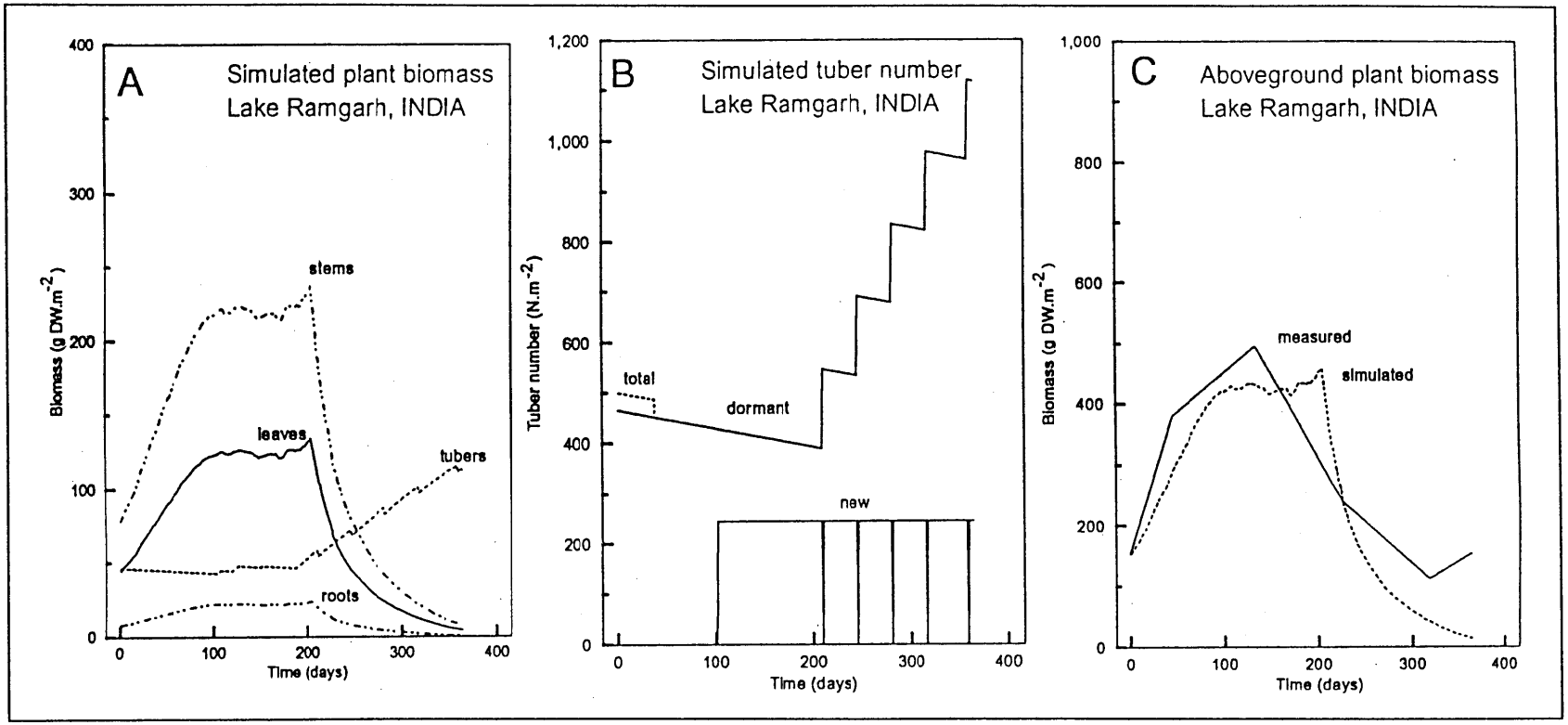

Figure 10. Simulated biomass of plant organs and tubers, simulated tuber numbers, and measured aboveground plant biomass of a *Hydrilla* community in Lake Ramgarh, India (Initial values on aboveground plant biomass and tuber number extrapolated to Julian daynumber 1, 1967-68 (Sahai and Sinha 1973). Climatological data 1978, Patancheru, India (longitude 78° 28'E, latitude 17° 27'N). Measured biomass data 1967-68 (Gorakhpur, longitude 83° 26'E, latitude 26° 5'N; Sahai and Sinha 1973))

5 Sensitivity Analysis

A sensitivity analysis of a simulation model is required to assess the parameters likely to strongly affect model behavior. The present analysis was based on the effect of a change in a parameter when all other parameters are kept the same. As reference level, the nominal parameter values were chosen as presented in Table 2, under Lake Orange, Florida, conditions at 1-m water depth. In a 1-year simulation starting with a 500 tubers.m^{-2} tuber bank, the value of the parameter understudy was changed. The results were compared with those of a standard run. Each parameter was once increased by 20 percent and once decreased by 20 percent. The relative sensitivity (RS) of a parameter was then defined as the relative change in the variable on which the effect was tested divided by the relative change in the parameter (Ng and Loomis 1984). The effects of eight parameters on three variables, all representing plant biomass aspects, were tested. A model variable is considered sensitive to a change in the value of a parameter at $RS > 0.5$ and < -0.5.

$$RS = \frac{(yield_i - yield_r)/yield_r}{(param_i - param_r)/param_r}$$

where

$yield_i$ = value at parameter value i

$yield_r$ = value at reference parameter value

$param$ = i and r idem

Maximum plant biomass proved most sensitive to changes in AMX and very sensitive to changes in light-use efficiency, which is not surprising because the model is based on the carbon flow through the plant (Table 3). Changes in plant density were important determinants of maximum plant biomass, but far less than AMX and light-use efficiency. The biomass of tubers at the end of the year was strongly influenced by that at the beginning of the year, as was tuber number. Tuber number was also sensitive to changes in relative tuber growth rate and plant density, but less to changes in relative tuber death rate and in number of tubers initiated per plant.

Table 3
Relative Sensitivity of Three Model Variables to Deviations in Parameter Values From Their Nominal Values as Presented in Table 2 (Results were obtained in a 1-year simulation under Lake Orange, Florida, conditions, starting with a tuber bank of 500 tubers.m^{-2})

Parameter Name	Value	Relative Sensitivity		
		Maximum Live Plant Biomass	Tuber Weight at End of Year	Tuber Number at End of Year
Potential CO_2 assimilation rate at light saturation for shoot tips	0.0158			
	0.01896	3.40	0	0
	0.01264	3.16	0	0
Light-use efficiency	0.000011			
	0.0000132	1.47	0	0
	0.0000088	1.61	0	0
Relative death rate leaves, stems, and roots	0.033			
	0.0396	0	0	0
	0.0264	0	0	0
Initial tuber number.m^{-2}	500			
	600	0	0.60	0.62
	400	0	0.60	0.62
Relative tuber growth rate	0.40			
	0.48	-0.11	0.74	0
	0.32	-0.10	0.46	0.97
Relative tuber death rate	0.360			
	0.432	0	-0.48	-0.49
	0.288	0	-0.47	-0.49
Tuber number initiated.$plant^{-1}$	7			
	9	0	0.09	-0.29
	5	0	0.03	0.10
Plant density.m^{-2}	35			
	42	0.62	0.15	-0.62
	28	0.73	-0.20	-0.54

6 Environmental Factor Analysis

The impacts of various changes in environmental factors were assessed using the relative sensitivity of the affected variables as "measure." For this purpose, changes in the parameters were based on value ranges taken from the literature that usually differed more than 20 percent from the nominal parameter value given in Table 2.

Climate

Climate greatly affects plant species distribution, phenological cycle, and biomass production. HYDRIL can be used to calculate climate change effects on the chronological timing of the phenological events and on biomass production. It cannot be used to assess climate change effects on (a) plant species distribution and (b) the phenological cycle itself since the phenological cycle has been used for calibration (see Chapter 3). Running the model under tropical climate conditions, i.e., changing the latitude from 29° to 17° N, demonstrated that peak biomass is far more sensitive to this climate change than tuber weight and number (Table 4).

Light Reflection Coefficient at Water Surface

The irradiance reflected at the water surface usually averages about 6 percent daily. The values of this parameter tested were 0 and 1. Reflection may theoretically have the value 0 when no reflection occurs at a 90-deg incoming angle of the radiation on a completely calm water surface (wind and wave action are minimal). The highest value of 1 may occur at a close to 180-deg incoming angle of the radiation and at very rough water surfaces. Increasing the light reflection coefficient to 1 annihilated plant biomass within the year. The RS of peak biomass and tuber weight and numbers, however, is relatively low (Table 4).

Light Extinction Coefficient of Water Column

A light extinction coefficient of $0.83.m^{-1}$ is used for reference runs of the model (Lake Orange, Florida). The range over which this parameter was tested was 0.20 to 2.00. A value of $0.20.m^{-1}$ is close to the theoretical one for water virtually devoid of particles and color (Kirk 1983). Values around $2.00.m^{-1}$ are typical for eutrophic fen lakes with submerged community present (Best, DeVries, and Reins 1985).

Changing the light extinction coefficient of the water column over a range of 0.20 to $2.00.m^{-1}$ demonstrated large effects on plant biomass. A light extinction coefficient of 2 greatly reduced biomass within the year. The effects on the tubers were negligible over a 1-year period, but increased on a longer term. The RS of peak biomass to changes in the light extinction coefficient is substantial, those of tuber numbers and weight negligible.

Water Depth

HYDRIL has been calibrated for a water depth of 1 m, the rooting depth of the *Hydrilla* community in Lake Orange. The model has the capability to respond to fluctuations in water level with year, by assigning 80 percent of the total plant mass to the upper six water layers, 6 percent to the roots and dividing the remaining 14 percent plant mass equally over the remaining number of water layers. In shallower situations, at water depth < 0.6 m, 6 percent of the total plant mass is assigned to the roots and the rest is equally divided over the remaining water layers. This technique for biomass distribution over the vertical axis of the community works well and gives realistic outcomes over a depth range of 0.1 to 2.5 m. Effects on tuber biomass and numbers were not noticeable.

Running HYDRIL with a water depth of 0.5 m instead of 1 m showed a considerable effect on peak biomass, indicating that changes in water depth in the range of 0- to 0.6-m depth have profound effects on biomass formation. In contrast, running HYDRIL with a water depth of 2 instead of 1 m showed a very small effect on the maximum plant biomass, probably because that part of the community below 0.6-m water depth is relatively small and already light limited at water depth of 1 m. Effects on tuber biomass and numbers were not noticeable. The RS of peak biomass to changes in water depth is substantial, but less than for changes in light extinction coefficient.

Table 4
Environmental Factor Analysis, Expressed as Relative Sensitivity of Three Model Variables to Deviations in Parameter Values From Their Nominal Values as Presented in Table 2 (Results were obtained in a 1-year simulation under Lake Orange, Florida, conditions, starting with a tuber bank of 500 tubers.m^{-2})

Parameter		Relative Sensitivity		
Name	Value	Maximum Live Plant Biomass	Tuber Weight at End of Year	Tuber Number at End of Year
Climate				
Gainesville USA1.980	Latitude 29° N			
Patancheru IND1.978	Latitude 17° N	1.66	0.19	0.47
Light reflection coefficient at the water surface	0.06			
	1.00 (+1667%)	-0.06	-0.03	-0.03
	0.00* (-100%)	-0.09	0	0
Light extinction coefficient water column	0.83			
	2.00 (+141%)	-0.38	-0.01	0
	0.20 (-76%)	-0.47	0	0
Water depth	1.0			
	2.0 (+100%)	-0.07	0	0
	0.5 (-50%)	-0.20	0	0

Note: To enable calculation of the RS, a very low RC value of 0.000001 was used.

7 Application Possibilities

HYDRIL can be used to assess the behavior of a *Hydrilla* community under various climatological and site-specific conditions, and it can be run with user-specified input values for plant biomass and tuber bank density.

Effects of man-made control activities, like harvesting at different times and at various water depths, can also be calculated (Table 5). Thus, in the latter case it can be used as a tool for aquatic plant management agencies. From Table 5 it can be concluded that harvesting at the end of July to a water depth of 0.8 m requires removal of a relatively low amount of biomass, but yields the lowest tuber bank density at the end of the year. This situation can be seen as favorable to control *Hydrilla*. In contrast, harvesting later in the year requires removal of relatively more plant biomass and allows for a relatively higher tuber bank density. Removing only the top layer of the plant community later in the year may lead even to increased numbers of tubers at the end of the year, probably due to a higher light penetration within the community.

Table 5
Effects of Mechanical Harvesting Date and Depth on Plant Biomass and Tuber Bank (Results were obtained in a 1-year simulation under Lake Orange, Florida, conditions, starting with a tuber bank of 500 tubers.m^{-2} and no aboveground plant biomass. Climatological data 1980, Gainesville, FL)

Harvest Day	Depth m	Live Plant Biomass Day 260 g DW.m^{-2}	Preharvest Biomass g DW.m^{-2}	Postharvest Biomass g DW.m^{-2}	Day With Zero Plant Biomass	Final Tuber Biomass g DW.m^{-2}, no
212	0.8	0.0	72.8	7.6	257	51 (330)
243	0.8	6.3	127.5	13.2	273	56 (490)
273	0.8	160.3	124.0	12.3	287	65 (490)
273	0.1	160.3	124.0	95.5	>365	82 (804)
304	0.8	160.3	65.2	6.5	316	73 (647)

The present version of HYDRIL has been developed as a stand-alone simulation model. It can be relatively easily modified to communicate with ecosystem models, because it is written in FORTRAN77 and its structure is simple. It is planned to link HYDRIL to a Geographical Information System through an appropriate interface like AEGIS+ (Luyten et al. 1994). To facilitate use of the present model, a user manual has been prepared (Boyd and Best 1996).

8 Discussion

The present model gives a reasonable description of the dynamics in plant biomass and tuber bank density of an established *Hydrilla* population under a variety of field conditions. As can be expected, the model is very sensitive to environmental changes affecting the light climate and, consequently, the carbon flow through the plant.

Extinction of light by periphyton has not been included in HYDRIL because (a) the plant canopy tends to be at the water surface during most of the growth season, (b) irradiance in the euphotic zone of the plant canopy (upper layers) is often saturating (i.e., >600 uE.m^{-2}.s^{-1}; Van, Haller, and Bowes 1976; Van, Haller, and Bowes 1978; Bowes, Holaday, and Haller 1979), and (c) no field data on periphyton available. It is expected that light attenuation by periphyton largely affects submersed macrophytes with most of their biomass concentrated just above the hydrosoil (like *Ceratophyllum demersum*; Best and Dassen 1987; Best and Jacobs 1990) and macrophytes with biomass never reaching the water surface (like *Vallisneria americana*; Titus and Adams 1979).

Senescence, resulting in decreasing photosynthetic activity in ageing plant parts, has been included into the model formulation. Since no data quantifying these effects in *Hydrilla* were available, data collected for another submersed macrophyte, *Ceratophyllum demersum* (Best and Dassen 1987), were used to calibrate the reduction factor accounting for ageing. Running the model demonstrated that virtually no effect on peak biomass was noticeable, probably largely due to the typical umbrella-type biomass distribution over the water column, with not only most biomass in the upper portion of the community but also most young plant parts.

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Appendix A
Model Listing

```
*-----------------------------------------------------------------------------*
* SUBROUTINE MODEL                                                            *
* Authors: Elly Best & Will Boyd                                              *
* Date  : 18 August 1995                                                      *
*                                                                             *
* FORMAL PARAMETERS:  (I=input,O=output,C=control,IN=init,T=time)             *
* name        type    meaning                                  units   class  *
* -------     ----    -----------                              -----   -----  *
* DELT        R4      Time step of integration                 d       I      *
* DOY         R4      Day number within year of simulation (REAL) d   I      *
* FILEIN      C*      Name of file with input model data       -       I      *
* FINTIM      R4      Finish time of simulation (=day number)  d       I      *
* IDOY        I4      Day number within year of simulation (INTEGER) d I      *
* ITASK       I4      Task that subroutine should perform      -       I      *
* IUNITD      I4      Unit of input file with model data       -       I      *
* IUNITO      I4      Unit of output file                      -       I      *
* IUNITL      I4      Unit number for log file messages        -       I      *
* IYEAR       I4      Year of simulation (INTEGER)             y       I      *
* LAT         R4      Latitude of site                         dec.degr. I    *
* LONG        R4      Longitude of site                        dec.degr. I    *
* ELEV        R4      Elevation of site                        m       I      *
* OUTPUT      L4      Flag to indicate if output should be done -      I      *
* RAIN        R4      Daily amount of rainfall                 mm.d-1  I      *
* RDD         R4      Daily shortwave radiation                J m-2 d-1I     *
* STTIME      R4      Start time of simulation (=day number)   d       I      *
* TERMNL      L4      Flag to indicate if simulation is to stop -      I/O    *
* TMMN        R4      Daily minimum temperature                degrees C I    *
* TMMX        R4      Daily maximum temperature                degrees C I    *
* VP          R4      Early morning vapour pressure            kPa     I      *
* WN          R4      Daily average windspeed                  m s-1   I      *
* WSTAT       C6      Status code from weather system          -       I      *
* WTRTER      L4      Flag whether weather can be used by model -      O      *
* YEAR        R4      Year of simulation (REAL)                y       I      *
*                                                                             *
* Fatal error checks    : if one of the characters of WSTAT = '4',            *
*                         indicates missing weather                           *
* Warnings              : none                                                *
* Subprograms called    : models as specified by the user                     *
* File usage            : IUNITD,IUNITD+1,IUNITO,IUNITO+1,IUNITL              *
*-----------------------------------------------------------------------------*
```

```
      SUBROUTINE MODEL (ITASK , IUNITD, IUNITO, IUNITL,
     &                  FILEIN,
     &                  OUTPUT, TERMNL,
     &                  DOY   , IDOY  , YEAR  , IYEAR,
     &                  TIME  , STTIME, FINTIM, DELT ,
     &                  LAT   , LONG  , ELEV  , WSTAT , WTRTER,
     &                  RDD   , TMMN  , TMMX  , VP    , WN, RAIN)

*-----Title of the program
*     <Fill in your title here>
*     HYDRIL

      IMPLICIT REAL (A-Z)

*-----Formal parameters

      INTEGER  ITASK , IUNITD, IUNITO, IUNITL, IDOY, IYEAR
      LOGICAL  OUTPUT, TERMNL, WTRTER
      CHARACTER*(*) FILEIN, WSTAT
      REAL DOY, YEAR, TIME, STTIME, FINTIM, DELT
      REAL LAT, RDD, TMMN, TMMX, VP, WN, RAIN
      REAL TMAX(365), TMIN(365)

*-----Standard local declarations
      INTEGER IWVAR,ITOLD,IDAY
      CHARACTER WUSED*6

*-----State variables, initial values and rates
      REAL DVS   , NUL   , DVR
      REAL TMPSUM
      REAL TWLVD , IWLVD , DLV
      REAL TWLVG , IWLVG , NGLV
      REAL TWSTD , IWSTD , DST
      REAL TWSTG , IWSTG , NGST
      REAL TWRTD , IWRTD , DRT
      REAL TWRTG , IWRTG , NGRT
      REAL TWSO  , IWSO  , GSO
      REAL TMP2  , INTUB , CKCFUN

*-----Model parameters
      REAL AMX   , ASRQSO, CVT   , DAYEM , REDAM
      REAL NPL   , Q10
      REAL RC    , TBASE , DEPTH , NT
      REAL ROC   , TL    , RCSHST, EE    , RDTU
      REAL NNTUB , NGTUB , NTUBD , NDTUB , RTR
      REAL TWGTUB, TWNTUB, NTUBPD, NINTUB, TWCTUB
      REAL HAR   , HARDAY, HARDEP

*-----Auxiliary variables
      REAL AMAX  , AMTMP , ASRQ  , COSLD , WTMP
      REAL DAVTMP, DAY   , DAYL  , YRNUM , WST
      REAL DDTMP , DS0   , DSINB , DSINBE
      REAL DTEFF , DTGA  , FGROS , FLV   , FRT
      REAL FRT1  , FRT2  , PI    , SUM
```

```
      REAL FSO   , FST   , GLV   , GPHOT , GRT
      REAL GST   , GTW   , MAINT , MAINTS, RDR
      REAL RDS   , REMOB , SC    , NTM   , TGWM
      REAL SINLD , TGW   , TEFF  , TRANS
      REAL TW    , WLV   , WRT

*-----AFGEN functions
*     REAL AMDVST
*     INTEGER IMAMDV, ILAMDV
*     PARAMETER (IMAMDV = 40)
*     DIMENSION AMDVST(IMAMDV)
      REAL AMTMPT
      INTEGER IMAMTM, ILAMTM
      PARAMETER (IMAMTM = 40)
      DIMENSION AMTMPT(IMAMTM)
      REAL FLT
      INTEGER IMFLT, ILFLT
      PARAMETER (IMFLT  = 40)
      DIMENSION FLT (IMFLT)
      REAL FLVT
      INTEGER IMFLVT, ILFLVT
      PARAMETER (IMFLVT = 40)
      DIMENSION FLVT (IMFLVT)
      REAL FRTT
      INTEGER IMFRTT, ILFRTT
      PARAMETER (IMFRTT = 40)
      DIMENSION FRTT (IMFRTT)
      REAL FSTT
      INTEGER IMFSTT, ILFSTT
      PARAMETER (IMFSTT = 40)
      DIMENSION FSTT (IMFSTT)
      REAL LT, KT
      INTEGER IMN1,ILT,IKT
      PARAMETER (IMN1   = 40)
      DIMENSION LT(IMN1), KT(IMN1)
      REAL NTMT, TGWMT
      INTEGER IMMEAS, ILMEAS
      PARAMETER (IMMEAS = 40)
      DIMENSION NTMT(IMMEAS), TGWMT(IMMEAS)
      REAL RDRT
      INTEGER IMRDRT, ILRDRT
      PARAMETER (IMRDRT = 40)
      DIMENSION RDRT  (IMRDRT)
      REAL RDST
      INTEGER IMRDST, ILRDST
      PARAMETER (IMRDST = 40)
      DIMENSION RDST  (IMRDST)
      REAL WTMPT
      INTEGER IMWTMP, ILWTMP
      PARAMETER (IMWTMP = 40)
      DIMENSION WTMPT (IMWTMP)
```

```
*-----Used functions
      REAL LINT  , INSW
      SAVE

      DATA ITOLD /4/
*-----Code for the use of RDD, TMMN, TMMX, VP, WN, RAIN  (in that order)
*     A letter 'U' indicates that the variable is used in calculations
      DATA WUSED/'UUU---'/

*-----Check weather data availability
      IF (ITASK.EQ.1.OR.ITASK.EQ.2.OR.ITASK.EQ.4) THEN
          DO 10 IWVAR=1,6
*-----Is there an error in the IWVAR-th weather variable ?
            IF (WUSED(IWVAR:IWVAR).EQ.'U' .AND.
     &         WSTAT(IWVAR:IWVAR).EQ.'4') THEN
                WTRTER = .TRUE.
                TERMNL = .TRUE.
                ITOLD  = ITASK
                RETURN
            END IF
10      CONTINUE
      END IF

      IF (ITASK.EQ.1) THEN
*
*               INITIALIZATION  SECTION
*              ============================
*-----Send title to output file

*-----Open input file
          CALL RDINIT (IUNITD, IUNITL, FILEIN)

*-----Read 1st value in MODEL.DAT file ... year number
          CALL RDSREA ('YRNUM ',YRNUM )

*-----Read initial states
          CALL RDSREA ('INTUB ',INTUB )
          CALL RDSREA ('IWLVD ',IWLVD )
          CALL RDSREA ('IWLVG ',IWLVG )
          CALL RDSREA ('IWRTD ',IWRTD )
          CALL RDSREA ('IWRTG ',IWRTG )
          CALL RDSREA ('IWSO  ',IWSO  )
          CALL RDSREA ('IWSTD ',IWSTD )
          CALL RDSREA ('IWSTG ',IWSTG )
          CALL RDSREA ('NUL   ',NUL   )
          CALL RDSREA ('REMOB ',REMOB )

*-----Read model parameters
          CALL RDSREA ('AMX   ',AMX   )
          CALL RDSREA ('ASRQSO',ASRQSO)
          CALL RDSREA ('CVT   ',CVT   )
          CALL RDSREA ('DAYEM ',DAYEM )
          CALL RDSREA ('DEPTH ',DEPTH )
          CALL RDSREA ('EE    ',EE    )
```

```
          CALL RDSREA ('HAR   ',HAR   )
          CALL RDSREA ('HARDAY',HARDAY)
          CALL RDSREA ('HARDEP',HARDEP)
          CALL RDSREA ('NINTUB',NINTUB)
          CALL RDSREA ('NPL   ',NPL   )
          If(YRNUM .EQ. 1.) CALL RDSREA ('NT    ',NT    )
          CALL RDSREA ('Q10   ',Q10   )
          CALL RDSREA ('RC    ',RC    )
          CALL RDSREA ('RCSHST',RCSHST)
          CALL RDSREA ('RDTU  ',RDTU  )
          CALL RDSREA ('REDAM ',REDAM )
          CALL RDSREA ('ROC   ',ROC   )
          CALL RDSREA ('RTR   ',RTR   )
          CALL RDSREA ('TBASE ',TBASE )
          CALL RDSREA ('TL    ',TL    )

*-----Read AFGEN functions
*       CALL RDAREA ('AMDVST',AMDVST,IMAMDV,ILAMDV)
          CALL RDAREA ('AMTMPT',AMTMPT,IMAMTM,ILAMTM)
          CALL RDAREA ('FLT   ',FLT   ,IMFLT ,ILFLT)
          CALL RDAREA ('FLVT  ',FLVT  ,IMFLVT,ILFLVT)
          CALL RDAREA ('FSTT  ',FSTT  ,IMFSTT,ILFSTT)
          CALL RDAREA ('FRTT  ',FRTT  ,IMFRTT,ILFRTT)
          CALL RDAREA ('KT    ',KT    ,IMN1  ,IKT   )
          CALL RDAREA ('LT    ',LT    ,IMN1  ,ILT   )
          CALL RDAREA ('NTMT  ',NTMT  ,IMMEAS,ILMEAS)
          CALL RDAREA ('RDRT  ',RDRT  ,IMRDRT,ILRDRT)
          CALL RDAREA ('RDST  ',RDST  ,IMRDST,ILRDST)
          CALL RDAREA ('TGWMT ',TGWMT ,IMMEAS,ILMEAS)
          CALL RDAREA ('WTMPT ',WTMPT ,IMWTMP,ILWTMP)

***             INITIAL CALCULATIONS          ***
*               ======================

*-----Initially known variables to output
*     Send title(s) to OUTCOM

*-----Initialize state variables
*     Start at the beginning of the developmental cycle
          DVS    = NUL
          TMPSUM = NUL

*-----Initialize weights of plant organs
          IF (YRNUM .EQ. 1.)THEN
          TWLVD  = IWLVD
          TWLVG  = IWLVG
          TWSTD  = IWSTD
          TWSTG  = IWSTG
          TWRTD  = IWRTD
          TWRTG  = IWRTG
          TWSO   = IWSO
          ENDIF
```

```
*-----Initialize tuber numbers and weight
          NNTUB  = 0.0
          IF (NT .LT. 35.)NPL = NT
          NGTUB  = NPL
          IF (YRNUM.EQ.1.)NTUBD  = RDTU * (NT-NGTUB) * TEFF
          NDTUB  = NT - (NGTUB+NTUBD)
          TWGTUB = NPL * INTUB
          TWNTUB = 0.0

      ELSE IF (ITASK.EQ.2) THEN

***               RATES OF CHANGE                ***
*               ================

*-----Weights of plant organs
          WLV   = TWLVG + TWLVD
          WST   = TWSTG + TWSTD
          WRT   = TWRTG + TWRTD
          TGW   = (TWLVG + TWSTG + TWRTG) / 0.86

*-----Total live weight never >900 g DW / m2
          TGW   = AMIN1 (TGW, 900.)

          TWSO  = TGW - (TWLVG + TWSTG + TWRTG)

***               RATE CALCULATIONS              ***
*               ====================

*-----Julian day number
          DAY = 1.+MOD (TIME-1.,365.)

*-----If water temperatures are available, temperature
*     dependent processes are related to water temperature;
*     otherwise they are related to air temperature with a
*     lag period of 7 days
          WTMP = LINT (WTMPT,ILWTMP,DAY)
          IDAY = DAY

          TMAX(IDAY) = TMMX
          TMIN(IDAY) = TMMN
      IF (DAY .LE. 7.0) THEN
          DAVTMP = 0.5 * (TMAX(1)+TMIN(1))
          DDTMP  = TMAX(1) - 0.25 * (TMAX(1)-TMIN(1))
      ELSE
          DAVTMP = 0.5 * (TMAX(IDAY-7)+TMIN(IDAY-7))
          DDTMP  = TMAX(IDAY-7) - 0.25 * (TMAX(IDAY-7)-TMIN(IDAY-7))
      ENDIF

          IF (WTMP .GT. 0.0) THEN
          DAVTMP = WTMP
          DDTMP  = WTMP
          ENDIF

          TEFF   = Q10**((DAVTMP-20.)/10.)
```

```
*-----Relative tuber growth rate
        RTRL  = RTR * TEFF

*-----Measured tuber numbers and measured total live plant dry weight
        NTM  = LINT (NTMT,ILMEAS,DAY)
        TGWM = LINT (TGWMT,ILMEAS,DAY)

*-----SBRT ASTRO call to introduce day length into MAIN
    CALL ASTRO
   $ (DAY,LAT,SC,DS0,SINLD,COSLD,DAYL,DSINB,DSINBE)

*------Tuber behaviour; carbohydrate remobilization for plant
*     formation from germinating tubers at proper day length
*     and temperature conditions; carbohydrate translocation
*     from plants to form new tubers provided plants are present

    TWTUB = (NT - (NGTUB+NTUBD)) * INTUB + TWNTUB
    IF (TWTUB .LE. 0.0)TWTUB = 0.00001

    IF (TWTUB .EQ. 0 .AND. DAY .EQ. 1)THEN
    WRITE(*,*)' There are no tubers !! -- Press <ENTER> '
    READ(*,*)
    STOP
    ENDIF
    IF (DVS .GE. .326) THEN
          TWGTUB = INTGRL (TWGTUB,- REMOB,DELT)
          TWGTUB = AMAX1(0.0,TWGTUB)
          REMOB  = TWGTUB * ROC * DTEFF

          IF (TWGTUB .EQ. 0.0) NGTUB = 0.0

    ELSE
          REMOB = 0.0
    ENDIF

         If (REMOB .EQ. 0.0) THEN
          If (DVS .GT. 1.0 .AND. DAYL .LT. 13.0)THEN
           If (DDTMP .GT. 14.0 .AND. DDTMP .LT. 33.0)THEN
*-----Set the new tuber number ... and total dry weight of the
*    new tubers
              If (NNTUB .EQ. 0. .AND. TGW .GT. 0.1) THEN
                  NNTUB  = NPL * NINTUB
                  TWCTUB = NNTUB * 0.08
                  TWNTUB = 0.0
*-----Otherwise, integrate to find weight of new tubers
              Else IF (TGW .GT. 0.1) THEN
                  TWNTUB = INTGRL (TWNTUB, RTRL, DELT)
              Endif

                  IF (TWNTUB .GE. TWCTUB .OR. TGW .LT. 0.1) THEN
                  IF (TWNTUB .GE. TWCTUB) THEN
*-----Add new tubers to the total number of dormant tubers
                  NDTUB = NDTUB + NNTUB
```

```
*-----Calculate a new value for dead tubers based on new tubers
*    added above
                NTUBD = NTUBD + (RDTU * NNTUB)
*-----Reset new tuber number and weight back to zero
                NNTUB  = 0.0
                TWNTUB = 0.0
                ENDIF
              ENDIF
              TRANS = RTRL * CVT
            ELSE
            TRANS = 0.0
            ENDIF
          ELSE
          TRANS = 0.0
          ENDIF
        ELSE
        TRANS = 0.0
        ENDIF

*-----Recalculate tuber numbers daily
        IF (DAY .GT. 1.0) THEN

*-----NNTUB not added because they were included in NDTUB when
*    reaching the total critical dry weight of new tubers TWCTUB
          NT = NDTUB + NGTUB - NTUBD
          NT = AMAX1 (0.0001,NT)
          NDTUB = NT - NGTUB
          ENDIF

*-----Dry matter and its partitioning over the plant organs
          TW  = TGW + (TWLVD + TWSTD + TWRTD)

          FLV = LINT(FLVT ,ILFLVT,DVS)
          FST = LINT(FSTT ,ILFSTT,DVS)
          FRT = LINT(FRTT ,ILFRTT,DVS)
          FL  = LINT(FLT  ,ILFLT ,DVS)
          FSO = 0.14*(FLV + FST + FRT)

*-----Growth of plant organs, maintenance respiration and translocation
          ASRQ = 1.46*FLV+1.51*FST+1.44*FRT+ ASRQSO*FSO
          MAINTS = 0.016*TWLVG+0.01*TWSTG+0.015*TWRTG+0.01*TWSO
          MAINT  = MAINTS * TEFF
          GTW = (.67*REMOB + GPHOT - TRANS - MAINT) / ASRQ
          GRT = FRT * GTW
          GST = FST * GTW
          GSO = FSO * GTW
          GLV = FLV * GTW

*-----Relative death rates
          RDR  = INSW (DVS-2.2,0.,LINT (RDRT,ILRDRT,DAVTMP))
          RDS  = INSW (DVS-2.2,0.,LINT (RDST,ILRDST,DAVTMP))
```

```
*-----Development rates
      IF(DAVTMP .LT. 3.0) THEN
           DVR = 0.0
      ELSE IF (DVS.LE.1.) THEN
           DVR = 0.012*DAVTMP/30
      ELSE IF (DVS.LE.4.0) THEN
           DVR = 0.012*DAVTMP/30
      ENDIF

*-----Calculation of astronomic daylength
      CALL ASTRO
     $ (DAY,LAT,SC,DS0,SINLD,COSLD,DAYL,DSINB,DSINBE)

*-----Temperature sum after 1.january
           DTEFF = AMAX1(0.,DAVTMP-TBASE)
           DLV   = TWLVG * RDR
           DST   = TWSTG * RDR
           DRT   = TWRTG * RDR

*-----Shoot photosynthesis at light saturation and daytime
*     temperature effect on shoot photosynthesis
           AMAX  = AMAX1(0.00001,AMX * AMTMP)
           AMAX  = AMAX * REDAM
           AMTMP = LINT(AMTMPT,ILAMTM,DDTMP)

*-----Before calling TOTASS, determine light extinction
*     coefficients of plants (K) and of water (L)
      L = LINT(LT,ILT,TIME)
      K = LINT(KT,IKT,DVS)

*-----Daily total gross assimilation

           CALL TOTASS
     $   (SC,DAYL,SINLD,COSLD,DSINBE,RDD,RC,L,K,AMAX,EE,
     $   TL,DEPTH,RCSHST,TGW,FGROS,FL,FLV,FST,FSO,WLV,WST,
     $   DAY,HAR,HARDAY,HARDEP,DTGA)

*-----If harvesting takes place, weights various plant organs must be
*     recalculated (TWSO,TWLVG,TWSTG,TWRTG,TW)
          IF(HAR .EQ. 1. AND. DAY .EQ. HARDAY) THEN
            TWSO  = 0.14 * TGW
            TWLVG = FLV * (TGW - TWSO)
            TWSTG  = FST * (TGW - TWSO)
            TWRTG = FRT * (TGW - TWSO)
            TW    = TGW + (TWLVD + TWSTD + TWRTD)
          ENDIF

*-----Conversion assimilated CO2 to CH2O
           GPHOT = DTGA * 30./44.
```

```
*-----Total and net growth rates
        GTW = (0.67*REMOB + GPHOT - TRANS - MAINT) / ASRQ
        GRT = FRT * GTW
        GST = FST * GTW
        GSO = FSO * GTW
        GLV = FLV * GTW

        NGLV = GLV - DLV
        NGST = GST - DST
        NGRT = GRT - DRT

*-----Finish conditions
        IF (DVS.GT.4.0 .OR. DAY .EQ. 365.) TERMNL = .TRUE.

*-----Output section
        IF (OUTPUT) THEN
          CALL OUTDAT (2,0,'DAVTMP',DAVTMP)
          CALL OUTDAT (2,0,'DAVL  ',DAVL  )
          CALL OUTDAT (2,0,'DDTMP ',DDTMP )
          CALL OUTDAT (2,0,'DVS   ',DVS   )
          CALL OUTDAT (2,0,'FGROS ',FGROS )
          CALL OUTDAT (2,0,'NDTUB ',NDTUB )
          CALL OUTDAT (2,0,'NGTUB ',NGTUB )
          CALL OUTDAT (2,0,'NNTUB ',NNTUB )
          CALL OUTDAT (2,0,'NT    ',NT    )
          CALL OUTDAT (2,0,'NTUBD ',NTUBD )
          CALL OUTDAT (2,0,'REMOB ',REMOB )
          CALL OUTDAT (2,0,'TGW   ',TGW   )
          CALL OUTDAT (2,0,'TGWM  ',TGWM  )
          CALL OUTDAT (2,0,'TRANS ',TRANS )
          CALL OUTDAT (2,0,'TW    ',TW    )
          CALL OUTDAT (2,0,'TWLVD ',TWLVD )
          CALL OUTDAT (2,0,'TWLVG ',TWLVG )
          CALL OUTDAT (2,0,'TWNTUB',TWNTUB)
          CALL OUTDAT (2,0,'TWRTG ',TWRTG )
          CALL OUTDAT (2,0,'TWSO  ',TWSO  )
          CALL OUTDAT (2,0,'TWSTD ',TWSTD )
          CALL OUTDAT (2,0,'TWSTG ',TWSTG )
          CALL OUTDAT (2,0,'TWTUB ',TWTUB )
        END IF

    ELSE IF (ITASK.EQ.3) THEN

*           INTEGRATION
*           =============
        DVS    = INTGRL (DVS   ,DVR   ,DELT)
        TMPSUM = INTGRL (TMPSUM,DTEFF ,DELT)
        TWLVD  = INTGRL (TWLVD ,DLV   ,DELT)
        TWLVG  = INTGRL (TWLVG ,NGLV  ,DELT)
        TWLVG  = AMAX1 (0.0, TWLVG)
        TWSTD  = INTGRL (TWSTD ,DST   ,DELT)
        TWSTG  = INTGRL (TWSTG ,NGST  ,DELT)
        TWSTG  = AMAX1 (0.0, TWSTG)
        WTRTD  = INTGRL (TWRTD  ,DRT   ,DELT)
```

```
            TWRTG  = INTGRL (TWRTG ,NGRT  ,DELT)
            TWRTG  = AMAX1 (0.0, TWRTG)
            NTUBPD = NTUBD
            NTUBD  = INTGRL (NTUBD, RDTU  ,DELT)
            NTUBD  = NTUBD - NTUBPD

        ELSE IF (ITASK.EQ.4) THEN

*               TERMINAL SECTION
*               ================

*-----Terminal calculations

*-----Terminal output

        CLOSE (IUNITD)

        END IF

        ITOLD = ITASK

        RETURN
        END
```

```
**********************************************************************************************
***                    3.1 ASTRO                                                           ***
*----------------------------------------------------------------------------------------------*
* SUBROUTINE ASTRO                                                                            *
* Authors: Daniel van Kraalingen                                                              *
* Date   : 9 August 1987                                                                      *
* Modified by Jan Goudriaan 4 Febr 1988                                                       *
* Modified by Jan Goudriaan and Kees Spitters 7 December 1989                                 *
* Purpose: This subroutine calculates astronomic daylength and photoperiodic daylength.      *
*          and diurnal radiation characteristics such as daily integral of sine of solar      *
*          elevation, solar constant. Measured daily total of global radiation is used to find*
*          atmospheric transmissivity and fraction diffuse radiation.                         *
* FORMAL PARAMETERS:  (I=input,O=output,C=control,IN=init,T=time)                              *
* name       meaning                                          units     class                 *
* -------    -----------                                      -------   -------               *
* DAY        Day number (Jan 1st = 1)                         -           I                   *
* LAT        Latitude of the site                             degrees     I                   *
* DTR        Measured daily total global radiation            J m-2 d-1   I                   *
* SC         Solar constant                                   J m-2 s-1   O                   *
* DS0        Daily extraterrestrial radiation                 J m-2 d-1   O                   *
* SINLD      Seasonal offset of sine of solar height          -           O                   *
* COSLD      Amplitude of sine of solar height                -           O                   *
* DAYL       Astronomical daylength (base = 0 degrees)        h           O                   *
* DSINB      Daily total of sine of solar height              s           O                   *
* DSINBE     Daily total of effective solar height            s           O                   *
*                                                                                             *
* FATAL ERROR CHECKS (execution terminated, message)                                          *
* condition                                                                                   *
*                                                                                             *
* LAT > 67, LAT < -67                                                                         *
*                                                                                             *
* SUBROUTINES and FUNCTIONS called : none                                                     *
*                                                                                             *
* FILE usage : none                                                                           *
*----------------------------------------------------------------------------------------------*

      SUBROUTINE ASTRO (DAY,LAT,SC,DS0,SINLD,COSLD,
     $                  DAYL,DSINB,DSINBE)
      IMPLICIT REAL (A-Z)

*-----PI and conversion factor from degrees to radians
      PARAMETER (PI=3.141592654, RAD=0.017453292)

*-----Check on input range of parameters
      IF (LAT.GT.67.)  STOP 'ERROR IN ASTRO: LAT > 67'
      IF (LAT.LT.-67.) STOP 'ERROR IN ASTRO: LAT <-67'

*-----Declination of the sun as function of daynumber (DAY)
      DEC = -ASIN(SIN(23.45*RAD)*COS(2.*PI*(DAY+10.)/365.))

*-----SINLD, COSLD and AOB are intermediate variables
      SINLD = SIN(RAD*LAT)*SIN(DEC)
      COSLD = COS(RAD*LAT)*COS(DEC)
      AOB   = SINLD/COSLD
```

```
*-----Daylength (DAYL)
      DAYL  = 12.0*(1.+2.*ASIN(AOB)/PI)

      DSINB = 3600.*(DAYL*SINLD+24.*COSLD*SQRT(1.-AOB*AOB)/PI)
      DSINBE= 3600.*(DAYL*(SINLD+0.4*(SINLD*SINLD+COSLD*COSLD*0.5))+
     $      12.0*COSLD*(2.0+3.0*0.4*SINLD)*SQRT(1.-AOB*AOB)/PI)

*-----Solar constant (SC) and daily extraterrestrial (DS0)
      SC  = 1370.*(1.+0.033*COS(2.*PI*DAY/365.))
      DS0 = SC*DSINB
      RETURN
      END
```

```
*** 3.2 TOTASS ***
*-----------------------------------------------------------------------------*
* SUBROUTINE TOTASS                                                           *
* Authors: Daniel van Kraalingen                                              *
* Date  : 1 December 1987                                                     *
* Modified by Jan Goudriaan 5-Febr-1988                                       *
* Modified by Jan Goudriaan and Kees Spitters 7 December 1989                 *
* Units modified by Elly Best & Will Boyd 28 July 1995                        *
* Purpose: This subroutine calculates daily total gross assimilation (DTGA) by performing*
*       a Gaussian integration over time. At three different times of the day, radiation is *
*       computed and used to determine assimilation whereafter integration takes place. *
*       (Source: Post-graduate Course 'Simulation of plant growth and crop production. *
*       Pontignano, Siena, Italy;3-12 November, 1992. Dept. Theor. Production Ecol. *
*       (TPE-WAU), Wageningen Agricultural University, and DLO-Centre for *
*       Agrobiological Research (CABO-DLO).)                                  *
*                                                                             *
* FORMAL PARAMETERS:  (I=input,O=output,C=control,IN=init,T=time)             *
* name      meaning                                          units     class  *
* -------   -----------                                      -------   ------ *
* SC        Solar constant                                   J m-2 s-1 I      *
* DAYL      Day length (base = 0 degrees)                    h         I      *
* SINLD     Intermediate variable in calculating solar  declination  -         I      *
* COSLD     Intermediate value in calculating solar height   -         I      *
* DSINBE    Daily total of effective solar height            s         I      *
* DTR       Measured daily total of global radiation         J m-2 d-1 I      *
* RC        Reflection coefficient of irradiation at water surface  -         I      *
*           (relative)                                                        *
* L         Water type specific light extinction coefficient -         I      *
* K         Plant species specific light extinction coefficient  -         I      *
* AMAX      Assimilation rate at light saturation for  g CO2 g DW-1 h-1 I      *
*           individual shoots                                                 *
* EE        Initial light use efficiency for individual shoots  g CO2 J-1  I      *
* TL        Thickness per plant layer                        m         I      *
* DEPTH     Water depth                                      m         I      *
* RCHSHST   Relation coefficient tuber weight-stem length    m g DW-1  I      *
* TGW       Total live plant dry weight                      g DW m-2  I      *
* FGROS     Instantaneous assimilation rate of whole  g CO2 m-1 soil h-1 O      *
*           canopy                                                            *
* FL        Leaf dry matter allocation to each layer of plant  -         I      *
* FLV       Fraction of total dry matter increase all. to leaves  -         I      *
* FST       Fraction of total dry matter increase all. to stems  -         I      *
* FSO       Fraction of total dry matter increase            -         I      *
*           allocated to storage compound                                     *
* WLV       Dry weight of leaves                             g DW m-2  I      *
* WST       Dry weight of stems                              g DW m-2  I      *
* HAR       Harvesting                                       -         I      *
* HARDAY    Harvesting day number                            d         I      *
* HARDEP    Harvesting depth                                 m         I      *
* DTGA      Daily total gross assimilation                   g CO2 m-2 d-1 O      *
*                                                                             *
* SUBROUTINES and FUNCTIONS called : ASSIM                                    *
* FILE usage : none                                                           *
*-----------------------------------------------------------------------------*
```

```
      SUBROUTINE TOTASS (SC,DAYL,SINLD,COSLD,DSINBE,DTR,RC,L,K,
     $            AMAX,EE,TL,DEPTH,RCSHST,TGW,FGROS,FL,
     $            FLV,FST,FSO,WLV,WST,DAY,HAR,HARDAY,
     $            HARDEP,DTGA)

      IMPLICIT REAL(A-Z)
      REAL XGAUSS(3), WGAUSS(3)
      INTEGER II, IGAUSS

      PARAMETER (PI=3.141592654)

      DATA IGAUSS /3/
      DATA XGAUSS /0.1127, 0.5000, 0.8873/
      DATA WGAUSS /0.2778, 0.4444, 0.2778/

*-----Assimilation set to zero & three different times of the day (HOUR)
      DTGA = 0.
      DO 10 II=1,IGAUSS

*-----At the specified HOUR, radiation is computed and used to compute
*     assimilation
      HOUR = 12.0+DAYL*0.5*XGAUSS(II)

*-----Sine of solar elevation
      SINB  = AMAX1(0.,SINLD+COSLD*COS(2.*PI*(HOUR+12.)/24.))

*-----Diffuse light fraction (FRDIF) from atmospheric transmission
*     (ATMTR)
      PAR   = 0.5*DTR*SINB*(1.+0.4*SINB)/DSINBE
      ATMTR  = PAR/(0.5*SC*SINB)
      FRDIF  = 1.47-1.66*ATMTR
      IF (ATMTR.LE.0.35.AND.ATMTR.GT.0.22) FRDIF=1.-6.4*(ATMTR-0.22)**2
      IF (ATMTR.LE.0.22) FRDIF=1.
      FRDIF  = AMAX1(FRDIF,0.15+0.85*(1.-EXP(-0.1/SINB)))
*-----Diffuse PAR (PARDIF) and direct PAR (PARDIR)
      PAR   = 0.5*DTR*SINB*(1.+0.4*SINB)/DSINBE
      PARDIF =  MIN (PAR,SINB*FRDIF*ATMTR*0.5*SC)
      PARDIR = PAR-PARDIF

      CALL ASSIM
     $ (PARDIR,PARDIF,RC,L,K,AMAX,EE,TL,DEPTH,RCSHST,TGW,
     $ FL,FLV,FST,FSO,WLV,WST,DAY,HAR,HARDAY,HARDEP,II,FGROS)

*-----Integration of assimilation rate to a daily total (DTGA)
      DTGA = DTGA+FGROS*WGAUSS(II)
10    CONTINUE

      DTGA = DTGA*DAYL

      RETURN
      END
```

```
*******************************************************************************
***                    3.3 ASSIM                                            ***
*-----------------------------------------------------------------------------*
*                                                                             *
* Authors: Elly Best & Will Boyd                                              *
* Date   : 28 July 1995                                                       *
* Purpose: This subroutine performs a instantaneous calculation of light profile in the *
*          water column, light absorbed by the available for photosynthesis, and assimilation*
*          at all these depth layers. The depth-integrated variable is FGROS. *
*          At harvesting, the plant material is removed per depth layer from the existing *
*          biomass                                                            *
*                                                                             *
* FORMAL PARAMETERS:  (I=input,O=output,C=control,IN=init,T=time)             *
* name        meaning                                          units    class *
* -------     -----------                                      -------  ------- *
* PARDIR      Instantaneous flux of direct radiation (PAR)     W m-2    I     *
* PARDIF      Instantaneous flux of diffuse radiation(PAR)     W m-2    I     *
* RC          Reflection coefficient of irradiation at                       *
*             water surface (relative)                         -        I     *
* L           Water type specific light extinction coefficient m-1      I     *
* K           Plant species specific light extinction coefficient m2 g-1DWI  *
* AMAX        Assimilation rate at light saturation for        g CO2    I     *
*              individual shoots                               g DW-1 h-1     *
* EE          Initial light use efficiency for individual shoots g CO2 J-1 I  *
* TL          Thickness per plant layer                        m        I     *
* DEPTH       Water depth                                      m        I     *
* RCHSHST     Relation coefficient tuber weight-stem length    m g-1DW  I     *
* TGW         Total live plant dry weight                      g DW m-2 I     *
* FL          Leaf dry matter allocation to each layer of  plant -      I     *
* FLV         Fraction of total dry matter increase            -        I     *
*             allocated to leaves                                            *
* FST         Fraction of total dry matter increase            -        I     *
*             allocated to stems                                             *
* FSO         Fraction of total dry matter increase            -        I     *
*             allocated to storage compound                                  *
* WLV         Dry weight of leaves                             g DW m-2 I     *
* WST         Dry weight of stems                              g DW m-2 I     *
* HAR         Harvesting                                       -        I     *
* HARDAY      Harvesting day number                            d        I     *
* HARDEP      Harvesting depth                                 m        I     *
* II          Counter in DO LOOP, indicates 1 of 3 times       -        I     *
*             per day (HOUR)                                                 *
* FGROS       Instantaneous assimilation rate of the plant     g CO2 m-2 h-1O *
*                                                                             *
* SUBROUTINES called : none                                                   *
* FUNCTIONS called : AFGEN                                                    *
*                                                                             *
* FILE usage : none                                                           *
*-----------------------------------------------------------------------------*

      SUBROUTINE ASSIM (PARDIR,PARDIF,RC,L,K,AMAX,EE,TL,
     $                  DEPTH,RCSHST,TGW,FL,FLV,FST,FSO,
     $                  WLV,WST,DAY,HAR,HARDAY,HARDEP,II,
     $                  FGROS)
```

```
      IMPLICIT REAL(A-Z)
      REAL DMPC(6), SC(100), IRZ(100) , IABS(100), IABSL(100)
      REAL HIG(100), AH(100), REDF(100), SumZ
      INTEGER IMN1, IRED, I, LOOP, Layers, LBelow, ILAY, II
      PARAMETER (IMN1   = 40)
      REAL REDFT(IMN1), DMPCT(IMN1)

*-----Read AFGEN functions
      CALL RDAREA ('REDFT ',REDFT ,IMN1  ,IRED  )
      CALL RDAREA ('DMPCT ',DMPCT, IMN1  ,ILAY  )

*-----Irradiation just beneath the water surface
      IRS = PARDIR + PARDIF
      IRZ(1) = IRS * (1.0 - RC)

*-----Canopy assimilation is set to zero
      FGROS = 0.

*-----Calculate stem length
      STEMLE = AMIN1(Depth+.0995, (RCSHST*(WLV+WST)))

      IF (STEMLE .GT. Depth+.08)THEN

*-----Determine total number of layers in the given water depth
      LOOP = INT (Depth/TL + 0.1) + 1

*-----Water depth must be greater than 0.8m to use this distribution
*     method; otherwise, go to ELSE which will distribute biomass equally
      IF (LOOP .GT. 9) THEN

*-----Distribute 80% of total plant biomass in 1st 6 layers
      DO 10 I = 1,6
      VAL = REAL (I)
      DMPC(I) = LINT (DMPCT,ILAY,VAL)
      SC(I) = TGW * DMPC(I)
   10 CONTINUE

*-----Distribute 14% of biomass in the lower layers (excluding last layer)
*     with biomass gradually decreasing toward the bottom
*     LOOP (integer) .. Number of 0.1m water layers
*     LAYERS (integer) .. Layers remaining after initial 6
*-----SUMZ (real) .. Summation of layers 7 through LOOP
*-----LBELOW (integer) .. Layer number going from bottom to top

*-----7 Is the 1st 6 layers + the bottom 1 layer (roots)
      LAYERS = LOOP - 7
      SUMZ = (LAYERS/2.0) * (LAYERS+1.0)

      DO 20 I = 7,LOOP-1
      LBELOW = LAYERS - (I-6) + 1.0
      SC(I) = (LBELOW/SUMZ) * (TGW * 0.14)
   20 CONTINUE
```

```
      ELSE

*-----If water depth is 0.8m or less, plant biomass is distributed
*     evenly over the existing layers
      DO 22 I = 1,LOOP-1
      SC(I) = TGW * (.94/(LOOP-1))
   22 CONTINUE

      ENDIF

*-----Distribute 6% of biomass in the last layer (roots)
      SC(LOOP) = TGW * 0.06

*-----Harvesting
      IF (HAR .EQ. 1. .AND. DAY .EQ. HARDAY)THEN
      IF (HARDEP .GT. DEPTH) HARDEP = DEPTH
      DO 25 I = 1,HARDEP/.1
      SC(I) = 0.0
   25 CONTINUE

*-----Reset total live weight (TGW) to zero
      IF(II .EQ. 1)TGW = 0.0
      ENDIF

      DO 50 I = 1,LOOP

*-----Total irradiation on top of stratum I
      IRZ(I+1) = IRZ(I) * EXP(-0.1* L - K* SC(I))
      IF(SC(I) .EQ. 0.0) GOTO 30

*-----Radiation absorbed by macrophyte community
      IABS(I) = (IRZ(I)-IRZ(I+1))*SC(I)*K/(K*SC(I)+0.1*L)

*-----Radiation absorbed by leaves, excluding bottom layer
      IF(I .LT. LOOP) IABSL(I) = IABS(I) * FL
      IF(IABSL(I) .EQ. 0.0)GOTO 30

*-----Height on top of stratum I measured from the water surface
      HIG(I) = TL * (LOOP - I)

*-----Absolute height of vegetation on top of stratum I, measured
*     from the top of the plant
      AH(I) = STEMLE - HIG(I)

*-----Reduction factor over the vertical of the vegetation
      REDF(I) = LINT(REDFT,IRED,AH(I))

*-----Instantaneous CO2 assimilation rate per depth layer
      FGL = SC(I)*AMAX*REDF(I)*(1.-EXP(-EE*IABSL(I)*3600. /
     $ (AMAX*REDF(I)*SC(I))))
      GOTO 40
   30 FGL = 0.0
   40 FGROS = FGROS + FGL
```

```
*-----If plants are harvested, live plant weight is recalculated
      IF (HAR.EQ.1 .AND. DAY.EQ.HARDAY .AND. II.EQ.1) THEN
      TGW = TGW + SC(I)
      ENDIF
   50 CONTINUE
      ENDIF

      RETURN
      END
```

```
* MODEL DAT file
* contains:      - Initial constants as far as specified with INCON statements,
*                - Model parameters,
*                - AFGEN functions,
*                - A SCALE array in case of a general translation
*
* File: HYDRIL.FOR
*
* Initial constants
* -----------------
INTUB      = 0.1
IWLVD      = 0.
IWLVG      = 0.
IWRTD      = 0.
IWRTG      = 0.
IWSO       = 0.
IWSTD      = 0.
IWSTG      = 0.
NUL        = 0.
REMOB      = 0.

* Model parameters
* ------------------------
YRNUM      = 1.
AMX        = 0.0158
ASRQSO     = 1.41
CVT        = 1.1
DAYEM      = 1.
DEPTH      = 1.0
EE         = 0.000011
HAR        = 0.
HARDAY     = 212.
HARDEP     = 0.8
NINTUB     = 7.0
NPL        = 25.
NT         = 500.
Q10        = 2.
RC         = .06
RCSHST     = 12.0
RDTU       = 0.36
REDAM      = 0.581
ROC        = 0.0576
RTR        = .4
TBASE      = 3.
TL         = 0.1
```

```
* AFGEN functions
* -------------------------
* AMDVST      = 0.001, 1., 3.5, 1., 4.0, 1.
 AMTMPT      = -30., 0.00001, 0., 0.00001, 16.,0.53, 20., 0.97, 24.,1.,
                 32., 0.94, 45., 0.86, 50., 0.00001
* DVRT        = -15., 0., 0., 0., 30.,0.012
 FLVT        = 0., 0.34, 5.0, 0.34
 FSTT        = 0., 0.60, 5.0, 0.60
 FRTT        = 0., 0.06, 5.0, 0.06
 FLT         = 0., 0.36, 5.0, 0.36
 KT          = 0., 0.01, 5.0, 0.01
 LT          = 0., .83, 365., .83
 RDRT        = 0., 0.033, 50., 0.033
 RDST        = 0., 0.033, 50., 0.033
 REDFT       = 0.0, 1.0, 5.0, 1.0
 DMPCT       = 1.0, .21, 2.0, .21, 3.0, .10, 4.0, .10, 5.0, .09, 6.0, .09
 WTMPT       = 1., 0.0, 46., 0.0, 135., 0.0, 227., 0.0, 319., 0.0, 365., 0.0
 NTMT        = 1., 330., 46., 330., 135., 128., 227., 128., 319., 362., 365., 120.
 TGWMT  = 1., 154., 46., 380., 135., 495., 227., 239.2, 319., 112.1, 365., 154.
```

```
* TIMER file contains:
*       - The used DRIVER and TRACE in case of GENERAL translation
*       - The TIMER variables used in both translation modes
*       - Additional TIMER variables in case of GENERAL translation
*       - The WEATHER control variables if weather data are used
*       - Miscellaneous FSE variables in case of FSE translation
*
* File: HYDRIL.FOR
*
* TIMER variables used in GENERAL and FSE translation modes
* ------------------------------------------------------------------------------
 STTIME      = 1.        ! start time
 FINTIM      = 365.      ! finish time
 DELT        = 1.        ! time step (for Runge-Kutta first guess)
 PRDEL       = 1.        ! output time step
 IPFORM      = 4         ! code for output table format:
                         ! 4 = spaces between columns
                         ! 5 = TAB's between columns (spreadsheet output)
                         ! 6 = two column output

       ! The string array PRSEL contains the output variables for which formatted tables
       ! have to be made. One or more times there is a series of variable names terminated
       ! by the word <TABLE>.The translator writes the variables in each PRINT statement
       ! to PRSEL =   ! a separate table.
* 'DAVTMP',
* 'DAYL  ',
* 'DDTMP ',
* 'DVS   ',
* 'FGROS ',
* 'NDTUB ',
* 'NGTUB ',
* 'NNTUB ',
  'NT    ',
* 'NTUBD ',
* 'REMOB ',
  'TGW   ',
* 'TGWM  ',
* 'TRANS ',
  'TW    ',
* 'TWLVD ',
  'TWLVG ',
* 'TWNTUB',
  'TWRTG ',
  'TWSO  ',
* 'TWSTD ',
  'TWSTG ',
  'TWTUB ',
       '<TABLE>'
 COPINF = 'N'            ! Switch variable whether to copy the input files
                         ! to the output file ('N' = do not copy, 'Y' = copy)
 DELTMP = 'N'            ! Switch variable what should be done with the
                         ! temporary output file ('N' = do not delete, 'Y' = delete)
 IFLAG  = 1101           ! Indicates where weather error and warnings
                         ! go (1101 means errors and warnings to log
```

```
                                ! file, errors to screen, see FSE manual)
*IOBSD = 1991,182               ! List of observation data for which output is
                                ! required. The list should consist of pairs
                                ! <year>,<day> combination

* WEATHER control variables
* ----------------------------------------
WTRDIR      = 'C:\SYS\WEATHER\'
CNTR        = 'USA'             ! Country code
ISTN        = 1                 ! Station code
IYEAR       = 1980              ! Year
```

```
* CONTROL data file contains:
*        - File names to be used by FSE 2.1
*        - The input files (except FILEIR) may used in reruns; up to five input
*          data files may be used (FILEI1-5)

  FILEON      = 'RES.DAT'        ! Normal output file
  FILEOL      = 'MODEL.LOG'      ! Log file
  FILEIR      = 'RERUNS.DAT'     ! Reruns file
  FILEIT      = 'TIMER.DAT'      ! File with timer data
  FILEI1      = 'MODEL.DAT'      ! First input data file

* FILEI2      = ' '              ! Second input data file (not used)
* FILEI3      = ' '              ! Third input data file (not used)
* FILEI4      = ' '              ! Fourth input data file (not used)
* FILEI5      = ' '              ! Fifth input data file (not used)
```

```
* RERUNS file contains information to produce multiple runs .
* File: HYDRIL.FOR
*
* RERUNS variables used in GENERAL and FSE translation modes
* ------------------------------------------------------------------------------
* YRNUM      = 2.
* HAR        = 1.
* HARDAY     = 74.
* HARDEP     = 1.0
* YRNUM      = 3.
* HAR        = 1.
* HARDAY     = 74.
* HARDEP     = 1.0
```

Appendix B
Variable Listing

Abbreviation	Explanation	Dimension
AH(i)	Absolute height of vegetation on top of stratum I, measured from the plant top	m
AMAX	Actual CO_2 assimilation rate at light saturation for individual shoots	$gCO_2.gDW^{-1}.hr^{-1}$
AMTMP	Daytime temperature effect on AMX (relative)	-
AMTMPT	Table of AMX as function of DVS	-, -
AMX	Potential CO_2 assimilation rate at light saturation for shoot tips	$gCO_2.gDW^{-1}.hr^{-1}$
ASRQ	Assimilate requirement for plant dry matter production	g CH_2O.g DW^{-1}
ASRQSO	Assimilate requirement for storage component production	gCH_2O.g DW^{-1} stor.organ
ATMTR	Atmospheric transmission coefficient	-
COSLD	Intermediate variable in calculating solar height	-
CVT	Conversion factor of translocated dry matter into CH_2O	-
DAVTMP	Daily average temperature	°C
DAY	Day number (January 1=1)	day
DAYEM	First Julian daynumber	day
DAYL	Daylength	hr
DDTMP	Daily average daytime temperature	°C
DEC	Declination of the sun	radians
DEPTH	Water depth	m
DLV	Death rate of leaves	g DW. $m^{-2}.day^{-1}$
DMPC(i)	Dry matter allocation to each plant layer (relative)	-
DSINB	Integral of SINB over the day	$s.day^{-1}$
DSINBE	Daily total of effective solar height	$s.day^{-1}$
DRT	Death rate of roots	g DW. $m^{-2}.day^{-1}$
DSO	Daily extra-terrestrial radiation	$J.m^{-2}.day^{-1}$
DST	Death rate of stems	g $DW.m^{-2}.day^{-1}$
DTEFF	Daily effective temperature	°C
DTGA	Daily total gross CO_2 assimilation of the plant	g $CO_2.m^{-2}.day^{-1}$
DTR	Measured daily total global radiation	$J.m^{-2}.day^{-1}$
DVR	Development rate	day^{-1}
DVRT	Table of DVR as function of temperature	day^{-1},°C
DVS	Development phase of the plant	-
EE	Initial light use efficiency for shoots	g CO_2 . J^{-1}
FGROS	Instantaneous CO_2 assimilation rate of the plant	g $CO_2.m^{-2}.hr^{-1}$
FGL	Instantaneous CO_2 assimilation rate per depth layer	g $CO_2.m^{-2}.hr^{-1}$
FL	Leaf dry matter allocation to each layer of the plant (relative)	-
FLT	Table to read FL as function of DVS	-, -
FLV	Fraction of total dry matter increase allocated to leaves	-
FLVT	Table to read FLV as function of DVS	-
FRDIF	Diffuse radiation as a fraction of total solar radiation	-
FRT	Fraction of total dry matter increase allocated to roots	-

FRTT	Table to read FRT as function of DVS	-, -
FSO	Fraction of total dry matter increase allocated to storage compounds	-
FST	Fraction of total dry matter increase allocated to stems	-
FSTT	Table to read FST as function of DVS	-, -
FTUB	Fraction of total dry matter increase allocated to tubers	-
GLV	Dry matter growth rate of leaves	g $DW.m^{-2}.day^{-1}$
GPHOT	Daily total gross CH_2O assimilation rate of the community	g $CH_2O.m^{-2}.day^{-1}$
GRT	Dry matter growth rate of roots	g $DW.m^{-2}.day^{-1}$
GSO	Dry matter growth rate of storage component	g $DW.m^{-2}.day^{-1}$
GST	Dry matter growth rate of stems	g $DW.m^{-2}.day^{-1}$
GTW	Dry matter growth rate of the crop (plant excluding tubers)	g $DW.m^{-2}.day^{-1}$
HAR	Harvesting (0=no harvesting, 1=harvesting)	-
HARDAY	Harvesting day number	day
HARDEP	Harvesting depth (measured from water surface)	m
HIG(i)	Height on top of stratum I (measured from water surface	m
HOUR	Selected hour during the day	hr
I	Counter in DO LOOP	-
IABS(i)	Total irradiance absorbed per plant layer	$J.m^{-2}.s^{-1}$
IABSL(i)	Total irradiance absorbed by plant shoots	$J.m^{-2}.s^{-1}$
IDAY	Integer equivalent of variable DAY	day
INTUB	Initial dry weight of a tuber	g $DW.tuber^{-1}$
IRS	Total irradiance on top of the water surface	$J.m^{-2}.s^{-1}$
IRZ(i)	Total irradiance on top of depth layer I	$J.m^{-2}.s^{-1}$
IWLVD	Initial dry matter of dead leaves	g $DW.m^{-2}$
IWLVG	Initial dry matter of green (live) leaves	g $DW.m^{-2}$
IWRTD	Initial dry matter of dead roots	g $DW.m^{-2}$
IWRTG	Initial dry matter of green (live) roots	g $DW.m^{-2}$
IWSO	Initial dry matter of storage component	g $DW.m^{-2}$
IWSTD	Initial dry matter of dead stems	g $DW.m^{-2}$
IWSTG	Initial dry matter of green (live) stems	g $DW.m^{-2}$
K	Plant species specific light extinction coefficient	$m^2.g\ DW^{-1}$
KT	Table to read K as function of DVS	-, $m^2.g\ DW^{-1}$
L	Water type specific light extinction coefficient	m^{-1}
LAT	Latitude of the site	degrees
LT	Table to read L as function of day number	day, m^{-1}
MAINT	Maintenance respiration rate of the plant	g $CH_2O.m^{-2}.day^{-1}$
MAINTS	Maintenance respiration rate of the plant at reference temperature	g $CH_2O.m^{-2}.day^{-1}$
NDTUB	Dormant tuber number	$dorm.tubers.m^{-2}$
NGLV	Net growth rate of leaves	g $DW.m^{-2}.day^{-1}$
NGRT	Net growth rate of roots	g $DW.m^{-2}.day^{-1}$
NGST	Net growth rate of stems	g $DW.m^{-2}.day^{-1}$

NGTUB	Germinating tuber number	germ.tubers.m^{-2}
NINTUB	Tuber number concurrently initiated per plant	conc.in.tub.$plant^{-1}$
NNTUB	New tuber number	new tubers .m^{-2}
NPL	Plant density	plants .m^{-2}
NT	Initial tuber density	initial tubers.m^{-2}
NTM	Initial tuber density measured (field site)	tubers.m^{-2}
NTMT	Table to read NTM as function of day number	tubers.m^{-2}, day
NTUBD	Dead tuber number	dead tubers.m^{-2}
NUL	Zero (0)	-
NTUBPD	Dead tuber number previous day	dead p.d.tub.m^{-2}
PAR	Instantaneous flux of photosynthetically active radiation	$J.m^{-2}.s^{-1}$
PARDIF	Instantaneous flux of diffuse PAR	$J.m^{-2}.s^{-1}$
PARDIR	Instantaneous flux of direct PAR	$J.m^{-2}.s^{-1}$
PI	Ratio of circumference to diameter of circle	-
Q10	Factor accounting for increase in maintenance respiration with a 10 °C rise in temperature	-
RAD	Factor to convert degrees to radians	$radians.degree^{-1}$
RC	Reflection coefficient of irradiation at water surface (relative)	-
RCSHST	Relation coefficient tuber weight-stem length	m.g DW^{-1}
RDR	Relative death rate of leaves (on DW basis)	day^{-1}
RDRT	Table to read RDR as function of DAVTMP	day^{-1}, °C
RDS	Relative death rate of stems and roots (on DW basis)	day^{-1}
RDST	Table to read RDS as function of DAVTMP	day^{-1}, °C
RDTU	Relative death rate of tubers (on number basis)	day^{-1}
REDAM	Reduction factor to relate AMX to pH and oxygen levels of the water (relative)	-
REDF(i)	Reduction factor for AMX to account for senescence plant parts over vertical axis of vegetation (relative)	-
REMOB	Remobilization rate of carbohydrates	g $CH_2O.m^{-2}.day^{-1}$
ROC	Relative conversion rate of tuber into plant material	$gCH_2O.gDW^{-1}.day^{-1}$
RTR	Maximum relative tuber growth rate at 20 °C	g $DW.tuber^{-1}.day^{-1}$
RTRL	Relative tuber growth rate at ambient temperature	g $DW.tuber^{-1}.day^{-1}$
SC	Solar constant corrected for varying distance sun-earth	$J.m^{-2}.s^{-1}$
SC(i)	Standing crop in depth layer I	g $DW.m^{-2}.layer^{-1}$
SINB	Sine of solar elevation	-
SINLD	Intermediate variable in calculating solar declination	-
STEMLE	Stem length	m
TBASE	Base temperature for juvenile plant growth	°C
TEFF	Factor accounting for effect of temperature on maintenance respiration	-
TGW	Total live plant dry weight (excluding tubers)	g $DW.m^{-2}$
TGWM	Total live dry weight measured (field site)	g $DW.m^{-2}$
TGWMT	Table to read TGWM as function of day number	g $DW.m^{-2}$, day
TL	Thickness per plant layer	m
TMAX	Daily maximum temperature	°C

TMIN	Daily minimum temperature	°C
TMPSUM	Temperature sum after 1 January	°C
TRANS	Translocation rate of carbohydrates	g $CH_2O.m^{-2}.day^{-1}$
TW	Total live + dead plant dry weight (excluding tubers)	g $DW.m^{-2}$
TWCTUB	Total critical dry weight of new tubers	g $DW.m^{-2}$
TWGTUB	Total dry weight of germinating tubers	g $DW.m^{-2}$
TWLVD	Total dry weight of dead leaves	g $DW.m^{-2}$
TWLVG	Total dry weight of live leaves	g $DW.m^{-2}$
TWNTUB	Total dry weight of new tubers	g $DW.m^{-2}$
TWRTD	Total dry weight of dead roots	g $DW.m^{-2}$
TWRTG	Total dry weight of live roots	g $DW.m^{-2}$
TWSO	Total dry weight storage component	g $DW.m^{-2}$
TWSTD	Total dry weight of dead stems	g $DW.m^{-2}$
TWSTG	Total dry weight of live stems	g $DW.m^{-2}$
TWTUB	Total dry weight of tubers	g $DW.m^{-2}$
WLV	Dry weight of leaves (live + dead)	g $DW.m^{-2}$
WRT	Dry weight of roots (live + dead)	g $DW.m^{-2}$
WST	Dry weight of stems (live + dead)	g $DW.m^{-2}$
WTMP	Daily water temperature	°C
WTMPT	Table to read WTMP as function of day number	°C, day
YRNUM	Year number simulation (1-5)	year

Appendix C
Manipulation of Literature Data Used for the Model Equations

Morphology, Development, and Phenological Cycle

The relationship between developmental rate and temperature is linear, increasing from 0 at 0 °C to 0.012 at 30 °C. A reference temperature of 30 °C is believed to be suitable for *Hydrilla*, since it originates from the tropics.

Plant Density

No additional information.

Wintering and Sprouting of Tuber Bank

Tubers of various size classes have been found in natural systems, usually around 0.1 g DW.tuber^{-1} (Van, Haller, and Bowes 1978).[1] Heavier tubers have been found also (Bowes et al. 1977), even up to five times as heavy, but the latter ones occurred only under experimental, N-fertilized, conditions (McFarland and Barko 1990).

Although the chemical composition of tubers is presently not known, starch concentrations up to 70 percent DW have been found to be common.[2]

---

1 References cited in this appendix are located at the end of the main text.

2 Personal Communication, 1995, J. D. Madsen, Research Biologist, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Growth of Sprouts to Water Surface

Elongation of sprouting tubers

Bowes et al. 1977 established relationships between tuber weight class (fresh weight), survival, and shoot elongation in the dark at 25 °C. Apparently, large tubers survived longer than small ones. The reasons for this phenomenon were not given.

Bowes' dataset was used as basis for calculations to (a) clarify which tuber size is likely to survive in the tuber bank for long periods and, thus, can initiate new plants in spring, and (b) establish a relationship between tuber size and chemistry, sprouting, and sprout elongation.

The maintenance respiration at 25 °C of the tuber size classes used for Bowes' experiment has been calculated, using a maintenance coefficient of 0.01 at 25 °C (typical for nonstructural carbohydrates; increasing with a Q_{10} of 2 per 10 °C increase; Table C1). These calculations indicate that tubers with fresh weights <0.280 g must have been respired within 61 days after planting. Planting activities probably broke tuber dormancy, switched on their maintenance respiration, and, in the absence of light, exhausted their carbohydrate reserves making survival impossible. Since winters usually last longer than 2 months in Florida, and tuber banks can be rather easily disturbed so that dormancy is interrupted, it is feasible that mostly the tubers > 0.280 g survive in the tuber bank, and that these give rise to a new macrophyte community in following growth season(s).

The potential elongation per gram sprouting tuber has been calculated for the various tuber size classes listed in Table C1, using the plant lengths measured 61 days after planting. Mean values found for, respectively, the lightest and the heaviest tubers per size class are presented in Table C1.

An example is given for, respectively, the lightest and the heaviest tubers of the largest size class. The dry weight content of the tubers is 14 percent (Van der Zweerde 1981). It is assumed that tubers consist of 70 percent DW of starch; that the sprouts grown from the tubers are composed of a species-specific mixture of nonstructural carbohydrates, proteins, fats, cellulose, organic acids, and minerals; and that the ratio of plant biomass formed over glucose consumed is 0.649 $g.g^{-1}$ (see Light, Photosynthesis, Maintenance, Growth, and Assimilate Partitioning). Therefore, a tuber of 0.3 g FW contains $0.3 \times 0.14 = 0.042$ g DW and can produce $0.042 \times 0.7 \times 0.649 = 0.019$ g DW sprout material. The sprout length measured for the 0.3- to 0.4-g tuber size class was 0.425 m. Since it was not indicated in literature which tuber weight produced which sprout length, only a range in unit sprout length produced per unit tuber weight can be derived from these data. Thus, (a) each tuber of 0.300 g FW can produce $(1/0.042) \times 0.425 = 10.1$-m sprout length, and (b) each tuber of 0.400 g FW can produce $(1/0.036) \times 0.425 = 7.5$-m sprout length.

Table C1
Measured Data on Tuber Weight Class, Survival, and Sprout Length Produced (Bowes et al. 1977) and Calculated Data on Tuber Dry Weight, Maintenance Respiration, and Relation Coefficient Between Tuber Dry Weight and Sprout Length (RCHST; Best and Boyd, this study)

		61 Days Alter Planting			122 Days Alter Planting			
Size Class g FW.tuber^{-1}	Size Class g DW.tuber^{-1}	Survival %	Shoot Length, m	Maintenance Respiration, g DW.tuber^{-1}	Survival %	Shoot Length, m	Maintenance Respiration, g DW.tuber^{-1}	RCHST m.g DW^{-1}
0.080-0.125	0.011-0.018	20	0.257	0.007-0.011	0	--	0.014-0.022	18.8
0.150-0.200	0.021-0.028	25	0.262	0.013-0.017	0	--	0.026-0.034	10.9
0.200-0.280	0.028-0.039	49	0.346	0.017-0.024	0	--	0.034-0.048	10.5
0.300-0.400	0.042-0.056	82	0.425	0.026-0.034	11	0.725	0.052-0.068	8.8

In HYDRIL, RCSHST has been set at 12-m sprout length.g DW^{-1}, being close to the average of the range found. Thus, all sprouting tubers usually present have the capacity to elongate over a distance of about 12 m. Reasons why they do not may be that (a) all nonstructural carbohydrates have been respired before the sprouts are self-supporting, (b) the light climate may not be suitable (daylength, light quantity and quality), (c) temperature interference with elongation (see Barko and Smart 1981), and (d) the conditions in the sediment may not be suitable.

Light probably barely affects elongation of germinating tubers; the potential influence of temperature on elongation is far larger. Barko and Smart (1981) found that elongation increases with a factor of 7 with temperature increasing from 7 to 16 °C (data not shown). The latter relationship is not likely to play a role in early growth of *Hydrilla*, because tuber sprouting only occurs at water temperatures > 18 °C. However, temperature may affect elongation considerably under natural conditions at temperatures > 18 °C in later growth phases (Table C2).

Table C2
Data on Shoot Length of *Hydrilla* Plants Reached at Various Temperatures Under Experimental Conditions (Barko and Smart 1981)

Temperature, °C	Shoot Length, cm	Shoot Length, relative
16	19	0.13
20	64	0.45
24	86	0.61
28	110	0.78
32	142	1

Calculation of relative conversion rate of tubers into adolescent plants (ROC, hr^{-1})

The light compensation point (LCP) decreases in young, growing *Hydrilla* shoots to a final value of 12 $uE.m^{-2}.sec^{-1}$ in adolescent plants (Bowes et al. 1977). Assuming that plants reach adolescence 35 days after tuber sprouting, and that the LCP decreases exponentially from a very high value of 100 to 12 $uE.m^{-2}.sec^{-1}$ in that period, a ROC value of $0.0025.hr^{-1}$ (~ 0.0576 g $CH_2O.g\ DW^{-1}.day^{-1}$) was calculated using the following equation

$$LCP_t = LCP_o.e^{-ROC(35 \cdot 24)}$$

Light, Photosynthesis, Maintenance, Growth, and Assimilate Partitioning

Light

Light extinction coefficients of water and of Hydrilla community

The light intensity or irradiance, I_z, at depth z is a function of intensity at the surface (I_0) to the log base of the negative extinction coefficient (E) at the depth distance, z, in meters.

$$I_z = I_o.e^{-E.z} \qquad or \qquad ln\ I_o - ln\ I_z = E_z$$

The light intensity at h m depth from the upper surface of the community, designated by I_{z+h}, may be approximated by the following equation

$$I_{z+h} = I_o.e^{(-E_c.h)}$$

where

I_z, I_o, and h = same meaning as stated above

E_c = extinction coefficient of water+plant material

Light profiles have been measured in Lake Trafford within a *Hydrilla* community and in open water. At that time, aboveground *Hydrilla* biomass was 890 g DW.m^{-2} (Bowes, Holaday, and Haller 1979). From the irradiance data of Table C3, extinction coefficients of 0.83.m^{-1} for water and of 12.32 m^{-1} for water+plant material were calculated. The extinction coefficient of the plant material only was calculated using Ikusima's (1970) equation as follows.

$$E_p = (E_c.h - E_s.h)/w_h$$

where

E_p = extinction coefficient of plant material, m^2.g DW^{-1}

E_s = extinction coefficient of water, m^{-1}

E_c and h = same meaning as stated above

w_h = plant weight, g DW, at depth h, m

Table C3
Light Penetration in a *Hydrilla* Mat as Compared With Open Water in Lake Trafford, Florida, in August 1977 (Data full noon sun. The data are representative of similar trends in Lake Orange (Bowes, Holaday, and Haller 1979). The data on biomass distribution over the vertical axis have been derived from the total measured aboveground biomass present in Lake Trafford, by assuming a typical umbrella-type vertical distribution as reported in literature (Ambasht and Ram 1976; Ikusima 1970))

Probe Depth, m	Irradiance, uE.m^{-2}.sec^{-1}		Depth From Top of Community, m	Biomass Distribution, % total aboveground	Biomass g DW.m^{-2}
	Community	Open Water			
Air	2,400	2,270			
Water surface	1,625	1,550	0-0.2	42	374
0.3	25	1,100	0.2-0.4	19	169
0.6	1	900	0.4-0.6	18	160
1.0	0	675	0.6-0.8	13	116
			0.8-1.0	8	71

Substituting the extinction coefficients of water and of water+plant material in Ikusima's equation and inserting the dry weight of the *Hydrilla* community present above 0.6-m depth, a plant-specific extinction coefficient of 0.0098 was calculated. In the model a value of 0.01 m^2.g DW^{-1} has been used. The latter value has also been found by Ikusima (1970) for *Hydrilla verticillata* Caspary.

Photosynthesis

Potential CO_2 assimilation rates for shoot tips (AMX)

Photosynthetic activity at light saturation in water in equilibrium with atmospheric CO_2 is 4.6 μmol O_2.mg $chl^{-1}.hr^{-1}$ (Van, Haller, and Bowes 1976, 1978). This value is very close to values measured in May in Lakes Orange and Trafford, Florida (Bowes, Holaday, and Haller 1979). Light- as well as carbon-saturated photosynthetic activity is far higher (Van, Haller, and Bowes 1976), suggesting that photosynthetic activity in the mentioned lakes in Florida, where the DIC concentrations are in the range of 0.8 to 1.0 mmol, is carbon limited.

Conversion of the light-saturated photosynthetic rate to mg CO_2.g $DW^{-1}.hr^{-1}$ yields 15.75 mg CO_2.g $DW^{-1}.hr^{-1}$. Conversion to 0.585 kg CO_2.ha

leaf^{-1}.hr^{-1} indicates that this value is about 1 percent of that of 50 kg CO_2.ha leaf^{-1}.hr^{-1} usually found for terrestrial plants (Mayus 1990). Published relationships used for conversions are (a) PQ = 1; (b) Chlorophyll concentration of *Hydrilla* is 1 to 1.3 mg.g FW^{-1}, being highest in plant tissue receiving the highest irradiance (Van, Haller, and Garrard 1978); 1.3 mg.g FW^{-1} used; (c) Dry weight of *Hydrilla* shoots is 6 percent of wet weight (Bowes, Holaday, and Haller 1979); (d) 1 kg DW *Hydrilla* leaf ~ 0.02692 ha leaf (assuming the same surface:DW ratio as in *Elodea nuttallii* (Dvorak and Best 1982).

Initial light use efficiency for shoot tips (EE)

Although it has been demonstrated that carbon can be fixed through the C_3 as well as through the C_4 photosynthetic pathway in *Hydrilla*, it is likely that the C_3 pathway is the major pathway into operation most of the time (Van, Haller, and Bowes 1976; Bowes, Holaday, and Haller 1979; Bowes 1985). Therefore, a light-use efficiency of 11.10^{-6} g CO_2.J^{-1}, typical for C_3 plants (Penning de Vries and Van Laar 1982), has been used in the model.

Photosynthesis limiting factors : pH and oxygen (REDAM)

The photosynthetic rate of *Hydrilla* decreases strongly between pH 4.5 and pH 8 and remains very low, but similar, between pH 8 and 9 at a DIC concentration of 0.6 mM. It is 2.6 × higher at pH 6.5 than at pH 8, i.e., 0.041 versus 0.016 g CO_2.g DW^{-1}.hr^{-1} (Van, Haller, and Bowes 1976). The relationship between photosynthetic rate and pH is linear over the alkalinity range of Lake Orange (0.8-1 mM).

In the upper m^3 of a dense *Hydrilla* mat, pH typically changes during a summer-day over a range of 7.6 to 10.1 (Van, Haller, and Bowes 1976; Bowes, Holaday, and Haller 1979), and thus the question had to be answered of which limiting factor had to be used to correct the AMX for daily changes in pH. For this, the light part of the day was divided into 2 pH-classes, and the duration of each pH-class was calculated from the field data: class pH 7.6 covered 6.5 hr and class pH 10 covered 7.5 hr. These pH classes were chosen because they proved suitable measures to describe the daily pH-range. Thus, plants photosynthesizing for 6.5 hr with AMX 0.023 g CO_2.g DW^{-1}.hr^{-1} contribute 0.150 g CO_2.g DW^{-1}.period $^{-1}$ to the daily photosynthesis; plants photosynthesizing for 7.5 hr with AMX 0.016 g CO_2.g DW^{-1}.hr^{-1} contribute 0.120 g CO_2.g DW^{-1}.period $^{-1}$ to the daily photosynthesis. Both periods combined represent 0.837 of the photosynthesis that would have occurred when AMX of 0.023 g CO_2.g DW^{-1}.hr^{-1} could be achieved during the 14-hr light period. The value of 0.837 is, therefore, used to correct AMX for daily changes in pH.

In the upper cubic meter of a dense *Hydrilla* mat, the oxygen concentration typically changes during a summer-day over a range of 5 to 18 mg O_2.l^{-1}

(Van, Haller, and Bowes 1976; Bowes, Holaday, and Haller 1979). A similar approach as for pH was chosen to account for the effects of changes in O_2 concentration on photosynthesis. For this, the light part of the day was divided into three O_2 concentration classes, each class having a photosynthesis-inhibiting factor derived from the Van, Haller, and Bowes (1976) measured relationship between photosynthetic activity and O_2 concentration. Thus, photosynthesis in plants at an O_2 concentration < 7.9 mg $O_2.l^{-1}$ is inhibited by a factor 0.9 of potential (4 hr), at an O_2 concentration >7.9 and <15.7 mg $O_2.l^{-1}$ by a factor 0.7 (4 hr) and at an O_2 concentration >15.7 and 23.6 mg $O_2.l^{-1}$ by a factor 0.6 (6 hr; total light period 14 hr). The value of 0.7 is, therefore, used to correct AMX for daily changes in pH.

Combination of both photosynthesis limiting factors brings the value used for REDAM at 0.581.

Effect of daytime temperature on photosynthesis (AMTMP)

To calibrate the relationship between temperature and photosynthetic activity, the measured values given in Table C4 were converted to relative values.

Table C4
Photosynthetic Activity, of *Hydrilla* Shoots in Response to Temperature (W. T. Haller, IFAS, Gainesville, FL: unpubl. 1984). Conditions were light-saturating, and water was in equilibrium with atmospheric CO_2)

Temperature, °C	Photosynthetic Rate	
	Absolute, μmol CO_2.mg chl^{-1}.hr^{-1}	Relative, %
8	1.33	0.57
18	1.75	0.75
36.5	2.33	1.00
40	1.33	0.57
Note: Relative to the maximum photosynthetic rate at 36.5 °C.		

Growth

Assimilate requirement for dry matter production (ASRQ)

The value of the conversion factor for growth of plant biomass, weighted according to its composition, can be computed in a simple way from the fractions of carbohydrates, proteins, fats, cellulose, organic acids, and minerals (Table C5). This method has been employed to calculate *Hydrilla*'s assimilate requirement for biomass production.

Table C5
Estimated Chemical Composition of *Hydrilla* Plants (Best and Boyd, this study), and Conversion Efficiencies Typical for Agricultural Crops, Showing How Much Glucose is Used for the Synthesis of Each Organic Matter Component (Penning de Vries and Van Laar 1982b)

Component	Contribution to Biomass, % DW	Conversion Factor	Assimilate Requirement g CH_2O.g DW^{-1}
Nonstructural	14	1.242	17.388
Carbohydrates			
Proteins	17	1.704	28.968
Fats	8	3.106	24.848
Cellulose	33	2.174	71.742
Organic acids	11.2	0.929	10.404
Minerals	16.8	0.050	0.840

Note: As the conversion factor for cellulose was not known, that for lignin has been used. Carbohydrates range from 6.5- to 15-percent DW.

Biomass allocation to plant organs

Biomass allocation to *Hydrilla* organs is set in the model to the following values: 34 percent of total biomass to leaves, 60 percent to stems, and 6 percent to roots. These values are based on the following literature references: (a) young shoots reach a stem weight of 3.2 g DW and a leaf weight of 1.9 g DW after 5 weeks of growth (Van, Haller, and Bowes 1978). The stem:leaf ratio is therefore 1.684, or 63 percent of the biomass produced goes to the stems and 37 percent to the leaves; (b) in a well-developed *Hydrilla* community in Florida, a stem weight of 56.5 g DW and leaf weight of 31.1 g DW were found (Haller and Sutton 1976), implying that 64 percent of the biomass produced goes to the stems and 36 percent to the leaves; (c) in young plants, roots made up 6 percent and shoots 94 percent of the total biomass (Van der Zweerde 1981; Van, Haller, and Garrard 1978).

Biomass distribution over the vertical axis (DMPC)

In adolescent plants, 80 percent of the aboveground biomass is usually present in the upper 0.6-m water layer, and it is distributed as 21 percent in layers 1 and 2, as 10 percent in layers 3 and 4, and as 9 percent in layers 5 and 6 (Ambasht and Ram 1976; Bowes, Holaday, and Haller 1979). These values form the basis for the dry matter allocation per 0.1-m-thick layer over the vertical axis from the water surface to 0.6 m below. The remaining biomass is divided equally over the lower 0.1-m water layers. DMPC stands for dry matter partitioning coefficient.

Maximum biomass

In the model, maximum of biomass has been set to 900 g $DW.m^{-2}$. This value is based on the following: Highest aboveground biomass is 890 g $DW.m^{-2}$ (Bowes, Holaday, and Haller 1979). Underground biomass is typically 6 percent of total, and tubers are not present in late summer; thus, total maximum biomass is 947 g $DW.m^{-2}$.

Induction and Formation of Tubers

Number of tubers concurrently initiated

Recalculation of data measured in various independent studies (Table C6) indicated that *Hydrilla* plants probably aim at forming 7 to 11 tubers per plant, at a rate of 0.05 to 0.12 $tubers.plant^{-1}.day^{-1}$ (one plant composed by 22 to 28 shoots).

Table C6
Calculation of Numbers of Tubers Formed per Plant (Aboveground plant biomass and tuber data per m^2 measured by Bowes, Holaday, and Haller (1979), Lake Orange, Florida. Plant density and tuber formation per plant were calculated by Best and Boyd (this study) using typical plant weights published by Barko and Smart (1981))

Day	Tubers $N.m^{-2}$	Tubers $N.plant^{-1}$	Tuber Formation $N.plant^{-1}.day^{-1}$	Tuber Formation $N.plant^{-1}.day^{-1}$	Plant Density $N.m^{-2}$
46	--				2.1-3.2
135	58	4.8-7.4	0.65	0.054-0.083	7.8-12.1
227	245	4.6-7.1	2.0	0.050-0.077	34.6-53.6
319	510	7.0-10.8	2.9	0.076-0.117	47.2-73.0

Senescence

No additional information on senescence.

Site-Specific Environmental Conditions

pH, alkalinity, and trophic state

pH, alkalinity, and trophic state are important factors influencing primary production in aquatic systems. pH and alkalinity determine carbon availability for photosynthesis, and trophic state gives an indication of algal production and consequent light attenuation within the water column. The model is calibrated for dissolved inorganic carbon concentrations > 0.8 mmol (alkalinity Lake Orange 0.8 to 1.0 mmol).[1] pH affecting potential photosynthetic rate at light saturation through REDAM can be modified by the user (see Light, Photosynthesis, Maintenance, Growth, and Assimilate Partitioning). The model is calibrated for a light extinction coefficient of the water of $0.83.m^{-1}$ (see Light, Photosynthesis, Maintenance, Growth, and Assimilate Partitioning); the value of this parameter (L) can be modified by the user.

Water temperature

The temperature has been measured in the surface water of Lake Orange at several points in time (Bowes, Holaday, and Haller 1979). For Day 365, a temperature of 15 °C is used, being the average of the maximum and minimum temperature measured in winter in Lake Orange, Florida.

Table C7
Seasonally Measured Daytime Temperatures in Surface Water of Lake Orange, Florida

Day, Number	Temperature, °C
46	16
135	26
227	30
319	17
365	15

Temperature profiles within *Hydrilla* mats have also been measured at several occasions, but published data are few (Bowes, Holaday, and Haller 1979). The latter data indicate that on a warm summer day the temperature can be 3 °C higher at the surface of a dense *Hydrilla* mat than in open water; temperature differences at greater depth are usually smaller. However, in the present model, the surface water temperature is taken as representative for the water temperature in the whole water body.

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[1] Personal Communication, 1995, G. Bowes, University of Florida, Gainesville.

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13. ABSTRACT *(Maximum 200 words)*

A simulation model for the biomass dynamics of the submersed macrophyte *Hydrilla verticillata* (dioecious biotype) is presented. The model HYDRIL is based on carbon flow within a 1-m^2 water column. It includes several aspects that affect biomass dynamics, such as latitude, seasonal changes in climate, pH and oxygen effects on CO_2 assimilation rate at light saturation, wintering strategies, grazing (removal of aboveground and tuber biomass), and mechanical control (removal of aboveground biomass). The characteristics of the community and of the site can be easily modified by the user.

HYDRIL incorporates insights into the processes affecting the dynamics of a *Hydrilla* community in relatively shallow, hard water (0.1- to 2.5-m depth; DIC concentration > 0.8 mmol). It has been calibrated on data pertaining to a *Hydrilla* community in Lake Orange, Florida. At that site, no aboveground wintering biomass is present and growth starts from the tuber bank. Peak biomass is reached late in August and tuber formation takes place in autumn, replenishing the tuber bank.

HYDRIL simulates the dynamics of plant biomass and tuber bank density at Lake Orange well over a period of 1 to 5 years. It has been used to calculate plant biomass and tuber density for other sites in subtropical (Florida) and tropical (India) areas, where it simulated biomass ranges similar to those measured in the field.

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Sensitivity analysis shows that peak biomass of a *Hydrilla* community is most sensitive to changes in photosynthetic activity at light saturation and very sensitive to changes in light-use efficiency. Sensitivity analysis indicates that changes in climate greatly affect the simulated data on peak biomass and, although less, tuber numbers. Peak biomass proved sensitive to changes in water transparency and, to less extent, in water depth, while tuber weights and numbers were not in 1-year simulations. However, simulations indicated that all three parameters were sensitive on a longer term (periods > 1 year).

The model can be used as a tool to predict the dynamics of a *Hydrilla* community over 1- to 5-year periods. Running the model with different parameter values specific for any particular site and/or treatment, e.g., biomass removal to a certain water depth, helps in gaining insight into the predominant mechanisms regulating submersed plant dynamics.