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A Simulation Model for Growth of the Submersed Aquatic Macrophyte Eurasian Watermilfoil (*Myriophyllum spicatum* L.)

by Elly P. H. Best, William A. Boyd

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Prepared for Headquarters, U.S. Army Corps of Engineers

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Preface

The work reported herein was sponsored by the Aquatic Plant Control Research Program (APCRP), Work Unit 32440. The APCRP is sponsored by Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Research and Development Center (ERDC) 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 Center for Aquatic Plant Research and Technology (CAPRT), Dr. John W. Barko, Director. Mr. Robert C. Gunkel, Jr., was Assistant Director, CAPRT. Technical Monitor during this study was Mr. Timothy Toplisek, HQUSACE.

Principal Investigator for this work unit was Mr. R. M. Stewart, Ecosystem Processes and Effects Branch (EPEB), Environmental Processes and Effects Division (EPED), EL, ERDC. The work described herein was performed by Dr. Elly P. H. Best, Fate and Effects Branch, EPED, with programming assistance from Mr. William A. Boyd, EPEB. Ms. Anne B. Stewart, AScI Corporation, assisted with the graphics. Dr. Best and Mr. Boyd prepared this report. Dr. F. G. Wortelboer (National Institute for Environmental Research, De Bilt, The Netherlands) provided an external technical review. The report was reviewed internally by Drs. John D. Madsen and Robert Kennedy, EPEB.

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

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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 physicochemical factors. Therefore, predictions of the environmental impact of management measures concerning aquatic communities should be based on accurate estimates of (a) plant species and mass and its pertinent physiological properties, (b) the contribution of plants to the various food chains, and (c) the contribution of the decay of plants 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.

Although the number of simulation models for growth of monotypic, submersed macrophyte communities is increasing (e.g., Titus et al. 1975; Best 1981; Collins and Wlosinski 1985; Best and Jacobs 1990; Hootsmans 1991, 1994; Scheffer, Bakema, and Wortelboer 1993; Best and Boyd 1996), it is still relatively low compared with that for terrestrial vegetation. The current model has been developed because none of the existing models were suitable to simulate the behavior of a monotypic milfoil community under various environmental and climatological conditions over a period ranging from season to several years.

Distribution of Eurasian Watermilfoil within the United States

The submersed, rooted aquatic macrophyte *Myriophyllum spicatum* L. or Eurasian watermilfoil belongs to the dicotyledonous family Haloragaceae. It has the ability to survive unfavorable environmental conditions and has been demonstrated to outcompete many other submersed aquatic plant species in temperate, subtropical, and tropical areas. This species has consequently a very large distributional area. It may be considered as the most aggressive member of a circumboreal complex of closely related taxa (Patten 1954). A problem in discussing the distribution and rapid spread of Eurasian watermilfoil is that this plant species is morphologically very similar to the native North American

milfoil variously named *Myriophyllum exalbescens* Fern., *M. spicatum* var. *exalbescens* (Fern.), and *M. spicatum* subsp.*exalbescens* (Fern.) Hult. The taxonomic distinction probably has not been made in all cases when these two species have been discussed in literature. Hereafter, Eurasian watermilfoil will be referred to simply as milfoil.

Milfoil is a native of Eurasia. It has been present in the United States since 1948 (Couch and Nelson 1985). This species was not considered a weed until the late 1950s. Since that time, it has spread from the east to the west coast in both the United States and Canada (Reed 1977; Aiken, Newroth, and Wile 1979), and it has been documented in 44 of the States and 3 Canadian provinces (Engel 1993). Spreading of species over large distances was partly related to aquarium and aquatic nursery trade (Reed 1977). Short-distance dispersal probably occurred by transport of plant fragments between lakes on boats or trailers (Scales and Bryan 1979). The explosive growth appears to follow major environmental disruptions (Nichols and Shaw 1986). For example, the Chesapeake Bay population increased only in the 1950s and early 1960s (Allen 1973; Bayley et al. 1978) after hurricanes hit the area repeatedly causing temporarily increased salinity, sedimentation, and inflow of nonpoint source pollutants. Increased milfoil growth in Cayuga Lake, New York, and Lake Mendota and Lilly Lake, Wisconsin, is attributed to major natural or human caused disruption (Lind and Cottam 1969; Oglesby et al. 1976; Nichols 1984). Dramatic population fluctuations appear to be characteristic, since they have been reported not only in the native Eurasian range of milfoil (Lundegardh-Ericson 1972; Jeschke and Muther 1978) but also in the Chesapeake Bay area and in Lake Wingra. In the Chesapeake Bay area, milfoil declined first in the most recently colonized areas rather than in the original epicenters of growth (Bayley et al. 1978), as such suggesting a pattern of spreading from optimal growth areas to less optimal ones (Nichols and Shaw 1986). Causes of declines are still under discussion, but initial stages of declines are commonly attributed to a large decrease in water transparency as a consequence of increases in total suspended-solids concentrations and in algal growth, respectively.

Milfoil is considered a nuisance plant in parts of the United States, since it may interfere with human utilization of freshwater resources, become aesthetically displeasing, or displace desirable indigenous communities. From a shoreline perspective, the biomass in a dense “mat” of submersed 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.

The simulation model developed in this study concerns Eurasian water-milfoil. 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. A user manual is published separately (Best and Boyd, in preparation).

2 MILFO: Description of Model

Modeling Concepts

The MILFO (Version 1.0) model simulates growth of a typically monoecious Eurasian watermilfoil community. In the model, growth is considered the plant dry matter accumulation including rhizome/root crown formation, under ample supply of nitrogen and phosphorus, in a pest-, disease-, and competitor-free environment under the prevailing weather conditions. Two or three plant cohorts in, respectively, temperate or tropical areas wax and wane per season with one and the same rhizome/root crown system as a common basis. 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 a system composed of root crowns attached to a rhizome system in the sediment with or without aboveground plant biomass present. All calculations are performed on a m^2 basis. Since environmental factors and plant growth characteristics vary with depth, in the model the water column and associated growth-related processes have been partitioned in 0.10-m depth classes (Titus et al. 1975).

Seed formation has not been included in the model because its role in maintaining an existing milfoil community at the same location is minimal (Hartleb, Madsen, and Boylen 1993). Dispersal and colonization of new habitats by plant fragments and seeds are recognized, important characteristics of Eurasian watermilfoil. 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).

MILFO requires as input physiological properties of the plant community (in this case of milfoil) and of the actual environmental and weather conditions at the site, characterized by 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

MILFO 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 Δt 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 most rapid 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 uncertainty, and that uncertainties in parameter

estimates 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 current knowledge in a dynamic simulation model. By studying the behavior of such a model, better insight in the real system is gained.

Implementation

The MILFO model was implemented as a FORTRAN77 program. For numerical integration, the Runge-Kutta technique is used, which allows employing a variable time-step. The program, as it is being run, integrates the equations once per day in the main subroutines (MODEL, CHRT2, CHRT3; see Figure 1), once per second in the subroutines calculating day length and instantaneous irradiance (ASTRO) and instantaneous gross assimilation (ASSIM), and at three times of the day in the subroutine calculating daily total gross assimilation (TOTASS; Gaussian integration). Instantaneous gross assimilation is calculated per second and converted to hourly rates within ASSIM.

Model approach and organization are similar to those used for agricultural crops (SUCROS1; Goudriaan, Van Keulen, and Van Laar 1992). Several features of a simulation model for hydrilla (HYDRIL; Best and Boyd 1996; Boyd and Best 1996) and of a general growth model for submersed angiosperms (SUBANG; Best and Jacobs 1990) have been used.

MILFO 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- ATs 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 MILFO are as follows:

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

b. Plant growth starts from the rhizome/root crown system alone or from the same system with wintering plants.

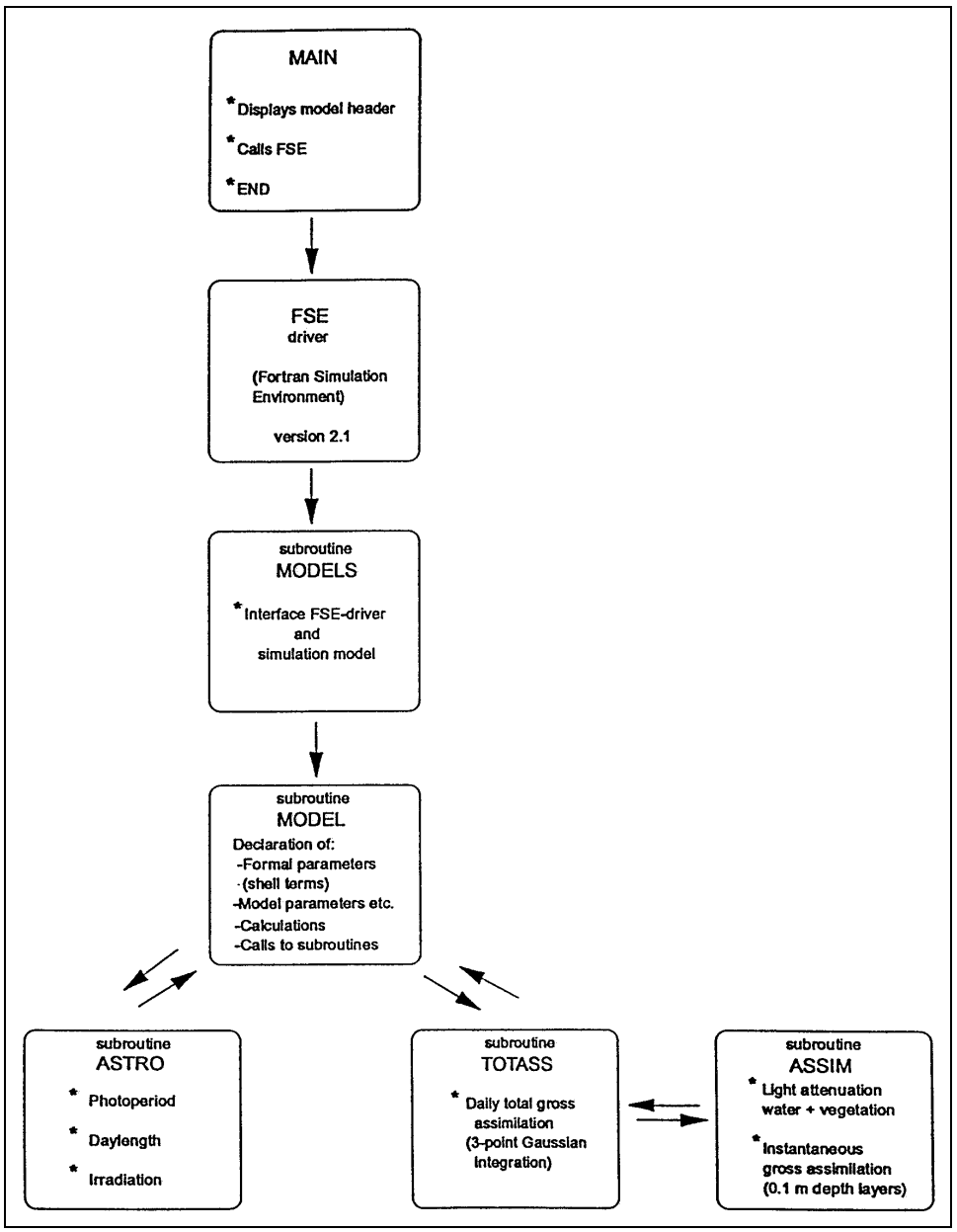

Figure 1. Relational diagram of MILFO and its subroutines in combination with FSE shell (Each plant cohort is represented by a cohort-specific subroutine (cohort 1 by MODEL, cohort 2 by CHRT2, and cohort 3 by CHRT3; only one shown), all using same subroutines ASTRO, TOTASS, and ASSIM)

c. Two plant cohorts are active in a temperate climate and three cohorts in the tropics, depending on the seasonal input variables.

d. Photosynthetic response is to instantaneous irradiance.

e. Removal of biomass through mechanical harvesting can be calculated.

f. Air or water temperatures must be used to run the model.

g. The model can be used for communities at various water depths, ranging from 0.5 to 6.0 m.

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

3 Model Processes

Morphology, Phenological Cycle, and Development

Morphology and phenological cycle of milfoil

Eurasian watermilfoil is a rooted perennial with long, flexible stems and finely dissected leaves. The leaves are arranged in whorls around the stems. The plant stems may reach lengths in excess of 4 m in summer, branching close to the water surface (canopy formation). It has been found in water depths ranging from 0.2 to 6 m (Grace and Wetzel 1978; Madsen, Eichler, and Boylen 1988). It occasionally forms small emergent shoots from fragments starting on the shore.[1] The current model does not describe plants in emergent habit.

Milfoil is able to propagate itself by seeds, by vegetative fragmentation, and in an evergreen condition. Flowering of milfoil in the northern hemisphere occurs from June to November; one (Aiken, Newroth, and Wile 1979; Grainger 1947; Carpenter 1980), two (Nichols 1971; Lind and Cottam 1969; Patten 1956), and three (Grace and Wetzel 1978) flowering periods per year have been reported. Flowering periods in southern areas have been described as "less predictable" (Grace and Wetzel 1978), while they are suggested to occur in the tropics during the whole growth season (Zutschi and Vass 1973). Flowering usually coincides with peak biomass and is followed immediately by autofragmentation/sloughing. The production of viable seeds requires emersion of the typically monoecious flowering spikes (Patten 1954) with transfer of pollen by wind as the dominant pollination mechanism (Hutchinson 1975). Seeds are important in long-distance dispersal and as insurance against local extinction, but seed germination may be delayed (Guppy 1897; Patten 1955) or decreased by desiccation (Standifer and Madsen 1997); seedling establishment appears to be a particularly fragile stage in the life cycle (Patten 1956; Hartleb, Madsen, and Boylen 1993). Shoot fragmentation is usually the result of abscission just after flowering, but it can also be accidental (by boat contact or wave action). Although shoot fragmentation can be substantial, the number of

[1] Personal Communication, 1998, J. E. Titus, University of Binghamton, New York.

established, new plants originating from shoot fragments is relatively low (Madsen and Smith 1997). Fragmentation is probably the most important means of dispersal within a water body or between nearby water bodies. Milfoil most frequently winters in an evergreen form as root crowns and/or lower shoots attached to the rhizome system (Grace and Wetzel 1978; Madsen, Eichler, and Boylen 1988; Madsen 1997) and may maintain considerable winter biomass (Stanley et al. 1976). This species does not form turions described as important hibernacula of other *Myriophyllum* species (*M. exalbescens, M. verticillatum, M. heterophyllum*; Grace and Wetzel 1978).

Description of development and phenological cycle in MILFO

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, 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. 1989b, 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 current model is in accordance with the degree-day hypothesis (Thornley and Johnson 1990a). The idea is as follows. The mean temperature T_i for each day i is measured, and a sum h is formed according to

$$h = \sum_{i=1}^{j} (\overline{T_i} - T_c)$$

which includes only those terms where 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 milfoil, 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 found in agricultural crops 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 milfoil in Lake Wingra, Wisconsin, in 1970 as an example (Adams and McCracken 1974). 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 MILFO. The development phase is dimensionless, and its value increases gradually within a growing season. The development rate has the dimension d^{-1}. The multiple of rate and time period yields an increment in phase. In the model, the temperature that affects development of milfoil can be chosen as equal to the daily average air temperature at the height of the growing point of the shoots, with a user-defined lag-period to correct for deviations in temperature of the water body in which the aquatic community grows compared with air temperatures (7 days is nominal). 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, MILFO can be run using either one.

The rate of phenological development can be affected by temperature differently in the vegetative phase and in the reproductive phase. These differences indicate that the physiological process of development may not be the same before and after anthesis. Descriptions in literature of number of flowering periods per year and their timing in milfoil indicate that from June to November usually two flowering periods, in June and July, occur in temperate climates, sometimes three in southern regions, and usually three in tropical climates (Zutschi and Vass 1973).

The following development rates were derived from the Lake Wingra field data, pertaining to two plant cohorts each with its own flowering period (Adams and McCracken 1974): of 0.022 d^{-1} prior to the first flowering period and of 0.015 d^{-1} subsequently, at a reference temperature of 30 °C and a temperature threshold of 3 °C. These development rates are considered as typical for temperate regions.

For milfoil populations in the tropics, the same development rates and timings as in temperate regions were applicable, but a third plant cohort had to be added to accommodate the third flowering period and usually high August biomass in India (Zutschi and Vass 1973). The milfoil development rates are somewhat higher than those found for hydrilla (0.012 d^{-1} at the same reference temperature and threshold temperature as used for milfoil).

The development phase has the value zero when the simulation starts at the first Julian day number (Tables 1 and 2). The simulation starts using observed

Table 1
Relationship Between Development Phase (DVS) of Milfoil, Day of Year, and 3 °C Day-Degree Sum for a Temperate Climate (DVRVT= 0.022; DVRRT= 0.015)

Developmental phase			
Description	**DVS Value**	**Day Number**	**3 °C Day-Degree Sum**
First Julian day number -> sprouting, initiation elongation, and leaf expansion COHORT1	0 -> 0.375	0 -> 114	1 -> 191
Sprouting, initiation elongation, and leaf expansion -> floral initiation, anthesis, and induction of senescence COHORT1	0.376 -> 1.000	115 -> 162	192 -> 900
Floral initiation, anthesis, and induction of senescence -> senescence COHORT1	1.001 ->1.630	163 -> 212	901 -> 2012
Senescence -> senesced COHORT1	1.631-> 2.000	213 -> 245	2013-> 2669
Sprouting, initiation elongation, and leaf expansion -> floral initiation, anthesis, and induction of senescence COHORT2	1.001-> 1.630	163 -> 212	901-> 2012
Floral initiation, anthesis, and induction of senescence -> anthesis and senescence COHORT2	1.631 -> 2.000	213 -> 245	2013 -> 2669
Senescence -> senesced COHORT2	2.001 -> 2.570	246 -> 365	2670 -> 3508
Senesced COHORT 1 and 2	2.570	365	3508

Note: Calibration was on field data on biomass (Adams and McCracken 1974) and on water transparency, temperature, and irradiance from Lake Wingra, WI, 1970 (Lee and Kluesener 1972).

weights of plants and rhizome/root crowns as initial values. Initial plant weights have been set equal to the observed shoot weight early in spring, which is believed to give a fair approximation. Since the initial weight of the rhizome/ root crown system had not been measured in the calibration data set, this weight has been set equal to 50 g DW m^{-2} found for a similar milfoil community in the same lake in 1977 (Smith and Adams 1986). The rhizome/root crown system is the common basis from which milfoil plant cohorts develop. Plant cohorts are plant groups exhibiting the same phenological cycle, and plants are considered as units composed of roots, stems, and leaves, excluding the rhizome/root crown system. If simulation of the community at another site is desired, the simulation can start from other initial biomass values, either from the rhizome/root crown system only or with wintering plant biomass present.

For a milfoil community in a temperate climate (Table 1), the sprouting of the rhizome/root crown system, i.e., the initiation of growth activity, occurs at DVS 0.375. Sprouts of plant cohort 1 develop through remobilization of carbohydrates from the rhizome/root crown system. The sprouts elongate rapidly to the water surface and form a canopy in the upper-water layers. Anthesis of cohort 1 is initiated at DVS 1.000 and finishes at DVS 1.630, just before downward carbohydrate translocation and senescence are initiated. Translocation and senescence of cohort 1 set in at DVS 1.631 and continue until DVS 2.000. Sprouting of cohort 2 starts when translocation and scenescence of cohort 1 have set in. This timing is based on the assumption that at that time, apical dominance by the existing, senescing shoots is broken and, consequently, new shoots can develop.

Table 2
Relationship Between Development Phase (DVS) of Milfoil, Day of Year, and 3 °C Day-Degree Sum for a Tropical Climate (DVRVT= 0.022; DVRRT= 0.015)

Developmental phase			
Description	**DVS Value**	**Day Number**	**3 °C Day-Degree Sum**
First Julian day number -> sprouting, initiation elongation, and leaf expansion COHORT1	0 -> 0.375	0 -> 25	1 -> 431
Sprouting, initiation elongation, and leaf expansion -> floral initiation, anthesis, and induction of senescence COHORT1	0.376 -> 1.000	26 -> 61	432 -> 1163
Floral initiation, anthesis, and induction of senescence -> senescence COHORT1	1.001 -> 1.630	62 -> 162	1164 -> 3844
Senescence -> senesced COHORT1	1.631 -> 2.000	163 -> 188	3845 -> 4490
Sprouting, initiation elongation, and leaf expansion -> floral initiation, anthesis, and induction of senescence COHORT2	1.001 -> 1.630	62 -> 162	1164 -> 3844
Floral initiation, anthesis, and induction of senescence -> anthesis and senescence COHORT2	1.631 -> 2.000	163 -> 188	3845 -> 4490
Senescence -> senesced COHORT2	2.001 -> 2.570	164 -> 233	4491 -> 5492
Sprouting, initiation elongation, and leaf expansion -> floral initiation, anthesis, and induction of senescence COHORT3	2.001 -> 2.447	164 -> 223	4491 -> 5273
Floral initiation, anthesis, and induction of senescence -> senescence COHORT3	2.448 -> 3.500	224 -> 307	5274 -> 7125
Senescence -> senesced COHORT3	3.501 -> 4.141	308 -> 365	7126 -> 8254
Senesced COHORT 1,2, and 3	4.141	365	8254

Note: Calibration was on field data on biomass from Kashmir lakes, India, 1970s (Zutschi and Vass 1973) and climatological data from Patancheru, India, 1978.

Sprouting of cohort 2 occurs from growing points on the rhizome/root crown system. Anthesis of cohort 2 is initiated at DVS 1.631 and finishes at DVS 2.000. Translocation and senescence of cohort 2 set in at DVS 2.001 and continue until the end of the year.

For a milfoil community in the tropics (Table 2), it proved impossible to generate the high levels of shoot and rhizome/root crown biomass reported (Zutschi and Vass 1973) with two plant cohorts active since the second plant cohort had already senesced in May. However, proper biomass levels and timing were attained with three plant cohorts active, the third cohort being switched on at latitudes less than 33 °N. It is possible that a particular plant process, like sprouting, is sensitive to day length and that this process decides for the population to activate another cohort. However, since the authors are not aware of publications on this topic for milfoil, the switch has been set at the cut-off latitude for tropical areas. Plant cohorts in tropical regions behave similar in terms of DVS to those in temperate regions, except that tropical cohorts require on average a 1.6 × higher 3° degree-day sum to complete their individual life cycle than temperate cohorts.

Maximum Biomass and Plant Density

Seasonal biomass maxima have been reported to vary considerably over time and space. In temperate climates, sometimes one, but usually two, biomass peak(s) were found per growth season. Biomass maxima appear to be related to flowering period. One distinct biomass maximum has been reported for tropical areas (India), while flowering started in May and continued during the growth season. The highest standing crop of 2,283 g DW m^{-2} has been found in Fish Lake, Wisconsin (Budd, Lillie, and Rasmussen 1995), and similar values have been reported for the more southern Lake Guntersville, Alabama, in 1972 (Stanley et al. 1976). This maximum biomass value found has been used to form the upper limit of plant biomass in the model.

Generally, biomass production of milfoil is far more constrained by plant-inherent factors, light and space availability and temperature, than by plant density. As the season progresses, the individual plant size increases along with the areal biomass, and thinning of shoots caused by intraspecific interference results in an inverse relationship between plant size and plant density (Lind and Cottam 1969).

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 3 to 32 so-called "plant clumps" m^{-2}, consisting of a variable number of stems, were determined for a milfoil community in Fish Lake, Wisconsin, in the summers of 1990-92 (Budd, Lillie, and Rasmussen 1995). The mean value of 11 plants m^{-2}, with clump used synonymously to plant, has been used in the model.

In MILFO, plant density has been set to 11 plants m^{-2}. This implies that plant density is always 11 m^{-2} at the beginning of the growth season, and that biomass is redistributed over 11 plants m^{-2} if wintering plants are present.

Wintering and Sprouting of Rhizomes/ Root Crowns and Growth of Sprouts to Water Surface

Rhizome/root crown tissues were the main storage area for carbohydrates in wintering milfoil. Starch concentrations may reach 20 percent, with total non-structural carbohydrates (TNC) concentrations of up to 30-40 percent (Titus and Adams 1979b; Madsen 1997). Rhizome/root crown biomass tended to be higher in spring and in autumn than during the rest of the year and showed an inverse relationship with plant cohort biomass. It fluctuated between 12 and 400 g DW m^{-2} because of seasonal changes (Madsen 1997). Rhizome/root crown biomass of the milfoil community in Lake Wingra amounted to 50 g m^{-2} in winter 1977 (Smith and Adams 1986), while it was relatively constant in tropical regions, varying between 32 and 48 g DW m^{-2} (Zutschi and Vass 1973).

In the model, rhizome/root crown weight decreases by sprouting of growing points, which transform into plants, by respiration, by a plant-inherent sloughing process, and, possibly, by grazing by waterfowl or other organisms, and it increases by downward carbohydrate translocation.

Sprouting or regrowth potential of the rhizome/root crown system is usually high and occurs early in the season. Sprouting in southern areas like Texas (latitude 33 °N, longitude 97 °E) has been reported to occur already in March (Madsen 1997). In northern areas, the timing of sprouting may be similar, but no observations confirming this have been made (or published) probably since at that time, water temperatures are still very low, impeding field work. Actual sprouting frequency under natural conditions is unknown. Sprouting frequency in an established community is probably not important, as long as the final plant density of 11 plants m^{-2} is somehow reached, since plant density tends to play a lesser role in biomass production compared with space availability (see Maximum Biomass and Plant Density). Sensitivity to day length at which the rhizome/root crown systems sprout, or triggering by red-far red ratio, has not been reported.

It is to be expected that the rhizome/root crown system requires continuous maintenance, but that maintenance processes proceed at a low level of activity because of the relatively high carbohydrate concentrations that are cheap in maintenance costs (Penning de Vries and Van Laar 1982b).

Sloughing or death rates of rhizomes/root crowns have not been published so far. A death rate value has been derived from observations on terrestrial rhizome systems where annual turnover rates were found to be approximately four times less than those of aboveground plant biomass in the growth season, but could drop with a factor of 1/100 in inactive periods (Vogt, Vogt, and Bloomfield 1991). Following this approach, a tentative relative death rate of 0.00042 d^{-1} was calculated (g DW g DW^{-1} d^{-1}), being 1/100 of the plant death rate. The latter value is far lower than that of 0.36 d^{-1} estimated for hydrilla tubers from simulations (Best and Boyd 1996). However, the death rate of hydrilla tubers may be an overestimate since death by grazing and/or disturbance of sediments was included in that overall death rate, and grazing of tubers, e.g., by waterfowl, is usually high (Jupp and Spence 1977; Scheffer, Bakema, and Wortelboer 1993). Effects of grazing on the milfoil rhizome/root crown systems are unknown, but expected to be far lower than on hydrilla tubers.

In MILFO, initial rhizome/root crown biomass has been set at 50 g AFDW m^{-2}, equal to the below-ground biomass measured at 1.5-m rooting depth in Lake Wingra in 1977 (Smith and Adams 1986) and equal to the lowest shoot biomass found in 1970 (Adams and McCracken 1974). Sprouting is a function of devel-opment phase through the 3 °C day-degree sum; it occurs between DVS 0.375 and the flowering period for cohort 1, between DVS 1.001 and the flowering period for cohort 2, and, when active, between DVS 2.001 and the flowering period for cohort 3. Sprouting frequency has been set equal to the number of plants per surface area, i.e., at 11 sprouts m^{-2} (sprout is used here synonymously with plant clump).

Remobilization can occur provided the weight of the rhizome/root crown system is greater than the critical rhizome weight. The critical rhizome weight value is the lowest value published, i.e., 12.0 g DW m^{-2} (Madsen 1997).

The rhizomes sprout by remobilization, i.e., conversion of part of their carbohydrate reserves into sprout material, via a relative conversion rate of rhizome-to-plant (ROC), with the same value as derived for conversion of hydrilla tubers (0.0576 g CH_2O g rhizome/root crown-DW^{-1} d^{-1}; for calculation, see Best and Boyd 1996). These carbohydrates are allocated to the plant organs 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, since potential sprout elongation has been estimated to be 12 m sprout-length g DW^{-1} (for hydrilla, cf. Best and Boyd 1996; it is assumed to be similar for milfoil).

After reaching the water surface, canopy formation takes place and photosynthesis proceeds.

Maintenance processes are treated in the next section.

The relative rhizome death rate has been set at 0.00042 d^{-1} (on dry weight basis).

A relational diagram illustrating the wintering and sprouting rhizomes/root crowns of milfoil is shown in Figure 2.

$$TWGRIZ = INTGRL\left(TWGRIZ, -\left[\left(\frac{-TRANS1 + REMOB1 + MAINRT}{1.242}\right) + (RDRIZ \times TGRIZ)\right], DELT\right)$$

IF (DVS. GE. 0.376. AND. DVS. LT. 1.0) THEN

IF (TWGRIZ. GT. CRRIZ) THEN

REMOB1 = ROC × TWGRIZ

TWRIZD = INTGRL (TWRIZD, RDRIZ, DELT)

where

TWGRIZ = total live dry weight of rhizome/root crown system of current day (g DW m^{-2})

REMOB1 = remobilization rate of carbohydrates cohort 1 (g CH_2O m^{-2} d^{-1})

MAINRT = maintenance respiration rate of rhizome/root crown system (g CH_2O m^{-2} d^{-1})

1.424 = assimilate requirement for rhizome dry matter production (g CH_2O g DW^{-1}; see Appendix C)

RDRIZ = relative death rate of rhizome/root crown system (d^{-1})

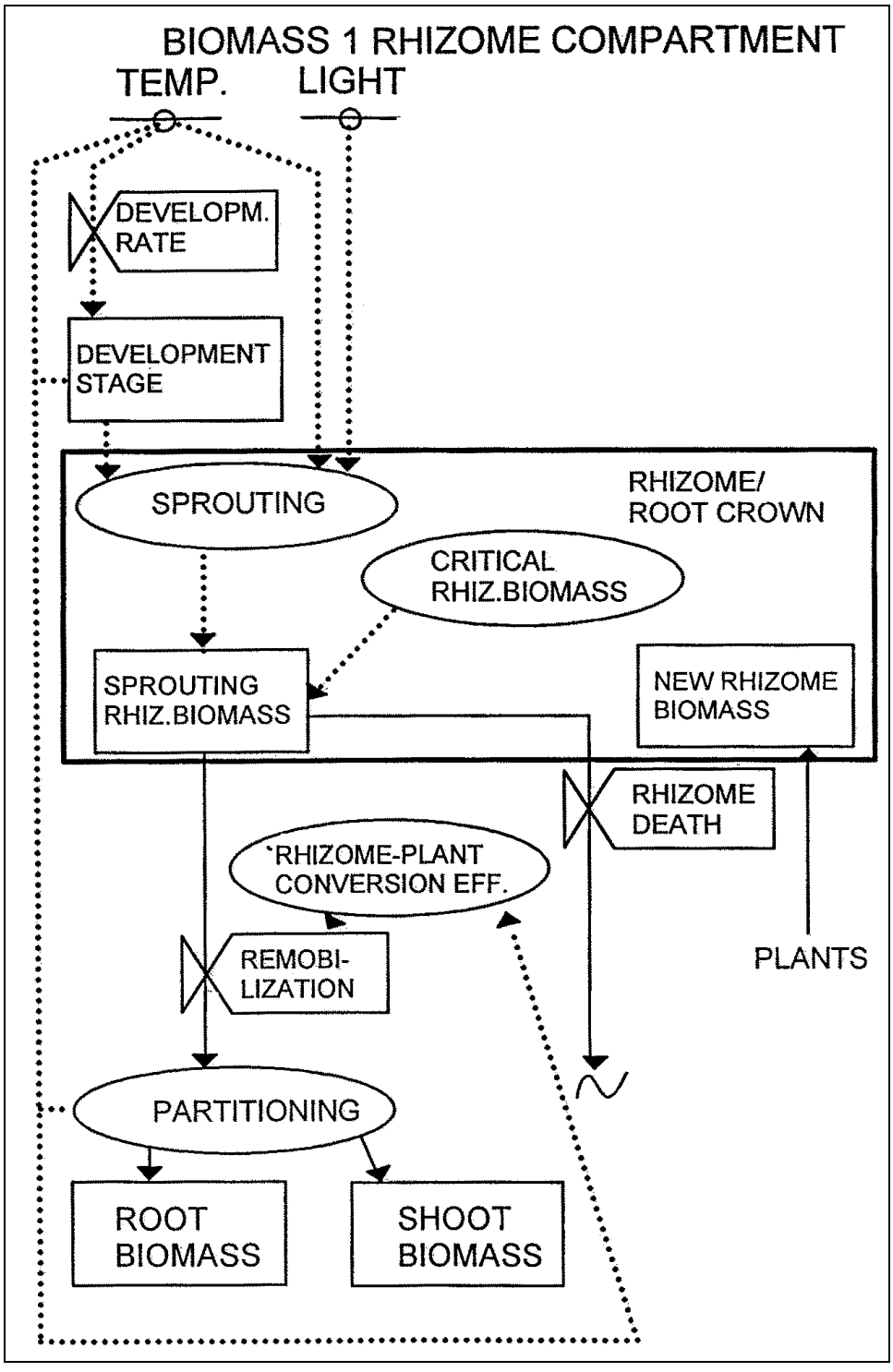

Figure 2. Relational diagram illustrating wintering and sprouting of rhizomes/root crowns in milfoil

TGRIZ = total live dry weight rhizome/root crown system of previous day (g DW m^{-2})

DVS = developmental phase of plant (-)

CRRIZ = critical weight of rhizome/root crown system (g DW m^{-2})

ROC = relative conversion rate of rhizome/root crown into plant material (g CH_2O g DW^{-1} d^{-1})

TWRIZD = total weight of dead rhizome/root crown system (g DW m^{-2})

Light, Photosynthesis, Maintenance, Growth, and Assimilate Partitioning in Milfoil Plants

Light

The measured daily total irradiance (wavelength 300-3,000 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 dissolved substances and particles within the water column resulting in 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* is assumed to be constant throughout the year and given a value of 0.006 m^2 g DW^{-1} measured in the milfoil community in Lake Wingra (Titus and Adams 1979a). Another higher, community-specific extinction coefficient of 0.01 m^2 g DW^{-1} has been published by Ikusima (1970) for a milfoil community in Japan, which may indicate that plants at lower latitudes have thinner leaves.

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

$$IRZ_{i+1} = IRZ_i \times e^{(-TL \times L - K \times SC_i)}$$

$$IABS_i = \frac{(IRZ_i - IRZ_{i+1}) \times SC_i \times K}{(K \times SC_i + TL \times L)}$$

$$IABSL_i = IABS_i \times FL$$

where

IRZ(i) = photosynthetic active part of total irradiance on top of depth layer *i* ($J\ m^{-2}\ s^{-1}$)

TL = thickness depth layer (0.10 m)

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 m^2 water column)

IABS(i) = total irradiance absorbed in depth layer *i* ($J\ m^{-2}\ s^{-1}$)

IABSL(i) = total irradiance absorbed by plant shoots in depth layer *i* ($J\ m^{-2}\ s^{-1}$)

FL = leaf dry matter allocation to each layer of the plant (relative)

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

$$FGL = SC_i \times AMAX \times (1 - \exp\,[\frac{-EE \times IABS_i \times 3600}{AMS \times SC_i}])$$

where

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

SC(i) = standing crop in depth layer *i* ($g\ DW\ m^{-2}$ layer $^{-1}$)

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

EE = initial light-use efficiency for shoots ($g\ CO_2\ J^{-1}$ absorbed)

For photosynthetic activity at light saturation (AMAX), the value of 0.0165 g CO_2 g DW^{-1} h^{-1} was used. This value is equal to the field AMAX measured in Lake Wingra in May 1971, at pH 8 and a total alkalinity of 190 mg L^{-1} (Adams and McCracken 1974). It is slightly higher than field values measured for hydrilla in water in equilibrium with atmospheric CO_2 (0.0158 g CO_2 g DW^{-1} h^{-1};

Bowes, Holaday, and Haller 1979; Van, Haller, and Bowes 1976). Light- and carbon-saturated photosynthetic rates can be far higher (Van, Haller, and Bowes 1976), suggesting that photosynthetic activity in lakes like Lake Wingra, where DIC concentrations are in the range of 0.8 to 3.5 mmol with a pH of 7.6 to 9.4 (Lee and Kluesener 1972), can be carbon limited.

For photosynthetic light-use efficiency (EE), a value of 11.10^{-6} g CO_2 J^{-1}, typical for C_3 plants, was used (Penning de Vries and Van Laar 1982a). Substituting the appropriate value for the absorbed photosynthetically active radiation yields the assimilation rate for each specific shoot layer.

Gross assimilation rate at light saturation shows a distinct seasonal pattern and tends to decrease with aging (Adams and McCracken 1974; Adams, Titus, and McCracken 1974). Although a function describing this relationship (AMDVST) has been included in the model, it is not active in the nominal version (it has the value of 1) since by running the model it turned out not to be quantitatively important. Gross assimilation in milfoil tends to decrease from apex to stem base (Adams, Titus, and McCracken 1974). A function describing this relationship (REDFT) has been included in the model, but is not active in the nominal version (it has the value of 1) since it also turned out not to be quantitatively important.

A reduction factor, REDAM, can be used to take the effects of daily changes in pH and oxygen concentrations on AMX into account, by reducing the AMX by a factor between 0 and 1 for the whole day. REDAM currently has the value of 0.5 since it appears that pH in milfoil communities in Lake Wingra usually oscillates around 8.8 (Adams and McCracken 1974), causing a 50-percent reduction in photosynthetic activity (Titus and Stone 1982). Milfoil appears to be relatively insensitive to changes in oxygen concentration (a reduction in the net photosynthetic rate of only 5 percent was observed because of a change in oxygen concentration from 1 to 21 percent at 15 µm CO_2; Van, Haller, and Bowes 1976).

A fitted, relative function, AMTMPT, describes the effect of daytime temperature on photosynthetic activity. This function has its optimum at 35 °C and is based on the photosynthetic response of milfoil to temperature (Titus and Adams 1979a; confirmed by Stanley and Nailor 1972; see 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 individually 0.1-m-high community layers.

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).

Maintenance, growth, and assimilate partitioning

Maintenance. Some of the carbohydrates formed are respired to provide energy for maintaining the existing plant components. The maintenance costs increase with metabolic activity, probably because of 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 determinations in agricultural crops. They typically range from 0.010 to 0.016 g CH_2O g $AFDW^{-1}$ d^{-1} (Penning de Vries and Van Laar 1982b).

In MILFO, the maintenance coefficients mentioned above are used to calculate the maintenance requirement of the plant cohorts. A lower maintenance coefficient of 0.005 g CH_2O g $AFDW^{-1}$ is used for the rhizome/root crown system, considered to be similar in respiration to stems with coefficients <0.007 (Penning de Vries et al. 1989a).

Higher temperatures expedite turnover rates of plant tissues and increase maintenance costs. A temperature increase of 10 °C usually increases maintenance respiration by a factor of about 2 up to temperatures that usually kill plants (45 to 60 °C; Q_{10} = 2 at a reference temperature 30 °C; Penning de Vries et al. 1989a).

Maintenance respiration in MILFO has been related to temperature by a factor, TEFF, which has the value of 1 between 5 and 20 °C (increases twofold with every 10 °C above a reference temperature of 20 ºC (Thornley and Johnson 1990a) and increases linearly from 0.0001 to 1 between 0 and 5 °C). The value of 2 appears to be a reasonable average, but lower and higher Q_{10} values have been reported also (Amthor 1984). The currently used Q_{10} value is lower in the 0 to 20 °C range than 2.28 found for a Q_{10} of dark respiration in milfoil (Grace and Wetzel 1978); however, the latter process includes growth processes.

Equations describing maintenance costs for milfoil plant cohorts (1, 2, or 3) are:

$$MAINTS = 0.016 \times TWLG + 0.010 \times TWSG + 0.015 \times TWRG$$

$$MAINT = MAINTS \times TEFF$$

where

MAINTS = maintenance respiration rate plant at reference temperature (g CH_2O m^{-2} d^{-1})

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

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

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

Equations describing maintenance costs for the rhizome/root crown system are:

$$MAINRT = 0.005 \times TWGRIZ \times TEFF$$

where

MAINRT = maintenance respiration rate rhizome/root crown system at reference temperature (g CH_2O m^{-2} d^{-1})

TWGRIZ = total dry weight of rhizome/root crown system of current day (g DW m^{-2})

Growth. 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 g CH_2O g DW^{-1} for leaves, 1.51 for stems, and 1.44 for roots (Penning de Vries and Van Laar 1982b; Penning de Vries et al. 1989a), confirmed by Griffin (1994). At higher temperatures, the conversion processes are accelerated, but the pathways are identical. The recently determined construction costs for several submersed plant species, using a different method (Williams et al. 1987), are generally lower, ranging from 0.99 to 1.11 (Spencer, Ryan, and Ksander 1997). However, the latter plants appear to be relatively poor in nitrogen, and transport costs have not been included, both factors that may have contributed to this lower cost calculated.

In MILFO, the construction costs typical for agricultural plants have been used since construction costs calculated for milfoil shoots with an average chemical composition were similar to those in agricultural plants, i.e., 1.54 CH_2O g DW^{-1} (see Appendix C).

The following equation describes growth:

$$GTW = \frac{((REMOB1 \times CVT) + GPHOT - TRANS1 - MAINT)}{ASRQ}$$

where

GTW = dry matter growth rate of vegetation (plants excluding rhizome/root crown system; g DW m^{-2} d^{-1})

GPHOT = daily total gross assimilation rate of community (g CH_2O m^{-2} d^{-1})

REMOB1 = remobilization rate of carbohydrates cohort 1 (g CH_2O m^{-2} d^{-1})

TRANS1 = translocation rate of carbohydrates cohort 1 (g CH_2O m^{-2} d^{-1})

MAINT = maintenance respiration rate of vegetation (g CH_2O m^{-2} d^{-1})

ASRQ = assimilate requirement for plant dry matter production (g CH_2O g DW^{-1})

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

In MILFO, the assimilate allocation pattern has been used synonymously with the biomass allocation pattern. This pattern is assumed to be followed after the shoot tips have reached the water surface and not to change with physiological age (only summer values on biomass partitioning were available). The assimilate allocation has been set at 0.47 of total net growth (excluding rhizome/root crown system) to leaves, 0.47 to stems, and 0.06 to roots. These values have been derived from the compartmentalization of biomass over plant organs in a well-developed milfoil community, with shoots composed of 50 percent by leaves and 50 percent by stems (Budd, Lillie, and Rasmussen 1995). A contribution of 0.06 to total biomass by roots was chosen since no information on the roots of the same vegetation was given, but root biomass is known to be usually small (similar to the contribution of roots to total plant biomass in hydrilla; Best and Boyd 1996). Contributions of leaves and stems to total biomass were recalculated proportionally.

The following equation describes biomass allocation to plant organs:

$$GRT = FRT \times GTW$$

$$GST = FST \times GTW$$

$$GLV = FLV \times GTW$$

where

GRT, *GST*, and *GLV* = dry matter growth rates of roots, stems, and leaves, respectively (g DW m^{-2} d^{-1})

FRT, *FST*, and *FLV* = fraction of total dry matter allocated to roots, stems, and leaves, respectively (relative)

GTW = dry matter growth rate of the vegetation (plants excluding rhizome/root crown system; g DW m^{-2} d^{-1})

In adolescent milfoil plants, shoot biomass is usually present for 61 percent in the upper 0.5-m water column, distributed for 10 percent in the upper 0.1-m layer, for 16 and 17 percent in both successive layers 2 and 3, and for 10 and 8 percent in both successive layers 4 and 5 (Adams, Titus, and McCracken

1974). These values form the basis for the dry matter allocation per depth layer over the vertical axis, from water surface to 0.5-m depth. The values of this function (DMPC) are read from the input file and can be changed by the user. Dry matter allocation to the lower water layers is equal up to a total biomass share of 5 percent. The remaining biomass is divided proportionally over all water layers. Vertical biomass distribution pattern is recalculated and redistributed by MILFO when a rooting depth other than the nominal one (1.5 m) is chosen.

A relational diagram illustrating photosynthesis, respiration, and biomass formation of milfoil is shown in Figure 3.

Flowering, Translocation, and Senescence

The occurrence of flowering affects subsequent metabolic activity of the vegetation. The timing of flowering is, therefore, extremely important for the physiological activity and biomass formation, while the actual investment of dry matter in flowers and seeds proves to be only minor (Madsen 1997).

After flowering, scenescence sets in, and a considerable part of net production is translocated downwards to the rhizome/root crown system, while the remainder of net production is allocated according to the above-mentioned key.

The translocated material consists mainly of carbohydrates and proteins and is largely equivalent with starch (Gijzen 1985). Conversion of starch to glucose increases the dry matter with a factor 10/9, whereas the transport of glucose costs dry matter, i.e., 36/38. Thus, the total transport "cost" of downward translocation is a factor CVT = 1.05 (10/9 × 36/38). Measured data on translocation are extremely scarce for terrestrial plants and absent for aquatic plants. Translocation proved to be 29 percent of net production in cassava (Gijzen 1985) and 35 percent in certain potato varieties (Kooman 1996). Estimates of translocation in submersed plants vary from 19 percent of net production in sea grasses (Wetzel and Neckles 1996) to about 40 percent in hydrilla (Best and Boyd 1996).

In MILFO, TRANS follows a hyperbolic relationship initially set to 35 percent (TRAFAC) of net production by the senescing plant cohort, multiplied by CVT, and decreasing exponentially to zero with concomitantly decreasing biomass of the translocating plant cohort and increasing biomass of the successive growing plant cohort.

Translocation is described by the following equation:

$$TRANS1 = CVT \times GPHOT \times ((TWLG2+TWSG2+TWRG2)/(TWLG1+TWSG1+TWRG1+TWLG2+TWSG2+TWRG2)) \times TRAFAC$$

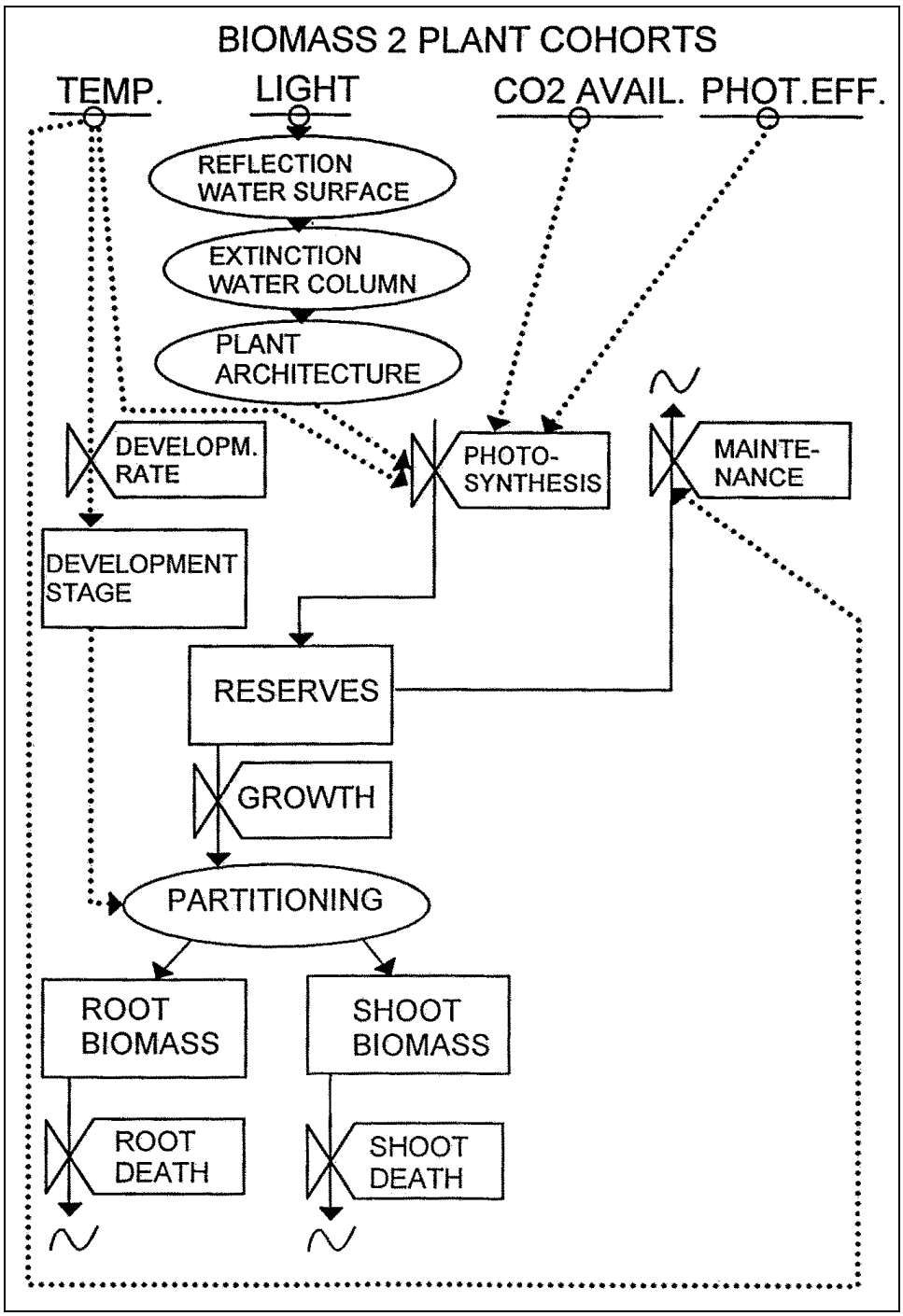

Figure 3. Relational diagram illustrating photosynthesis, respiration, and biomass formation in milfoil

where

TRANS1 = translocation rate cohort 1 (g CH_2O m^{-2} d^{-1})

CVT = conversion/transport factor (relative)

GPHOT = daily total gross CH_2O assimilation rate of community (g CH_2O m^{-2} d^{-1})

TWLG1 or *2* = total weight of green leaves cohort 1 or cohort 2 (g DW m^{-2})

TWSG1 or *2* = total weight of green stems cohort 1 or cohort 2 (g DW m^{-2})

TWRG1 or *2* = total weight of live roots cohort 1 or cohort 2 (g DW m^{-2})

TRAFAC = translocation factor (relative)

Senescence refers to the loss of capacity to carry out essential physiological processes and to the loss of biomass. The fundamental processes involve physiological aging 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. High temperature usually accelerates senescence.

In MILFO, a mechanistic approach to senescence has been chosen by setting the death rate at a certain fraction of plant biomass lost per day once the conditions for growth deteriorate. The timing and value of relative death rate (RDR) of plant cohorts 1 and 2 have been derived from field observations on shoot biomass in Lake Wingra, Wisconsin (Adams and McCracken 1974). For plant cohort 3, timing and relative death rate of the plant cohorts 1 and 2 performed well, and length of the third senescence period turned out to be similar to that of plant cohort 2.

The timing of onset of senescence was found by running the model repeatedly with different development rates, base and reference temperatures. Thus, initiation of senescence for cohort 1 was set at DVS 1.631, for cohort 2 at DVS 2.001, and for cohort 3 at 3.501.

The value for the relative death rate of the plants was found by applying the same differential equation as commonly used for simple exponential growth, to describe exponential decrease in biomass after flowering, with a negative specific decrease rate (Thornley and Johnson 1990b; Hunt 1982). An RDR of 0.042 d^{-1} was calculated following this approach.

The value for the relative death rate of the rhizome/root crown system was set at 0.00042 d^{-1} as described in the section Wintering and Sprouting of Rhizomes/ Root Crowns and Growth of Sprouts to Water Surface.

A relational diagram illustrating translocation and senescence is shown in Figure 4.

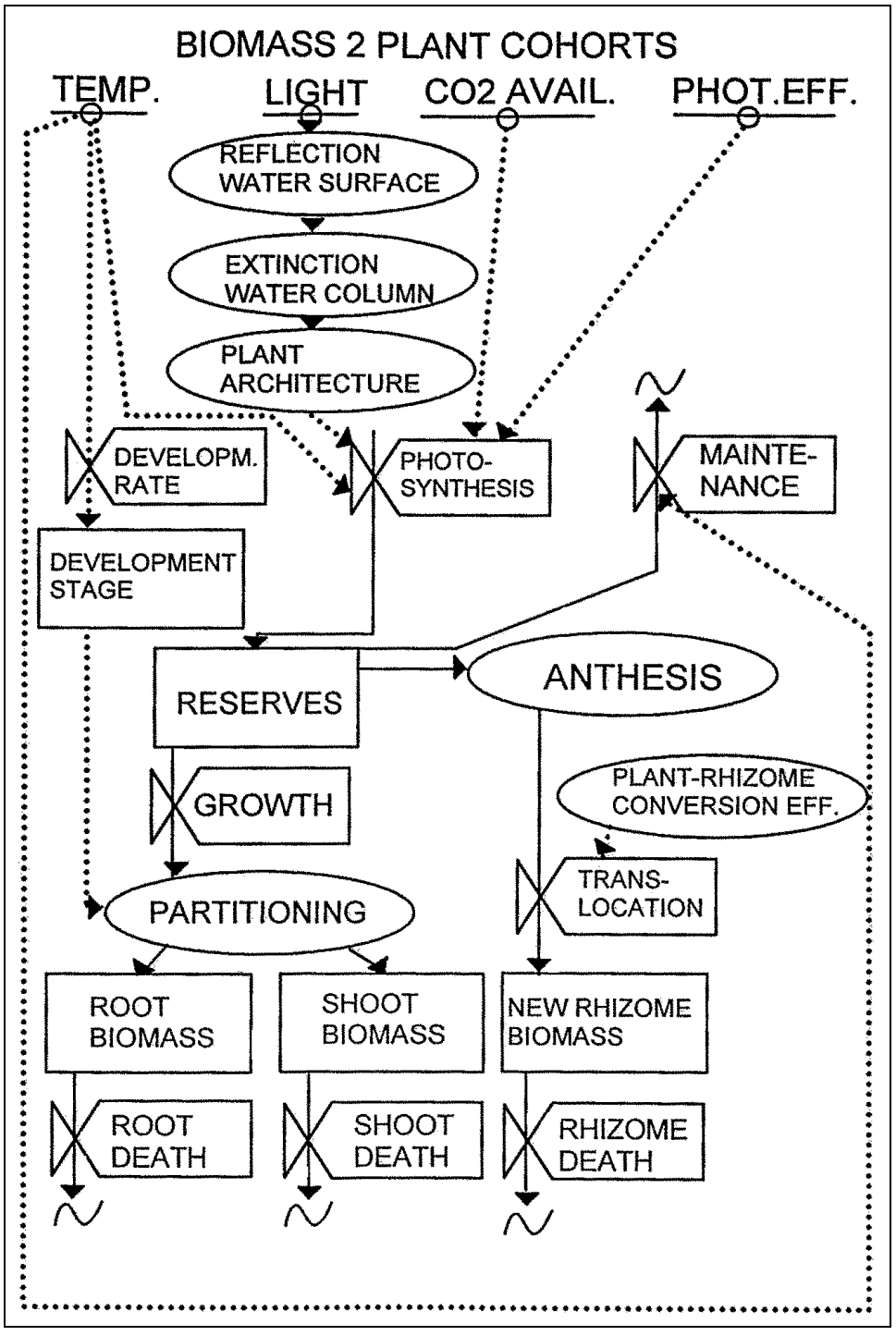

Figure 4. Relational diagram illustrating translocation and senescence following anthesis in milfoil

Choice of Parameter Values

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

Table 3
Parameter Values Used in MILFO

Parameter	Abbreviation	Value	Reference
Morphology, Phenological Cycle, and Development			
First Julian day number	DAYEM	1	
Development rate as function of temperature	DVR(T)*	0.015-0.022	Calibrated
Base temperature for juvenile plant growth	TBASE	3 ^{o}C	Calibrated
Maximum Biomass and Plant Density			
Maximum biomass	AMIN1 TGW	2,283 g DW m^{-2}	4
Plant density	NPL	11 m^{-2}	4
Wintering and Sprouting of Rhizomes/Root Crowns and Growth of Sprouts to Water Surface			
Critical rhizome weight	CRRIZ	12 g DW m^{-2}	8
Initial rhizome weight	IWGRIZ	50 g DW m^{-2}	10
Relation coefficient rhizome/root crown weight-stem length	RCSHST	12 m g DW^{-1}	3, 17
Relative death rate of rhizomes	RDRIZ	0.00042 d^{-1}	18
Relative conversion rate of rhizome/root crown weight into plant material	ROC	0.0576 g CH_2O. g DW^{-1} d^{-1}	3
Light and Photosynthesis of Plants			
Daytime temperature effect on AMX as function of DVS	AMTMP(T)	0 -1	13, 11
Potential CO_2 assimilation rate at light saturation for shoot tips	AMX	0.0165 g CO_2. g DW^{-1} h^{-1}	2, 16
Conversion factor for translocated dry matter into CH_2O	CVT	1.05	9
Initial light-use efficiency for shoot tips	EE	0.000011 g CO_2 J^{-1}	9
Reflection coefficient of irradiance at water surface	RC	0.06	5
Reduction factor to relate AMX to water pH	REDAM	0.5	7, 15
Reduction factor for AMX to account for senescence plant parts over vertical vegetation axis	REDF(T)	1.0	User def.
Plant species specific light-extinction coefficient	K(T)	0.006 m^2 g DW^{-1}	13
Water type specific light-extinction coefficient	L(T)	1.15 - 2.00 m^{-1}	7
Thickness per plant layer	TL	0.1 m	14
Maintenance, Growth, and Assimilate Partitioning of Plants			
Dry matter allocation to each plant layer	DMPC(T)	0 -1	1
Leaf dry matter allocation to each plant layer	FL(T)	0.50	1
Fraction of total dry matter increase allocated to leaves	FLV(T)	0.47	1
Fraction of total dry matter increase allocated to roots	FRT(T)	0.06	1
Fraction of total dry matter increase allocated to stems	FST(T)	0.47	1
Factor accounting for effect of daily effective temperature on maintenance respiration	TEFF(T)	0 - 12	12

(Continued)

Table 3 (Concluded)

Parameter	Abbreviation	Value	Reference
Flowering, Translocation, and Senescence			
Relative death rate of leaves (on DW basis)	RDR(T)	0.042 d^{-1}	2
Relative death rate of stems and roots (on DW basis)	RDS(T)	0.042 d^{-1}	2
Translocation (part of net photosynthetic rate)	TRAFAC	0.35	5
Site Information			
Lag period between water and air temperature	DELAY	7 d	User def.
Water depth (= rooting depth)	DEPTH	1.5 m	User def.
Total live dry weight measured (field site)	TGWM(T)	-, g DM m^{-2}	User def.
Daily water temperature (field site)	WTMP(T)	-, ^{o}C	User def.
Harvesting			
Harvesting	HAR	0 or 1	User def.
Harvesting day number	HARDAY	1-365	User def.
Harvesting depth (measured from water surface in m)	HARDEP	0.1 m<DEPTH	User def.

Notes: 1. Adams, Titus, and McCracken 1974; 2. Adams and McCracken 1974; 3. Bowes, Holaday, and Haller 1979; 4. Budd, Lillie, and Rasmussen 1995; 5. Golterman 1975; 6. Kooman 1995; 7. Lee and Kluesener 1972; 8. Madsen 1997; 9. Penning de Vries and Van Laar 1982a, b; 10. Smith and Adams1986; 11. Stanley and Nailor 1972; 12. Thornley and Johnson 1990a; 13. Titus and Adams 1979a; 14. Titus et al. 1975; 15. Titus and Stone 1982; 16. Van, Haller, and Bowes 1976; 17. Van der Zweerde 1981; 18. Vogt, Vogt, and Bloomfield 1991. *, Calibration function.

4 Performance Tests

Simulated and Measured Behavior of a Milfoil Community in Lake Wingra, Wisconsin

Nominal run

The seasonal changes in biomass of plant shoots and roots and of the rhizome/root crown system as simulated by MILFO are shown in Figure 5A and B. Simulated shoot biomass compared well with shoot biomass measured in Lake Wingra (Figure 5C). Peak biomass appeared to be reached somewhat earlier in the simulation than found in the lake; however, the latter may be due to the low frequency of field observations (no measurements between September and November). The simulated biomass of the rhizome/root crown system showed two maxima per year. Variation was within the range found in a milfoil community in the same lake in later years (Smith and Adams 1986).

Simulated transport of carbohydrates was substantial in the beginning and at the end of the growing period of each plant cohort, when carbohydrate remobilization from the rhizome/root crown system supports growth of the sprouts, and carbohydrate translocation from plant organs supports the filling of the rhizome/root crown system, respectively (Figure 6). Carbohydrate transport could be in the same range as net assimilation at the beginning and end of the growth season (Figure 7). Maintenance respiration was usually considerably lower than assimilation as well as carbohydrate transport, as can be expected at the relatively low water temperatures (Figure 7).

Running the model with the low assimilate requirements suggested to be typical for submersed aquatic vegetation by Spencer, Ryan, and Ksander (1997) showed that peak biomass of milfoil shoots would increase by a factor of 2, oscillations in biomass of the rhizome/root crown system would be greater, and final biomass of the rhizome/root crown system would be increased (Figure 8). However, as indicated in Chapter 3, the opinion of these authors is that a construction cost of 0.99 to 1.11 for milfoil plant tissues is on the low side, taking the usually high N concentrations of shoots into consideration.

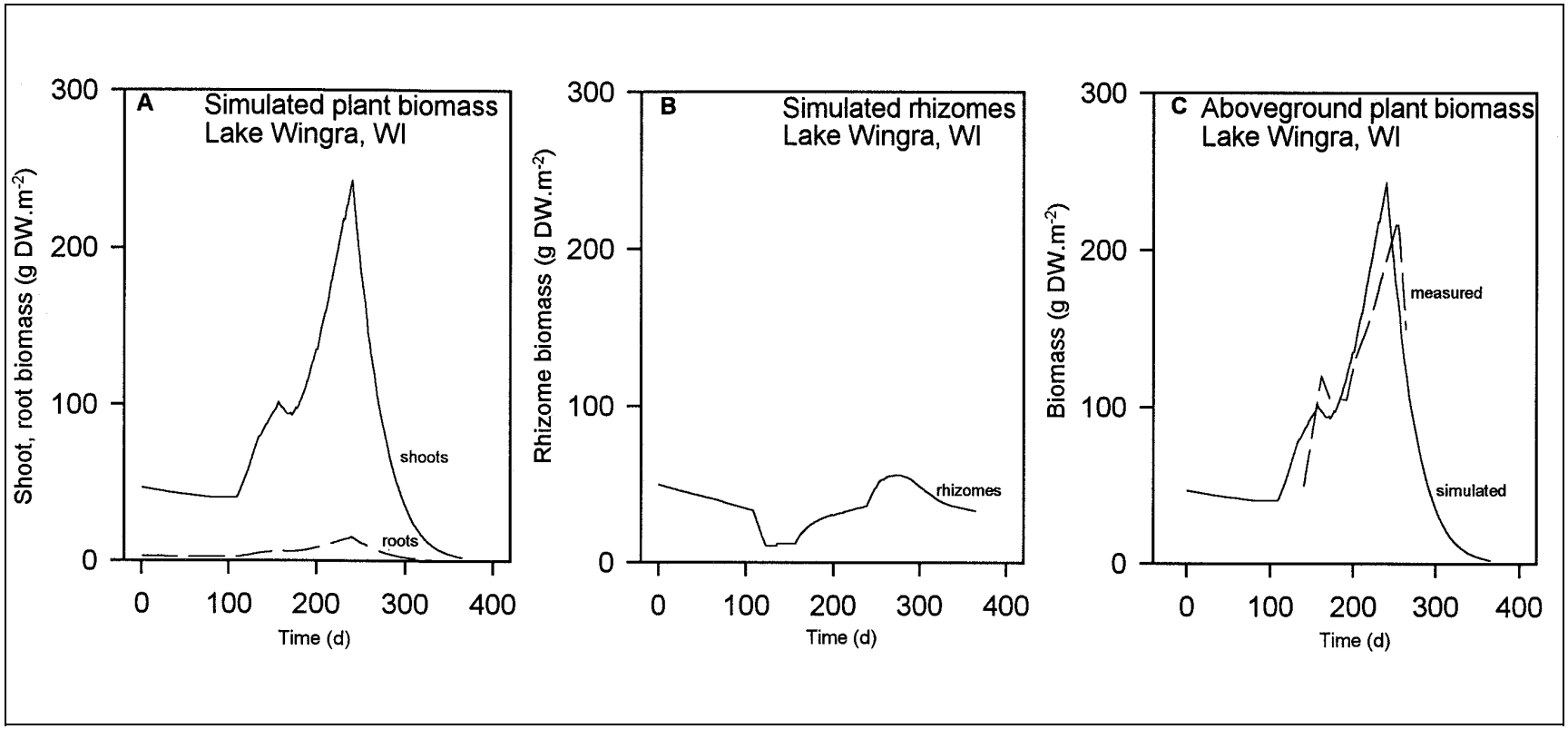

Figure 5. Simulated biomass of shoots, roots, and rhizomes/root crowns and measured shoot biomass of a milfoil community in Lake Wingra, Wisconsin (Nominal run) (Initial values of biomass on shoots (Adams and McCracken 1974) and rhizomes/root crowns (Smith and Adams 1986) extrapolated to Julian day number 1. Climatological data 1970, Lake Wingra, Wisconsin (longiude 89° 20' W, latitude 43° 08' N). Measured shoot biomass data 1970 (Adams and McCracken 1974))

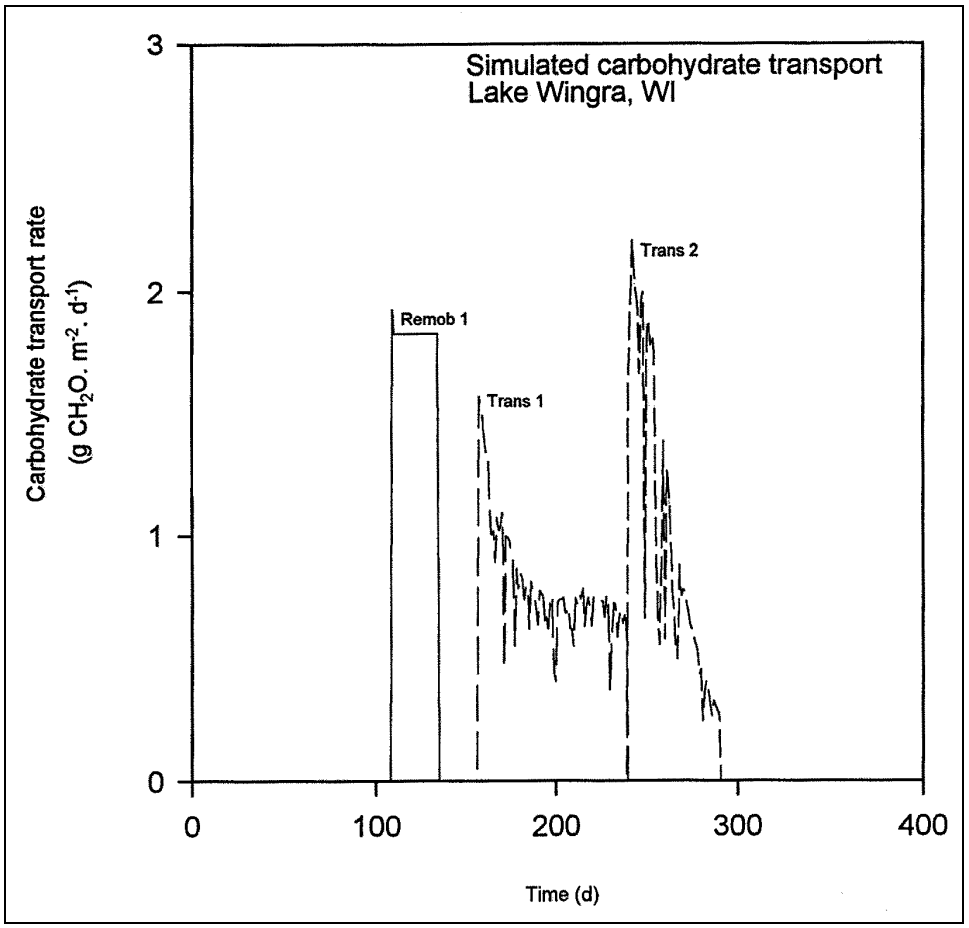

Figure 6. Simulated behavior of carbohydrate flow through plant compartments (Carbohydrate remobilization and upward transport from rhizomes/ root crowns are used for initial growth of each plant cohort. Down-Ward carbohydrate translocation into rhizomes/root crowns occurs during anthesis and senescence of each plant cohort (Initial biomass and climatological data as in nominal run))

Running the model for the same year and lake, but with only rhizomes/root crowns initially present (Figure 9B), showed that plant biomass of both cohorts was greatly reduced and critical weight of the rhizome/root crown system was reached more often than with initial plant biomass present (Figure 9A; nominal run). This large difference in peak biomass is due to the inability of the plant community to fully capture the high spring irradiance at this latitude of 43 °N without wintering shoots. Thus, wintering shoots provide a distinct advantage for this plant species.

Running the model with (24-hr average) air temperatures lagging 7 days behind water temperatures or measured water temperatures as forcing variables yielded similar biomass values, despite the fact that instantaneous assimilation rates varied less with water temperatures than with air temperatures, and assimilation rates had shifted somewhat in time (Figure 10). This illustrates the

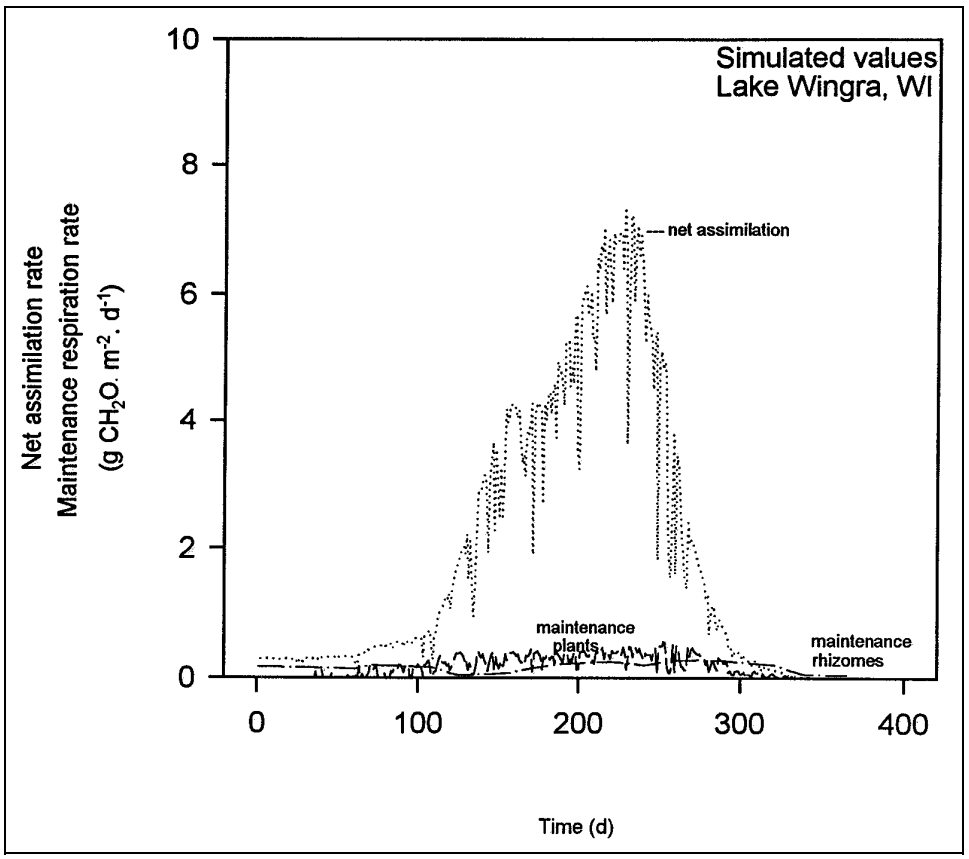

Figure 7. Simulated rates of daily net assimilation and maintenance respiration of a milfoil community in Lake Wingra, Wisconsin (Initial biomass and climatological data as in nominal run)

usefulness of inclusion of both temperature options in the model, facilitating use of the model by users who do not possess a full data set of water temperatures for the water body for which they desire to run the model. It has to be cautioned, however, that the relationship between the temperatures of air and of each water body concerned may differ since temperatures within each water body are influenced by catchment morphometry, wind speed, fetch, mixing processes, and upward seepage, etc. In the experience of these authors, however, a lag period of 7 days between air and water temperatures usually described this relationship well for shallow water bodies (up to 5-6 m), without large inflows of groundwater.

Effects of year-to-year differences in climate

The model was run with initial biomass values and local climatological data as inputs for a different year, 1972 (Figure 11). A run with water temperatures of a previous (1970) year yielded less biomass (Figure 11A) than actually measured (Figure 11C). A run with air temperatures of 1972, in contrast, yielded less biomass for the first plant cohort, but similar biomass as measured for the

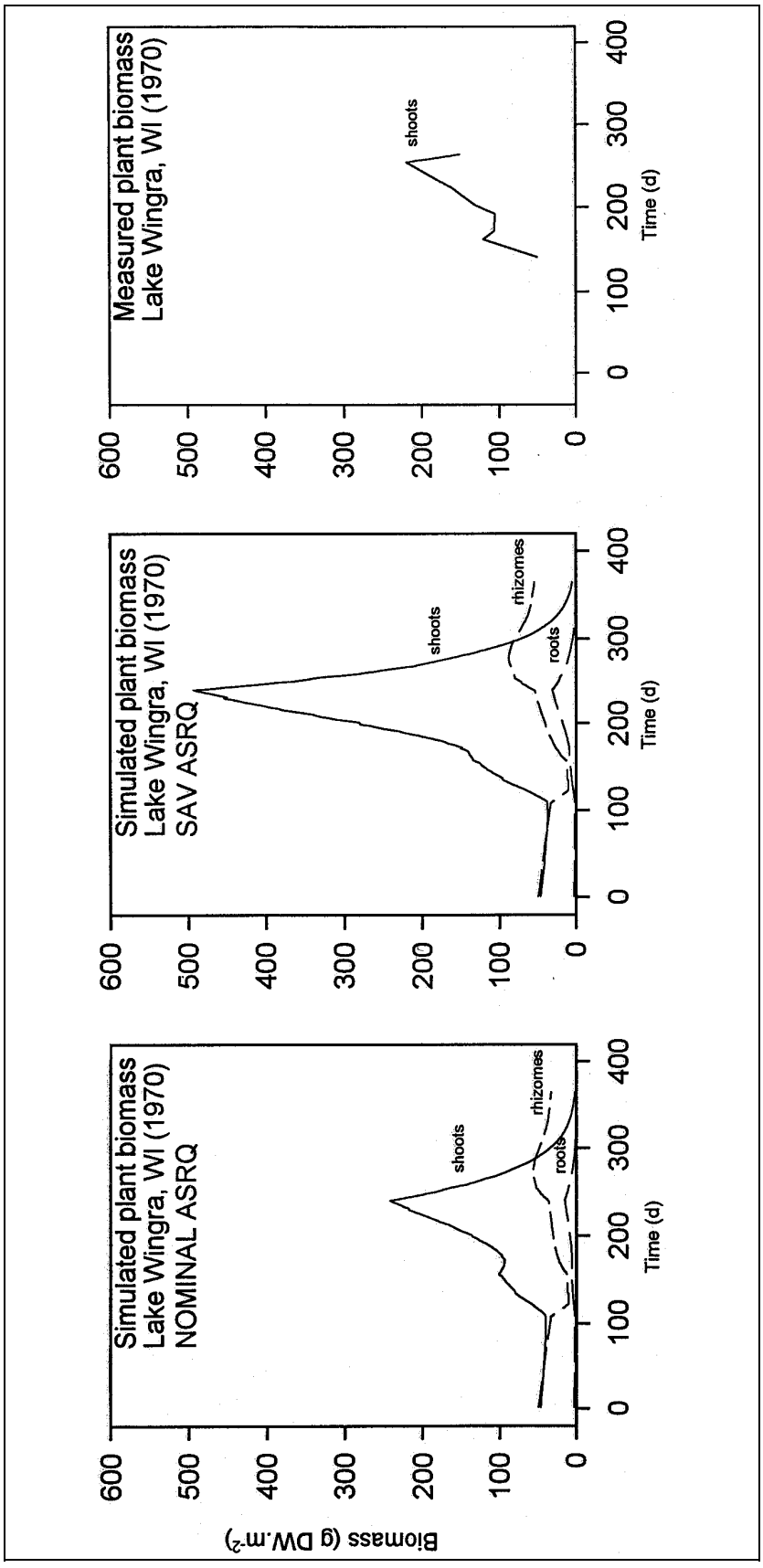

Figure 8. Simulated biomass with assimilate requirement for growth (ASRQ) value nominal or as suggested for submersed aquatic vegetation (SAV) and measured shoot biomass of a milfoil community in Lake Wingra, Wisconsin (ASRQ SAV data Spencer et al. 1977) (Initial biomass and climatological data as in nominal run)

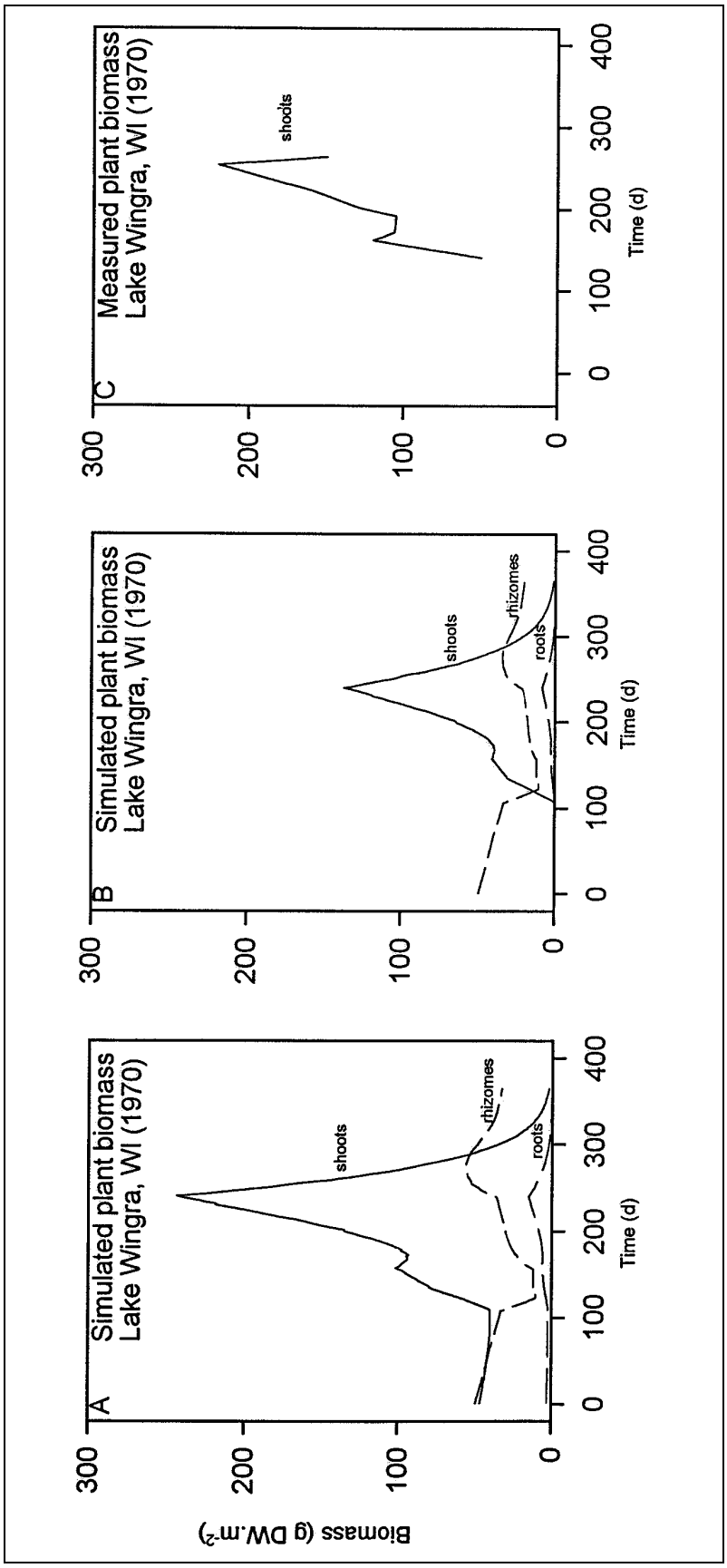

Figure 9. Simulated biomass with (A) and without (B) initial plant biomass and measured (C) shoot biomass of a milfoil community in Lake Wingra, Wisconsin ((A) Initial biomass values and climatological data as in nominal run; (B) initial plant biomass zero and rhizomes/root crowns as in nominal run. Measured shoot biomass 1970 (Adams and McCracken 1974). Climatological data as in nominal run)

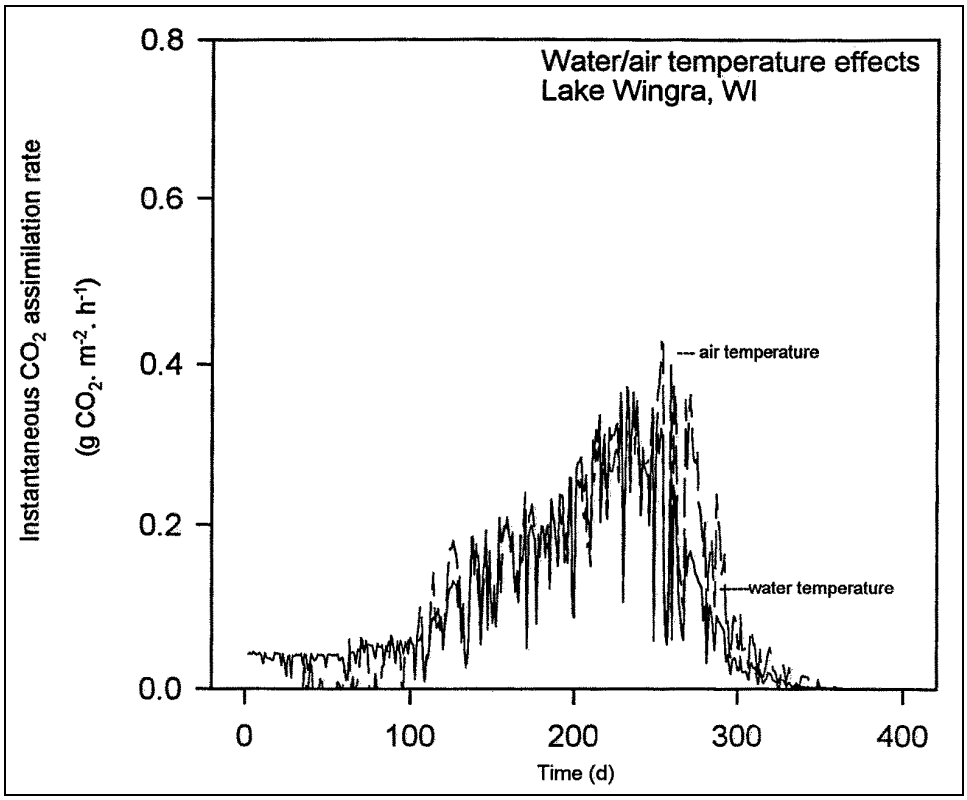

Figure 10. Simulated photosynthetic rates of a milfoil community in Lake Wingra, Wisconsin, with water or air temperatures as input (Initial biomass and climatological data as in nominal run)

second cohort (Figure 11B). However, irradiances in both years, 1970 and 1972, differed in that total irradiance and, consequently, temperature sum were higher in 1970 than in 1972 (particularly in spring), and, thus, higher biomass production was to be expected using water temperatures of 1970. This leads one to believe that the early peak biomass value measured in 1972 is an overestimate. The latter suggestion is supported by the fact that the measured biomass level could neither be attained by running the model with considerably decreased light-extinction coefficients tentatively indicative for the clear water phase in spring, which is typical for this lake.

Simulated and Measured Behavior of a Milfoil Community at Other Latitudes

To investigate whether the model was able to simulate behavior of a milfoil community at other sites, runs were made for a site at a more southern latitude, Lake Guntersville, Alabama. Behavior of milfoil in this lake is particularly interesting because the lake is long, oriented from north-east to south-west, and situated at a latitude around 34 °N, being very close to tropical (33 °N). Biomass of milfoil communities in this lake has been described as having a high

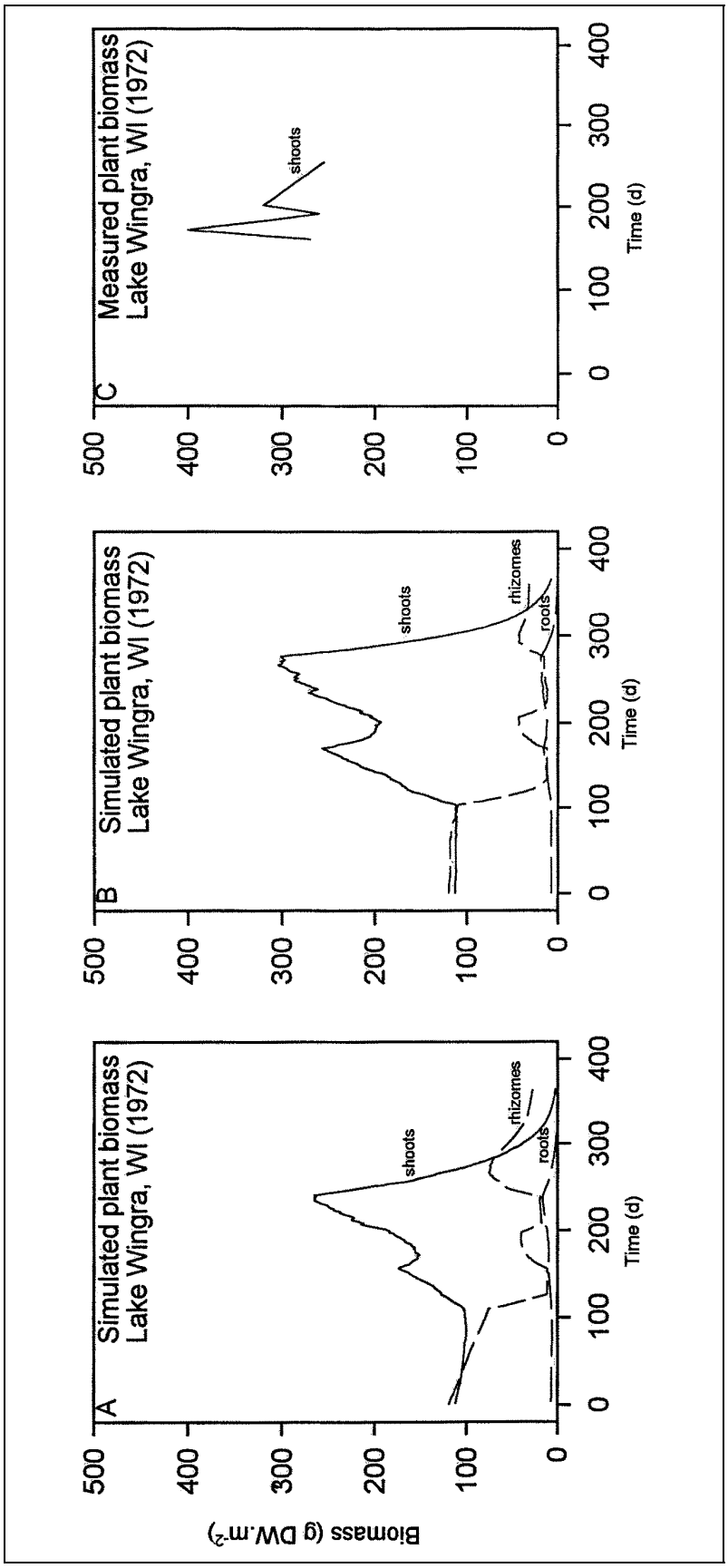

Figure 11. Simulated biomass with (A) water temperatures of a different year, 1970, or (B) air temperatures of the same year, 1972, as input and (C) measured shoot biomass, 1972, of a milfoil community of Lake Wingra, Wisconsin (Initial values on biomass of shoots and rhizomes/root crowns (A) and (B) extrapolated to Julian day number 1, 1972 (Titus et al. 1975). Climatological data 1972, Lake Wingra, Wisconsin. Measured shoot biomass 1972 (Titus et al. 1975))

variation in time and space (Grace and Wetzel 1978; Stanley et al. 1976); unfortunately, in these descriptions, no attention was paid to differences in latitude of the various sites within the lake nor to local differences in temperature or other environmental factors. It was mentioned, however, that flowering and the subsequent sloughing period were less predictable in southern locales than in northern ones.

Initial plant biomass values measured at a site in this lake studied in 1990 were very low, possibly because of grass carp herbivory the previous year,[1] and initial rhizome/root crown mass has been set at the critical value of 12 g DW m^{-2}. Rooting depth in the simulation was kept at 1.5 m, although in reality water depth may have varied over 1.0 $\pm$ 0.7 m within a year (Stanley et al. 1976).

Simulated biomass of the first plant cohort remained low. Only one apparent biomass peak could be distinguished, which originated from the second plant cohort. Simulated shoot biomass coincided in timing with measured shoot biomass, but the simulated peak was lower than the measured one (Figure 12). The latter difference may be a consequence of temporal decreases in water depth during the year; depth was kept constant in the simulation, leading to an underestimate of simulated plant biomass. Relatively small changes in water depth can cause large changes in net assimilation and biomass production (See Chapter 6).

To investigate which consequences a warm year for the milfoil community in this lake might have, when three instead of two plant cohorts are expected to be active, a model run was made with the same initial biomass and climatological data and a third cohort active (Figure 13). It turned out that in one year far higher shoot biomass values of approximately 950 g DW m^{-2} could be generated, similar in timing and value to maximum biomass values reported for the nearby Melton Hill Lake (Stanley et al. 1976), with rhizome/root crown biomass accumulating towards the end of the year. However, similar biomass values could also be reached earlier in the year when higher initial (nominal) biomass values were used as input, and only two cohorts active; in the latter case, biomass peaks of both plant cohorts appeared, and rhizome/root crown biomass was well above the critical level but not accumulating.

Simulation of a milfoil community in the Kashmir lakes, India, demonstrated that only one maximum in shoot biomass was generated (Figure 14), with a value somewhat higher than the measured range of 288 to 640 g DW m^{-2} and a rhizome/root crown biomass varying over a range close to the measured range of 32 to 160 (Zutschi and Vass 1973). The higher simulated shoot biomass may be due to the use of climatological data from Patancheru, which is located more south, and thus warmer, than the Kashmir lakes from which the measured biomass values originated (Patancheru 17 °N, Kashmir lake 32 °N); however, more northern climatological data from India were not available.

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[1] Personal Communication, M.S. Stewart, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

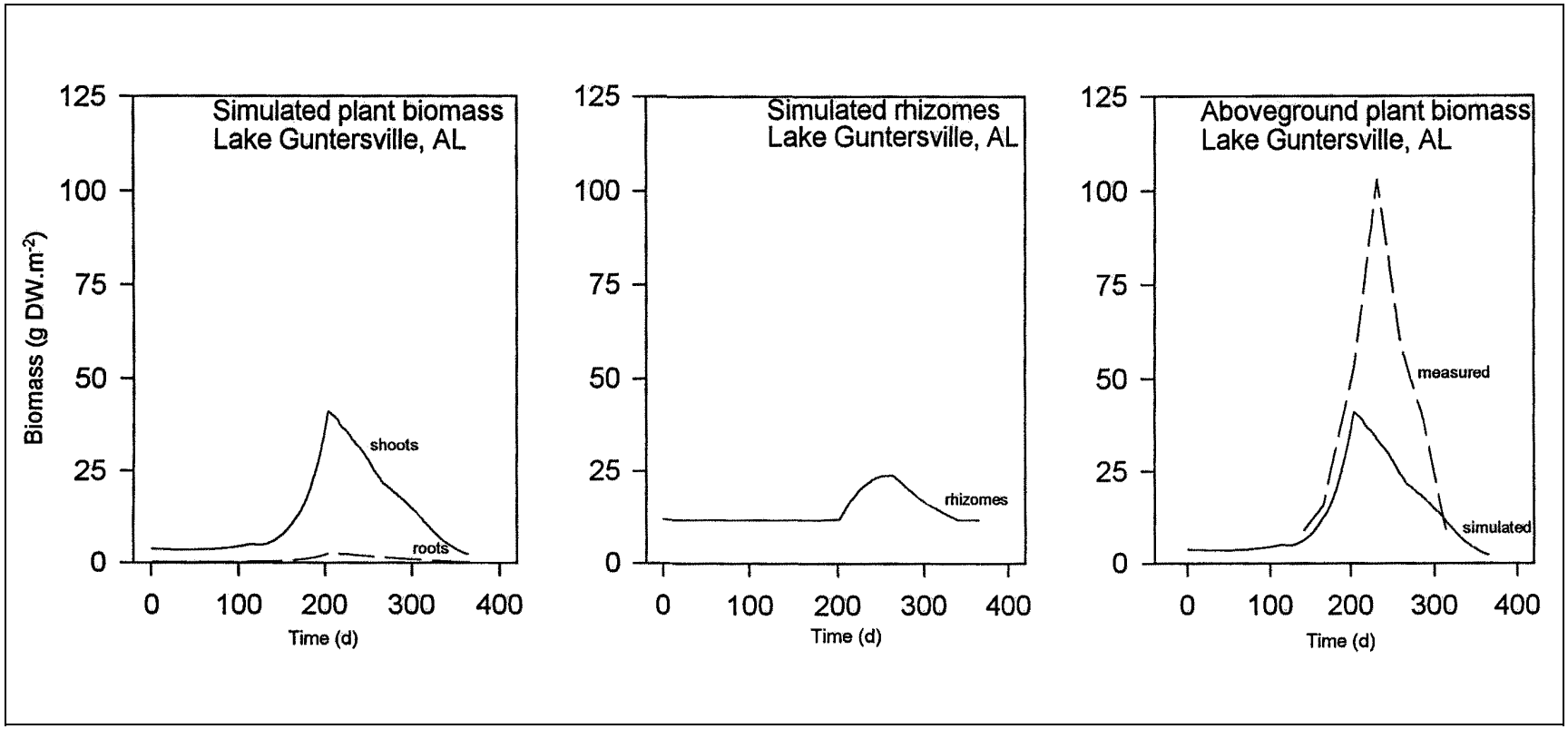

Figure 12. Simulated biomass of shoots, roots, and rhizomes/root crowns and measured shoot biomass of a milfoil community in Lake Guntersville, Alabama (Initial values on biomass of shoots and rhizomes/root corwns (M. S. Stewart 1990, unpublished) extrapolated to Julian day number 1. Climatological data 1990, Lake Guntersville, Alabama (longitude 85° 50' W, latitude 34° 08' N). Measured shoot biomass 1990 (M. S. Stewart 1990, unpublished))

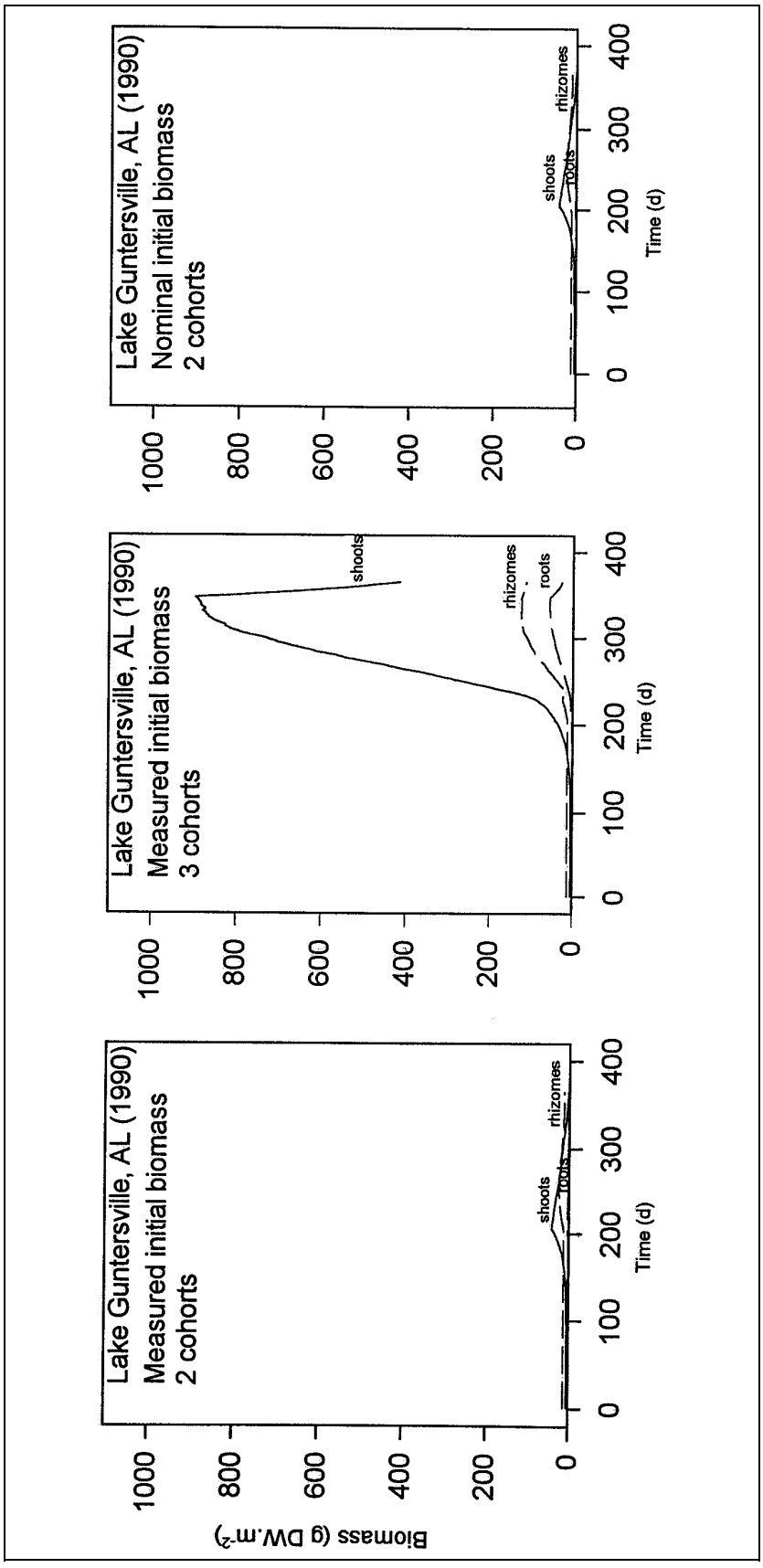

Figure 13. Simulated biomass of shoots, roots, and rhizomes/root crowns of a milfoil community in Lake Guntersville, Alabama, composed of two or three plant cohorts and using various initial biomass values (Measured initial biomass vlaues—cf. M. S. Stewart unpublished (1990) and nominal ones as for nominal run. Climatological data 1990, Lake Guntersville, Alabama)

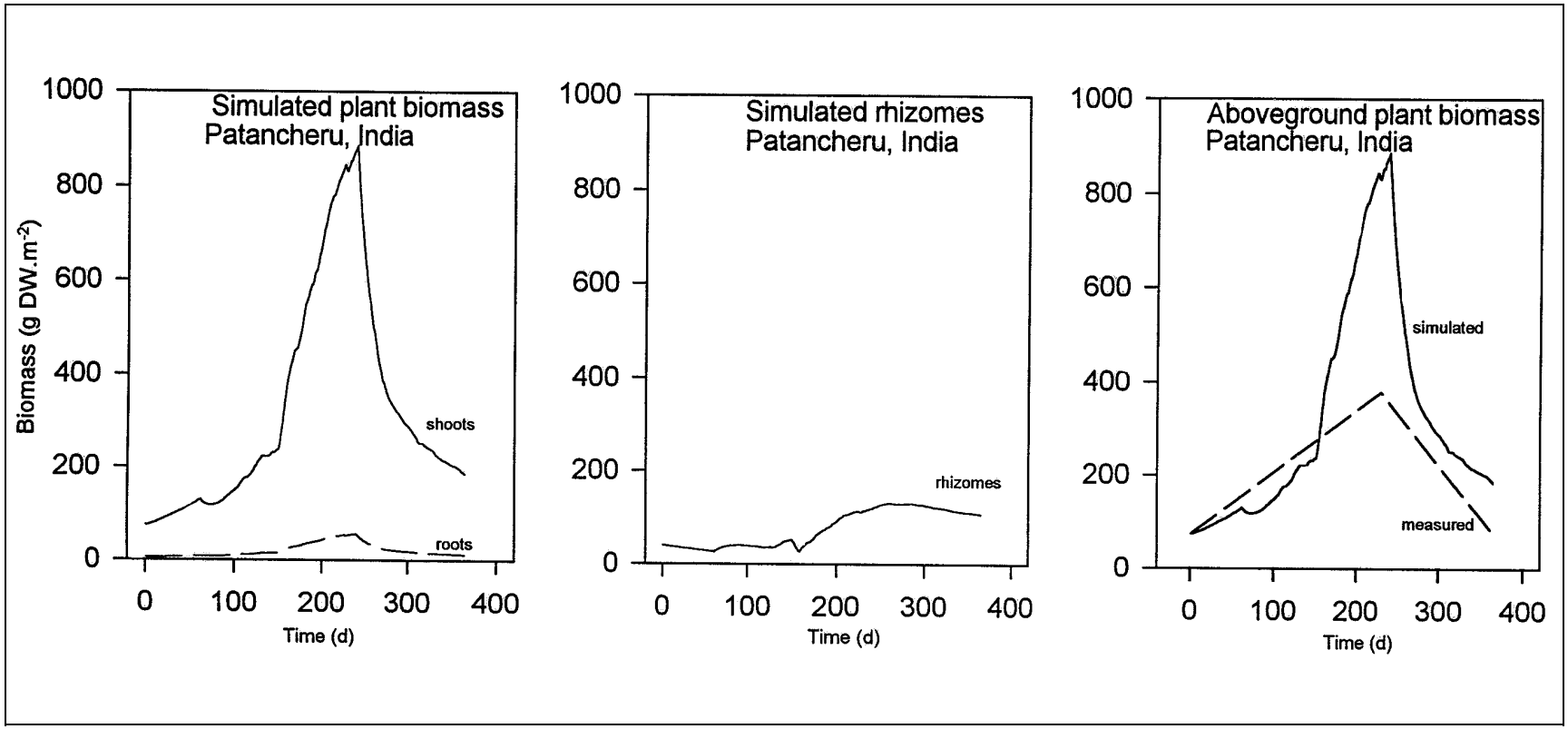

Figure 14. Simulated biomass of shoots, roots, and rhizomes/root crowns and measured shoot biomass of a milfoil community in Kashmir lakes, India (longitude 74 to 80° E, latitude 32° N; Initial values on biomass of shoots and rhizomes/root crowns mean of range published for 1970s (Zutschi and Vass 1973). Climatological data, 1978, Patancheru, India (longitude 78° 28' E, latitude 17° 27' N). Measured shoot biomass mean of range published for 1970s (Zutschi and Vass 1973))

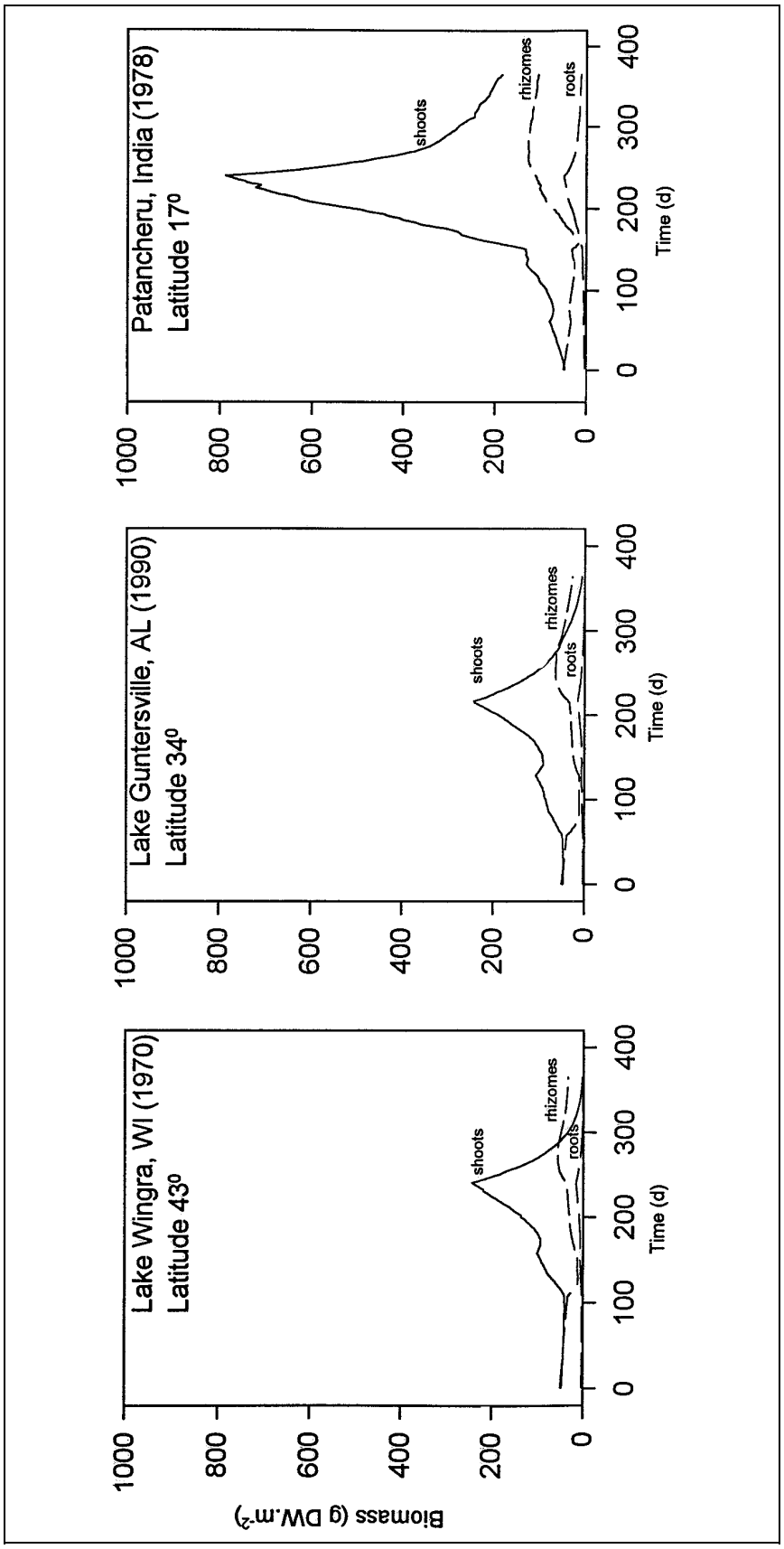

Figure 15. Simulated biomass of a milfoil community at various latitudes (Initial biomass values nominal. Climatological data, 1970, Lake Wingra, Wisconsin; 1990, Lake Guntersville, Alabama; 1978, Patancheru, India)

It was investigated whether milfoil benefits from adaptation to the tropics by producing thinner leaves. This was done because a higher leaf-surface area:dry weight ratio (K-value) has been found for milfoil in Japan (0.01 m^2 g DW^{-1}; Ikusima 1970) than in Wisconsin (0.006 m^2 g DW^{-1}; Titus and Adams 1979a). It turned out that timing was very similar and simulated plant biomass about 10 percent higher using the higher K-value (data not shown).

Running the model with nominal biomass values and climatological data typical for sites representative for temperate, temperate to tropical, and tropical climates (Figure 15) indicated that (a) in all climates one clear biomass peak is generated; (b) only in a temperate climate the biomass peak of both first and second cohorts can be distinguished; that is, from biomass values alone; flowering coinciding with every biomass maximum is always a suitable indicator, but it is often not noted in biomass studies; (c) peak biomass is expected to be highest in the tropics; that highest biomass values have been found at northern latitudes may be because most biomass studies on aquatic plants have been performed at the latter latitudes and biomass data from tropical areas are extremely scarce; and (d) end-of-year accumulation of rhizome/root crown biomass usually occurs in tropical, but not in temperate climates; that is, when three plant cohorts are active.

5 Sensitivity Analysis

A sensitivity analysis of a simulation model is required to assess the parameters likely to strongly affect model behavior. The current 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 3, under Lake Wingra, Wisconsin, conditions at 1.5-m water depth. In a 1-year simulation starting with 50 g DW m^{-2} biomass for both plants and rhizome/root crown system, the value of the parameter under study was changed (Table 4). The results were compared with those of a nominal 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 10 parameters on two variables, 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. The current sensitivity analysis was performed over a 1-year period.

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

where

$yield_i$ = value at parameter value i

$yield_r$ = value at reference parameter value

$param_i$ and $param_r$ as above

Maximum plant biomass proved most sensitive to changes in potential CO_2 assimilation at light saturation for shoot tips and very sensitive to changes in light-use efficiency. This is not surprising because the model is based on carbon flow through the plant. Changes in plant density did affect maximum plant biomass, but far less than photosynthetic activity at light saturation and light-use efficiency. Most parameter changes, except in critical rhizome weight, influencing rhizome/root crown biomass affected maximum plant biomass

substantially, for example, initial rhizome weight, conversion rate into plant material, and translocation rate. In general, the same parameters as those for maximum plant biomass were important determinants of end-of-year rhizome/root crown biomass, with potential CO_2 assimilation at light saturation, light-use efficiency, and relative death rate exhibiting the largest effects. This illustrates the utmost importance of the rhizome/root crown system for local survival and biomass production of milfoil.

Earlier or later flowering biotypes are suited to different environments. The effect of flowering date can be tested with the model by varying the development rate of the vegetation. Slower rates represent later and faster, earlier biotypes. Development rate slower or faster than the nominal rate leads to lower biomass. Faster development leads to a shorter growing season and less vegetative dry matter, incomplete light interception, and lower carbohydrate availability for organ formation. At the same time, however, the rate of organ formation increases, but the duration of each organ formation shortens. Intuitive prediction of biotype behavior under such highly variable climatic conditions is therefore hazardous. The model shows some promise in being able to reproduce some of these complex responses of the vegetation and may be useful in evaluating long-term implications of differences in development rate.

Although as far as is known, no publications exist on what the temperature requirements of aquatic plants are to traverse development from anthesis to senesced state; differences in postanthesis development rates for several wheat and rice cultivars are known to be small and have little effect on yield (Van Keulen 1976).

Maximum plant biomass proved only sensitive to a decrease in preanthesis development rate, while end-of-year rhizome/root crown biomass was sensitive to any change in preanthesis or postanthesis development rate.

Table 4
Relative Sensitivity of Two Model Variables to Deviations in Parameter Values from Their Nominal Values (As presented in Table 3) (Results were obtained in a 1-year simulation under Lake Wingra, Wisconsin, 1970 conditions, starting with both plant and rhizome biomass being 50 g DW m^{-2})

Parameter Name	Parameter Value	Relative Sensitivity	
		Maximum Live Plant Biomass	End-of-Year Rhizome/Root Crown Biomass
Potential CO_2 assimilation rate at light saturation for shoot tips	0.0165		
	0.0200	1.96	2.00
	0.0149	1.97	2.02
Light-use efficiency	0.000011		
	0.000013	1.10	1.14
	0.000008	1.22	1.25
Relative death rate leaves, stems, and roots	0.042		
	0.050	-0.62	-1.01
	0.034	-0.77	-1.36
Initial rhizome weight	50		
	60	0.20	0.17
	40	0.22	0.18
Critical rhizome weight	12		
	14.4	0	0.05
	9.6	0	0.06
Relative conversion rate of rhizomes into plant material	0.0576		
	0.069	0.19	0.17
	0.046	0.21	0.18
Translocation rate	0.35		
	0.42	-0.13	0.57
	0.28	-0.14	0.72
Plant density	11		
	13	0.16	-0.79
	9	-0.16	0.79
Preanthesis development rate	0.015		
	0.018	-0.23	-0.81
	0.012	-0.26	-0.99
Postanthesis development rate	0.015		
	0.018	-0.69	-0.89
	0.012	-0.79	0.66

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, parameter changes were based on value ranges taken from literature, which sometimes differed more than 20 percent from the nominal parameter value given in Table 3.

Climate

Climate greatly affects plant-species distribution, phenological cycle, and biomass production. MILFO 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 more southern climatological conditions, i.e., changing the latitude from 43 to 34° N demonstrated that end-of-year rhizome/root crown biomass is far more sensitive to this climate change than maximum plant biomass (Table 5).

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 ° 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 ° incoming angle of the radiation and at very rough water surfaces.

Increasing the light reflection coefficient to 1 annihilated plant biomass within the year. That nevertheless low RS values were found (Table 5) is an artifact of the calculation method employed. Decreasing the light-reflection

Table 5
Environmental Factor Analysis, Expressed as Relative Sensitivity of Two Model Variables to Deviations in Parameter Values from Their Nominal Values (As presented in Table 3) (Results were obtained in a 1-year simulation under Lake Wingra, Wisconsin, 1970 conditions, starting with both plant and rhizome/root crown biomass being 50 g DW m^{-2})

Parameter Name	Parameter Value	Relative Sensitivity	
		Maximum Live Plant Biomass	End-of-Year Rhizome/Root Crown Biomass
Climate			
Lake Wingra (1980)	Latitude 43° N	-	-
Lake Guntersville (1990)	Latitude 34° N	-0.01	0.89
Light-reflection coefficient at water surface	0.06		
	1.00 (+1567%)	-0.05	-0.04
	0.00* (-100%)	-0.07	-0.07
Light-extinction coefficient water column	1.80		
	2.16 (+20%)	-0.92	-1.01
	1.44 (-20%)	-1.12	-1.01
Water depth	1.5		
	1.8 (+20%)	-0.31	-0.31
	1.2 (-20%)	-0.34	-0.33

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

coefficient greatly increased maximum biomass and end-of-year rhizome/root crown biomass (Table 5).

Light-Extinction Coefficient of Water Column

A light-extinction coefficient of on average 1.80 m^{-1} is used for nominal runs of the model (Lake Wingra, Wisconsin).

Changing the light-extinction coefficient of the water column demonstrated large effects on maximum plant and end-of-year rhizome/root crown biomass. The often relatively small effect of an increase in light-extinction coefficient relative to the nominal value may be due to (a) the high nominal value and (b) the spatial distribution of milfoil plant biomass with typically 61 percent in the upper 0.5-m water layer. A nominal value of 2 m^{-1} has been found typical for eutrophic fen lakes where submersed vegetation can just persist (Best, De Vries, and Reins 1985). The large effect of a decrease in light-extinction coefficient can largely be explained by greatly increased growth of the first plant cohort,

boosting the rhizome/root crown system by translocation, thus providing a better start for the subsequent plant cohort(s) and resulting in a higher peak biomass.

Water Depth

MILFO has been calibrated for a water depth of 1.5 m, the rooting depth of an extensively studied milfoil community in Lake Wingra, Wisconsin. The model has the capability to respond to fluctuations in water level with year, by (re)distributing plant biomass over the desired water depth (number of water layers; see Chapter 3). This technique for biomass distribution over the vertical axis of the community works well and gives realistic outcomes over a depth range of 0.5 to 6 m.

Running MILFO at an increased or decreased water depth showed similar, relatively small effects on maximum plant and end-of-year rhizome/root crown biomass (Table 5).

The RS of peak plant biomass and end-of-year rhizome/root crown biomass to changes in water depth was relatively small and far lower than to changes in the light-extinction coefficient.

The current sensitivity and environmental analyses give indications of the sensitivity of maximum plant biomass and end-of-year rhizome/root crown systems for variations in plant parameters and environment over a 1-year period. It is to be expected, however, that the small changes that occurred over this relatively short period will increase with time and that these extrapolations in time will yield information on the likelihood for plant populations to ultimately persist or become extinct. Particularly, increases in water turbidity because of increased phytoplankton or periphyton growth stimulated by eutrophication, increased erosion/resuspension, and seasonal herbivory have been mentioned as decisive for the persistence of submersed plant populations.

7 Application Possibilities

MILFO can be used to assess behavior of a milfoil community under various site-specific and climatological conditions as demonstrated in Chapters 4, 5, and 6, and it can be run with user-specified input values for plant and rhizome/root crown biomass.

Effects of man-made control activities like harvesting at different times and at various water depths can be calculated also (Table 6). Thus, in the latter case it can be used as a tool for aquatic plant management agencies. From this table it can be concluded that harvesting at the end of May to a water depth of 0.8 m requires removal of a relatively low amount of biomass, but yields the lowest peak biomass and end-of-year rhizome/root crown biomass. This situation can be seen as favorable to control milfoil. In contrast, harvesting later in the year requires removal of relatively more plant biomass or allows for a relatively higher end-of-year rhizome/root crown biomass. Removing only the top layer of the plant community later in the year may even lead to increased maximum plant and end-of-year rhizome/root crown biomass, probably because of a temporarily higher light penetration within the community.

Table 6
Effects of Mechanical Harvesting Date and Depth on Plant and Rhizome/Root Crown Biomass (Results were obtained in a 1-year simulation under Lake Wingra, Wisconsin, 1970 conditions, starting with both plant and rhizome/root crown biomass being 50 g DW m^{-2})

Harvest Time	Harvest Depth m	Live Plant Biomass 28 August g DW m^{-2}	Preharvest Biomass g DW m^{-2}	Postharvest Biomass g DW m^{-2}	Day with Zero Plant Biomass	End-of-Year Rhizome/ Root Crown Biomass g DW m^{-2}
End of May	0.8	84	100	21	>365	13
End of June	0.8	143	106	5	>365	18
End of July	0.8	49	171	8	>365	14
End of July	0.1	300	171	141	>365	41
End of August	0.8	258	244	11	>365	18
End of September	0.8	258	100	4	>365	30
End of October	0.8	258	33	1	>365	33

The current version of MILFO 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 MILFO to a Geographical Information System through an appropriate interface like AEGIS+ (Luyten et al. 1994). To facilitate use of the current model, a user manual has been prepared (Best and Boyd, in preparation).

8 Discussion

The current model gives a reasonable description of the dynamics in plant and rhizome/root crown biomass of an established milfoil 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 MILFO 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 cm^{-2} s^{-1}; Van, Haller, and Bowes 1976), and (c) no field data on periphyton biomass concomitant with photosynthetic activity are available at this time. Light attenuation by periphyton is expected to have large effects on submersed macrophyte species with most of their biomass concentrated just above the hydro-soil (like *Ceratophyllum demersum*; Best and Dassen 1987; Best and Jacobs 1990) and macrophytes with biomass that usually remains below the water surface (like *Vallisneria americana*; Titus and Adams 1979a).

Senescence, resulting in decreasing photosynthetic activity in aging plant parts, has been included into the model formulation. Although data quantifying these effects in milfoil were available (Adams and McCracken 1974; Adams, Titus, and McCracken 1974), running the model demonstrated that virtually no effect on peak biomass was noticeable, probably largely because of 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   : 16 July 1997                                                                                       *
*                                                                                                             *
* 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          I *
* RDD           R4      Daily shortwave radiation                       J/m2/d        I *
* 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 wind speed                        m/s           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>
*     MILFO

      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, DDELAY
      CHARACTER WUSED*6

*-----State variables, initial values and rates
      REAL DVS   ,NUL   ,DVR   ,TMPSUM,TMP2
      REAL TWLG1 ,TWSG1 ,TWRG1 ,IWLG1 ,IWSG1,IWRG1
      REAL TWLD1 ,TWSD1 ,TWRD1 ,IWLD1 ,IWSD1,IWRD1
      REAL TWLG2 ,TWSG2 ,TWRG2 ,IWLG2 ,IWSG2,IWRG2
      REAL TWLD2 ,TWSD2 ,TWRD2 ,IWLD2 ,IWSD2,IWRD2
      REAL TWLG3 ,TWSG3 ,TWRG3 ,IWLG3 ,IWSG3,IWRG3
      REAL TWLD3 ,TWSD3 ,TWRD3 ,IWLD3 ,IWSD3,IWRD3
      REAL NGLV1 ,NGST1 ,NGRT1 ,DLV1  ,DST1 ,DRT1
      REAL NGLV2 ,NGST2 ,NGRT2 ,DLV2  ,DST2 ,DRT2
      REAL NGLV3 ,NGST3 ,NGRT3 ,DLV3  ,DST3 ,DRT3
      REAL TWLVG ,TWLVD ,TWSTG ,TWSTD ,TWRTG,TWRTD
      REAL TWGRIZ,TWRIZD,IWGRIZ,IWRIZD,TGRIZ

*-----Model parameters
      REAL AMX   ,CVT   ,DAYEM ,DELAY ,DEPTH ,EE
      REAL HAR   ,HARDAY,HARDEP
      REAL NPL   ,RC    ,RCSHST,REDAM , RDRIZ
      REAL ROC   ,TBASE ,TRAFAC,TL

*-----Auxiliary variables
      REAL AMAX  , AMTMP , ASRQ  , COSLD , WTMP
      REAL DAVTMP, DAY   , DAYL  , DDTMP , DSO
      REAL DSINB , DSINBE, DTEFF , DTGA  , FGROS
      REAL FLV   , FRT   , FRT1  , FRT2  , FST
      REAL GLV   , GPHOT , GRT   , GST   , GTW
      REAL MAINT , MAINTS, PI    , RDR   , RDS
      REAL REMOB1, REMOB2, REMOB3, SC    , SINLD
      REAL SUM   , TEFF  , TGW   , TGWM  , TRANS1
      REAL TRANS2, TRANS3, TREMOB, TW    , WLV
      REAL WST   , WRT   , MAINRT, YRNUM

*-----AFGEN functions
      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   =  730)
      DIMENSION LT(IMN1), KT(IMN1)
      REAL TGWMT
      INTEGER IMMEAS, ILMEAS
      PARAMETER (IMMEAS =  40)
      DIMENSION 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 TEFFT
      INTEGER IMTEFF, ILTEFF
      PARAMETER (IMTEFF =  40)
      DIMENSION TEFFT (IMTEFF)
      REAL WTMPT
      INTEGER IMWTMP, ILWTMP
      PARAMETER (IMWTMP =  730)
      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 ('CRRIZ ',CRRIZ )
          CALL RDSREA ('IWGRIZ',IWGRIZ)
          CALL RDSREA ('IWRIZD',IWRIZD)
          CALL RDSREA ('IWLD1 ',IWLD1 )
          CALL RDSREA ('IWLD2 ',IWLD2 )
          CALL RDSREA ('IWLD3 ',IWLD3 )
          CALL RDSREA ('IWLG1 ',IWLG1 )
          CALL RDSREA ('IWLG2 ',IWLG2 )
          CALL RDSREA ('IWLG3 ',IWLG3 )
          CALL RDSREA ('IWRD1 ',IWRD1 )
          CALL RDSREA ('IWRD2 ',IWRD2 )
          CALL RDSREA ('IWRD3 ',IWRD3 )
          CALL RDSREA ('IWRG1 ',IWRG1 )
          CALL RDSREA ('IWRG2 ',IWRG2 )
          CALL RDSREA ('IWRG3 ',IWRG3 )
          CALL RDSREA ('IWSD1 ',IWSD1 )
          CALL RDSREA ('IWSD2 ',IWSD2 )
          CALL RDSREA ('IWSD3 ',IWSD3 )
          CALL RDSREA ('IWSG1 ',IWSG1 )
          CALL RDSREA ('IWSG2 ',IWSG2 )
          CALL RDSREA ('IWSG3 ',IWSG3 )
          CALL RDSREA ('NUL   ',NUL   )
          CALL RDSREA ('REMOB1',REMOB1)

*-----Read model parameters
          CALL RDSREA ('AMX   ',AMX   )
          CALL RDSREA ('CVT   ',CVT   )
          CALL RDSREA ('DAYEM ',DAYEM )
          CALL RDSREA ('DELAY ',DELAY )
          CALL RDSREA ('DEPTH ',DEPTH )
          CALL RDSREA ('EE    ',EE    )
          CALL RDSREA ('HAR   ',HAR   )
          CALL RDSREA ('HARDAY',HARDAY)
          CALL RDSREA ('HARDEP',HARDEP)
          CALL RDSREA ('NPL   ',NPL   )
          CALL RDSREA ('RC    ',RC    )
```

```
      CALL RDSREA ('RCSHST',RCSHST)
      CALL RDSREA ('REDAM ',REDAM )
      CALL RDSREA ('RDRIZ ',RDRIZ )
      CALL RDSREA ('ROC   ',ROC   )
      CALL RDSREA ('TBASE ',TBASE )
      CALL RDSREA ('TL    ',TL    )
      CALL RDSREA ('TRAFAC',TRAFAC)

*-----Read AFGEN functions
      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 ('RDRT  ',RDRT  ,IMRDRT,ILRDRT)
      CALL RDAREA ('RDST  ',RDST  ,IMRDST,ILRDST)
      CALL RDAREA ('TEFFT ',TEFFT ,IMTEFF,ILTEFF)
      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

*-----Delay variable set from a REAL to an INTEGER
    DDELAY = DELAY

*-----Initialize weights of plant organs
      IF (YRNUM .EQ. 1.)THEN
      TWLD1  = IWLD1
      TWLD2  = IWLD2
      TWLD3  = IWLD3
      TWLG1  = IWLG1
      TWLG2  = IWLG2
      TWLG3  = IWLG3
      TWSD1  = IWSD1
      TWSD2  = IWSD2
      TWSD3  = IWSD3
      TWSG1  = IWSG1
      TWSG2  = IWSG2
      TWSG3  = IWSG3
      TWRD1  = IWRD1
      TWRD2  = IWRD2
      TWRD3  = IWRD3
      TWRG1  = IWRG1
```

```
          TWRG2  = IWRG2
          TWRG3  = IWRG3
          TWGRIZ = IWGRIZ
          TWRIZD = IWRIZD
          ENDIF

      ELSE IF (ITASK.EQ.2) THEN

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

*-----Weights of plant organs
        WLV = TWLG1 + TWLD1 + TWLG2 + TWLD2 + TWLG3 + TWLD3
        WST = TWSG1 + TWSD1 + TWSG2 + TWSD2 + TWSG3 + TWSD3
        WRT = TWRG1 + TWRD1 + TWRG2 + TWRD2 + TWRG3 + TWRD3
        TGW = TWLG1+TWSG1+TWRG1+TWLG2+TWSG2+TWRG2+TWLG3+TWSG3+TWRG3

*-----Total live weight never >2283 g DW / m2; cf. Budd et al.
          TGW   = AMIN1 (TGW, 2283.)

*-----Initialize rhizome weight
          TWRIZ  = TWGRIZ - TWRIZD

***             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 in day(s) to be chosen
*     by substituting number given for DELAY in MODEL.DAT

          WTMP = LINT (WTMPT,ILWTMP,DAY)
          IDAY = DAY

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

      IF (DAVTMP .LT. 5.0)DAVTMP = 5.0

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

```
      TEFF = LINT(TEFFT,ILTEFF,DDTMP)

*-----Measured total live plant dry weight
          TGWM = LINT (TGWMT,ILMEAS,DAY)

*-----Call to SBRT ASTRO to introduce day length into MAIN for tentative
*     relationship REMOB1-DAYL; otherwise this call can be made at *ASTRO
      CALL ASTRO
     $ (DAY,LAT,SC,DS0,SINLD,COSLD,DAYL,DSINB,DSINBE)

*-----Calculation of dry matter and its partitioning over the plant organs
      TW = TGW+(TWLD1+TWSD1+TWRD1+TWLD2+TWSD2+TWRD2+TWLD3+TWSD3+TWRD3)
      FLV = LINT(FLVT ,ILFLVT,DVS)
      FST = LINT(FSTT ,ILFSTT,DVS)
      FRT = LINT(FRTT ,ILFRTT,DVS)
      FL  = LINT(FLT  ,ILFLT ,DVS)

*-----Growth of plant organs, maintenance respiration and translocation
*     Calculation assimilate requirement for plant organ formation.
       ASRQ   = 1.54
       MAINTS = 0.016*TWLG1+0.01*TWSG1+0.015*TWRG1
       MAINT  = MAINTS*TEFF
       MAINRT = 0.005 * TWGRIZ * TEFF

*-----Carbohydrate behavior: remobilization from rhizomes for plant formation at proper day length and
*      temperature conditions (presently related to DVS); translocation from above-ground biomass
*     (i.e.'plants') to rhizomes, provided plants are present
      TRANS1 = 0.0
      TREMOB = 0.0

      TWGRIZ = AMAX1 (CRRIZ, TWGRIZ)
      TGRIZ  = TWGRIZ
      TWRIZD = INTGRL (TWRIZD, RDRIZ , DELT)

       IF (DVS.GE.0.376 .AND. DVS.LT.1.0) THEN
         IF (GPHOT .LT. MAINT)THEN
             IF (TWGRIZ .GT. CRRIZ) THEN
          TREMOB = INTGRL (TREMOB, REMOB1, DELT)
          REMOB1  = ROC * TWGRIZ
         ELSE
          WRITE (*,*) 'Vegetation is dying'
          REMOB1 = 0.000001
         ENDIF

         ENDIF

       ELSE
         REMOB1 = 0.000001
         ENDIF

*-----Relative death rates
       RDR = INSW (DVS-1.001,0.,LINT (RDRT,ILRDRT,DDTMP))
       RDS = INSW (DVS-1.001,0.,LINT (RDST,ILRDST,DDTMP))
```

```
*-----Development rates
      IF(DAVTMP .LT. 3.0) THEN
            DVR = 0.0
      ELSE IF (DVS.LE.1.) THEN
        DVR = 0.022*DAVTMP/30
      ELSE IF (DVS.LE.6.0) THEN
        DVR = 0.015*DAVTMP/30
      ENDIF

*-----Calculation of effective daytime temperature
            DTEFF = AMAX1(0.,DAVTMP-TBASE)

*-----Calculation of dead plant material per organ
            DLV1  = TWLG1 * RDR
            DST1  = TWSG1 * RDR
            DRT1  = TWRG1 * 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 plant material (K) and 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,WLV,WST,
     $   DAY,HAR,HARDAY,HARDEP,DTGA,IRS)

*-----If harvesting takes place, weights various plant organs must be recalculated
*     (TWLG1,TWSG1,TWRG1,TW)
            IF(HAR .EQ. 1. AND. DAY .EQ. HARDAY) THEN
      TWLG1 = FLV * TGW
      TWSG1 = FST * TGW
      TWRG1 = FRT * TGW
      TW = TGW+(TWLD1+TWSD1+TWRD1+TWLD2+TWSD2+TWRD2+TWLD3+TWSD3+TWRD3
            ENDIF

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

*-----Induction of flowering at DVS=1; flowering occurs 10 days after induction
*     Induction of flowering, translocation and senescence occur simultaneously
      IF (DVS .GE. 1.0)THEN

*-----If there is no above-ground plant biomass present, TRANS1 must stay at zero; otherwise it gets
*     a value
            IF ((TWLG1+TWSG1+TWRG1) .GT. 0.0)THEN
              IF (TGW .GE. TWGRIZ) THEN

        TRANS1 = CVT * GPHOT*((TWLG1+TWSG1+TWRG1)/
```

```
     $(TWLG1+TWSG1+TWRG1+TWLG2+TWSG2+TWRG2)) * TRAFAC

        ENDIF
       ENDIF

*-----If there is no plant biomass present, REMOB1 must stay at zero
          IF ((TWLG1+TWSG1+TWRG1) .EQ. 0.0)REMOB1 = 0.0
     ENDIF

*-----The total weight of the green rhizomes increases by translocation (TRANS1 from CHORT1) and
*      decreases by remobilization and rhizome maintenance respiration
       TWGRIZ = INTGRL (TWGRIZ, -(((-TRANS1 +REMOB1+ MAINRT)/1.242)
     $          +(RDRIZ*TGRIZ)), DELT)

*-----Total and net growth rates
GTW = ((REMOB1*CVT) + GPHOT - TRANS1 - MAINT)/ASRQ
          GRT = FRT * GTW
          GST = FST * GTW
          GLV = FLV * GTW

          NGLV1 = GLV - DLV1
          NGST1 = GST - DST1
          NGRT1 = GRT - DRT1

     CALL CHORT2   (AMAX ,AMTMP ,AMTMPT,AMX   ,ASRQ  ,COSLD ,CRRIZ ,
     &          CVT  ,DAVTMP,DAY   ,DAYL  ,DDTMP ,DELT  ,DEPTH ,
     &          DLV2 ,DRT2  ,DSINB ,DSINBE,DST2  ,DTEFF ,DTGA  ,
     &          DVR  ,DVS   ,EE    ,FGROS ,FL    ,FLT   ,FLV   ,
     &          FLVT ,FRT   ,FRTT  ,FST   ,FSTT  ,GLV   ,GPHOT ,
     &          GRT  ,GST   ,GTW   ,HAR   ,HARDAY,HARDEP,IKT   ,
     &          ILAMTM,ILFLT ,ILFLVT,ILFRTT,ILFSTT,ILRDRT,ILRDST,
     &          ILT  ,K     ,KT    ,L     ,LAT   ,LT    ,
     &          MAINRT,MAINT ,NGLV2 ,NGRT2 ,NGST2 ,RC    ,
     &          RCSHST,RDD   ,RDR   ,RDRIZ ,RDRT  ,RDST  ,REDAM ,
     &          REMOB1,REMOB2,ROC   ,SC    ,SINLD ,TBASE ,TEFF  ,
     &          TGRIZ ,TGW   ,TIME  ,TL    ,TRAFAC,TRANS1,TRANS2,
     &          TREMOB,TW    ,TWLD1 ,TWLD2 ,TWLG1 ,TWLG2 ,TWRD1 ,
     &          TWRD2 ,TWRG1, TWRG2 ,TWGRIZ,TWRIZD,TWSD1 ,
     &          TWSD2 ,TWSG1, TWSG2 ,WLV   ,WST   ,IRS)

     IF (LAT .LE. 33) CALL CHORT3
     &          (AMAX ,AMTMP ,AMTMPT,AMX   ,ASRQ  ,COSLD ,CRRIZ ,
     &          CVT  ,DAVTMP,DAY   ,DAYL  ,DDTMP ,DELT  ,DEPTH ,
     &          DLV3 ,DRT3  ,DSINB ,DSINBE,DST3  ,DTEFF ,DTGA  ,
     &          DVR  ,DVS   ,EE    ,FGROS ,FL    ,FLT   ,FLV   ,
     &          FLVT ,FRT   ,FRTT  ,FST   ,FSTT  ,GLV   ,GPHOT ,
     &          GRT  ,GST   ,GTW   ,HAR   ,HARDAY,HARDEP,IKT   ,
     &          ILAMTM,ILFLT ,ILFLVT,ILFRTT,ILFSTT,ILRDRT,ILRDST,
     &          ILT  ,K     ,KT    ,L     ,LAT   ,LT    ,
     &          MAINRT,MAINT ,NGLV3 ,NGRT3 ,NGST3 ,RC    ,
     &          RCSHST,RDD   ,RDR   ,RDRIZ ,RDRT  ,RDST  ,REDAM ,
     &          REMOB1,REMOB3,ROC   ,SC    ,SINLD ,TBASE ,TEFF  ,
     &          TGRIZ ,TGW   ,TIME  ,TL    ,TRAFAC,TRANS1,TRANS2,
     &          TRANS3,TREMOB,TW    ,TWLD1 ,TWLD2 ,TWLD3 ,TWLG1 ,
```

```
     &          TWLG2 ,TWLG3 ,TWRD1 ,TWRD2 ,TWRD3 ,TWRG1 ,TWRG2 ,
     &          TWRG3 ,TWGRIZ,TWRIZD,TWSD1 ,TWSD2 ,TWSD3 ,
     &          TWSG1 ,TWSG2 ,TWSG3 ,WLV   ,WST   ,IRS)

*-----Finish conditions
      IF(DVS .GT. 6.0 .OR. DAY .EQ. 365.) TERMNL = .TRUE.

*-----Output section
            IF (OUTPUT) THEN
              CALL OUTDAT (2,0,'DAVTMP',DAVTMP)
              CALL OUTDAT (2,0,'DAYL  ',DAYL  )
              CALL OUTDAT (2,0,'DDTMP ',DDTMP )
              CALL OUTDAT (2,0,'DTEFF ',DTEFF )
              CALL OUTDAT (2,0,'DTGA  ',DTGA  )
              CALL OUTDAT (2,0,'DVS   ',DVS   )
              CALL OUTDAT (2,0,'FGROS ',FGROS )
              CALL OUTDAT (2,0,'GPHOT ',GPHOT )
              CALL OUTDAT (2,0,'IRS   ',IRS   )
              CALL OUTDAT (2,0,'MAINRT',MAINRT)
              CALL OUTDAT (2,0,'MAINT ',MAINT )
              CALL OUTDAT (2,0,'REMOB1',REMOB1)
              CALL OUTDAT (2,0,'REMOB2',REMOB2)
              CALL OUTDAT (2,0,'REMOB3',REMOB3)
              CALL OUTDAT (2,0,'TEFF  ',TEFF  )
              CALL OUTDAT (2,0,'TGW   ',TGW   )
              CALL OUTDAT (2,0,'TGWM  ',TGWM  )
              CALL OUTDAT (2,0,'TMPSUM',TMPSUM)
              CALL OUTDAT (2,0,'TRANS1',TRANS1)
              CALL OUTDAT (2,0,'TRANS2',TRANS2)
              CALL OUTDAT (2,0,'TRANS3',TRANS3)
              CALL OUTDAT (2,0,'TREMOB',TREMOB)
              CALL OUTDAT (2,0,'TW    ',TW    )
              CALL OUTDAT (2,0,'TWGRIZ',TWGRIZ)
              CALL OUTDAT (2,0,'TWLD1 ',TWLD1 )
              CALL OUTDAT (2,0,'TWLD2 ',TWLD2 )
              CALL OUTDAT (2,0,'TWLD3 ',TWLD3 )
              CALL OUTDAT (2,0,'TWLG1 ',TWLG1 )
              CALL OUTDAT (2,0,'TWLG2 ',TWLG2 )
              CALL OUTDAT (2,0,'TWLG3 ',TWLG3 )
              CALL OUTDAT (2,0,'TWLVD ',TWLVD )
              CALL OUTDAT (2,0,'TWLVG ',TWLVG )
              CALL OUTDAT (2,0,'TWRD1 ',TWRD1 )
              CALL OUTDAT (2,0,'TWRD2 ',TWRD2 )
              CALL OUTDAT (2,0,'TWRD3 ',TWRD3 )
              CALL OUTDAT (2,0,'TWRG1 ',TWRG1 )
              CALL OUTDAT (2,0,'TWRG2 ',TWRG2 )
              CALL OUTDAT (2,0,'TWRG3 ',TWRG3 )
              CALL OUTDAT (2,0,'TWRIZ ',TWRIZ )
              CALL OUTDAT (2,0,'TWRIZD',TWRIZD)
              CALL OUTDAT (2,0,'TWRTG ',TWRTG )
              CALL OUTDAT (2,0,'TWSD1 ',TWSD1 )
              CALL OUTDAT (2,0,'TWSD2 ',TWSD2 )
              CALL OUTDAT (2,0,'TWSD3 ',TWSD3 )
              CALL OUTDAT (2,0,'TWSG1 ',TWSG1 )
```

```
            CALL OUTDAT (2,0,'TWSG2 ',TWSG2 )
            CALL OUTDAT (2,0,'TWSG3 ',TWSG3 )
            CALL OUTDAT (2,0,'TWSTD ',TWSTD )
            CALL OUTDAT (2,0,'TWSTG ',TWSTG )
            CALL OUTDAT (2,0,'WTMP  ',WTMP  )

          END IF

      ELSE IF (ITASK.EQ.3) THEN

              INTEGRATION
             =============
          DVS   = INTGRL (DVS   ,DVR   ,DELT)
          TMPSUM = INTGRL (TMPSUM,DTEFF  ,DELT)
          TWLD1  = INTGRL (TWLD1 ,DLV1   ,DELT)
          TWLD2  = INTGRL (TWLD2 ,DLV2   ,DELT)
          TWLD3  = INTGRL (TWLD3 ,DLV3   ,DELT)
          TWLG1  = INTGRL (TWLG1 ,NGLV1  ,DELT)
          TWLG2  = INTGRL (TWLG2 ,NGLV2  ,DELT)
          TWLG3  = INTGRL (TWLG3 ,NGLV3  ,DELT)
          TWLG1  = AMAX1 (0.0, TWLG1)
          TWLG2  = AMAX1 (0.0, TWLG2)
          TWLG3  = AMAX1 (0.0, TWLG3)
          TWSD1  = INTGRL (TWSD1 ,DST1   ,DELT)
          TWSD2  = INTGRL (TWSD2 ,DST2   ,DELT)
          TWSD3  = INTGRL (TWSD3 ,DST3   ,DELT)
          TWSG1  = INTGRL (TWSG1 ,NGST1  ,DELT)
          TWSG2  = INTGRL (TWSG2 ,NGST2  ,DELT)
          TWSG3  = INTGRL (TWSG3 ,NGST3  ,DELT)
          TWSG1  = AMAX1 (0.0, TWSG1)
          TWSG2  = AMAX1 (0.0, TWSG2)
          TWSG3  = AMAX1 (0.0, TWSG3)
          TWRG1  = INTGRL (TWRG1 ,NGRT1  ,DELT)
          TWRG2  = INTGRL (TWRG2 ,NGRT2  ,DELT)
          TWRG3  = INTGRL (TWRG3 ,NGRT3  ,DELT)
          TWRG1  = AMAX1 (0.0, TWRG1)
          TWRG2  = AMAX1 (0.0, TWRG2)
          TWRG3  = AMAX1 (0.0, TWRG3)
          TWRD1  = INTGRL (TWRD1 ,DRT1   ,DELT)
          TWRD2  = INTGRL (TWRD2 ,DRT2   ,DELT)
          TWRD3  = INTGRL (TWRD3 ,DRT3   ,DELT)
          TWRD1  = AMAX1 (0.0, TWRD1)
          TWRD2  = AMAX1 (0.0, TWRD2)
          TWRD3  = AMAX1 (0.0, TWRD3)

*-----If REMOB1 equals zero and TRANS1 equals zero and DVS greater that one, all biomass of
*     cohort 1 is added to Cohort 2. Therefore all biomass in cohort 1 is gone & shouldn't come back
      IF (DVS.GT.1.0 .AND. REMOB1.EQ.0.0 .AND. TRANS1.EQ.0.0)THEN
      TWLG2 = TWLG2 + TWLG1
      TWRG2 = TWRG2 + TWRG1
      TWSG2 = TWSG2 + TWSG1
      TWLG1 = 0.0
      TWSG1 = 0.0
      TWRG1 = 0.0
```

```
      ENDIF

*-----If REMOB2 equals zero and TRANS2 equals zero and DVS greater that two, all biomass of cohort
*       2 is added to cohort 3. Therefore all biomass in cohort 2 is gone & shouldn't come back
      IF (DVS.GT.2.0.AND.REMOB2.EQ.0.0.AND.TRANS2.EQ.0.0.AND.LAT.LE.33)
     &THEN
      TWLG3 = TWLG3 + TWLG2
      TWRG3 = TWRG3 + TWRG2
      TWSG3 = TWSG3 + TWSG2
      TWLG2 = 0.0
      TWSG2 = 0.0
      TWRG2 = 0.0
      ENDIF

*-----Total plant weights
        TWLVG = TWLG1 + TWLG2 + TWLG3
        TWLVD = TWLD1 + TWLD2 + TWLD3
        TWRTG = TWRG1 + TWRG2 + TWRG3
        TWRTD = TWRD1 + TWRD2 + TWRD3
        TWSTG = TWSG1 + TWSG2 + TWSG3
        TWSTD = TWSD1 + TWSD2 + TWSD3

      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 day length and photoperiodic day length *
*  (see CABO-TPE report #?) 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 day length (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  : 10 December 1987                                                    *
* Modified by Jan Goudriaan 5 February 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/m2/d        I  *
* RC         Reflection coefficient of irradiation at  water surface (relative)-  I  *
* L          Water type specific light extinction coefficient -             I  *
* K          Plant species specific light extinction coefficient -          I  *
* AMAX       Assimilation rate at light saturation for  individual shoots  g CO2/ g DW/h  I  *
* EE         Initial light use efficiency for individual shoots  g CO2/J    I  *
* TL         Thickness per plant layer                        m             I  *
* DEPTH      Water depth                                      m             I  *
* RCHSHST    Relation coefficient shoot weight-stem length    m/g DW        I  *
* TGW        Total live plant dry weight                      g DW/m2       I  *
* FGROS      Instantaneous assimilation rate of whole  canopy  g CO2/ m2 soil/h  O  *
* FL          Leaf dry matter allocation to each layer of  plant  -         I  *
* WLV        Dry weight of leaves                             g DW/m2       I  *
* WST        Dry weight of stems                              g DW/m2       I  *
* HAR        Harvesting                                       -             I  *
* HARDAY     Harvesting day number                            d             I  *
* HARDEP     Harvesting depth                                 m             I  *
* DTGA       Daily total gross assimilation                   g CO2/m2/d    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,
     $                   WLV,WST,DAY,HAR,HARDAY,HARDEP,DTGA,IRS)

      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,WLV,WST,DAY,HAR,HARDAY,HARDEP,II,FGROS,IRS)

*-----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   : 16 July 1997                                                   *
* Modified by Jan Goudriaan 5 February 1988                               *
*    Purpose: This subroutine performs an instantaneous calculation of light profile in the water *
*    column, light absorbed by the plant tissue 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/m2         I  *
* PARDIF      Instantaneous flux of diffuse radiation(PAR)     W/m2         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 DW    I  *
* AMAX        Assimilation rate at light saturation for individual shoots g CO2/ g DW/h I  *
* EE          Initial light use efficiency for individual  shoots g CO2/J    I  *
* TL          Thickness per plant layer                        m            I  *
* DEPTH       Water depth                                      m            I  *
* RCHSHST     Relation coefficient shoot weight-stem length    m/g DW       I  *
* TGW         Total live plant dry weight                      g DW/m2      I  *
* FL          Leaf dry matter allocation to each layer of  plant -          I  *
* WLV         Dry weight of leaves                             g DW/m2      I  *
* WST         Dry weight of stems                              g DW/m2      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 per day (HOUR) -    I  *
* FGROS       Instantaneous assimilation rate of the crop      g CO2/m2/h   O  *
*                                                                         *
* SUBROUTINES called : none                                               *
* FUNCTIONS called : AFGEN                                                *
*                                                                         *
* FILE usage : none                                                       *
*-------------------------------------------------------------------------*

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

      IMPLICIT REAL(A-Z)
      REAL DMPC(6), SC(100), IRZ(100) , IABS(100), IABSL(100)
      REAL HIG(100), AH(100), REDF(100), SumZ, BotBio
      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

*-----LOOP should never be less than 6 since DEPTH shouldn't be less than .5m
      IF (LOOP .LE. 5) LOOP = 6

*-----Distribute 61% of total plant biomass in 1st 5 layers
      DO 10 I = 1,5
      VAL = REAL (I)
      DMPC(I) = LINT (DMPCT,ILAY,VAL)
      SC(I) = TGW * DMPC(I)
   10 CONTINUE

*-----If water depth is at least 1m - use METHOD1 for distribution of
*     biomass beyond 1st 5 layers; otherwise, use METHOD2
*     METHOD 1
      If (LOOP .GE. 10)THEN

*-----Distribute 39% of biomass in the lower layers (including last layer)
*     with biomass gradually decreasing toward the bottom
*     LOOP (integer) .. Number of 0.1m water layers
*     LAYERS (integer) .. Layers remaining after initial 5
*-----SUMZ (real) .. Summation of layers 6 through LOOP
*-----LBELOW (integer) .. Layer number going from bottom to top

*-----5 in next statement is for the 1st 5 layers of the plant
      LAYERS = LOOP - 5
      SUMZ = (LAYERS/2.0) * (LAYERS+1.0)

      DO 20 I = 6,LOOP
      LBELOW = LAYERS - (I-5) + 1.0
      SC(I) = (LBELOW/SUMZ) * (TGW * 0.39)
   20 CONTINUE

*-----METHOD 2
      ELSE

*-----If water depth is less than 1m - put 5% of total biomass in each layer
*     remaining - subtract from the 39% biomass reserved for lower layers
      BotBio = TGW * 0.39
```

```
      DO 21 I = 6,LOOP
      SC(I) = TGW * 0.05
      BotBio = BotBio - SC(I)
   21 CONTINUE

*-----Redistribute difference "BotBio" over the top 5 layers proportionally
      DO 22 I = 1,5
      SC(I) = SC(I) + (DMPC(I)*BotBio)
   22 CONTINUE

      ENDIF

*-----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(-TL* 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) + TL*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
*******************************************************************************
***                                3.4 CHORT2                                ***
*-----------------------------------------------------------------------------*
*                                                                             *
* Authors: Elly Best & Will Boyd                                              *
* Date   : 16 July 1997                                                       *
* Purpose: This subroutine describes the behavior of the second  plant cohort *
*-----------------------------------------------------------------------------*

      SUBROUTINE CHORT2(AMAX ,AMTMP ,AMTMPT,AMX   ,ASRQ  ,COSLD,CRRIZ,
     &          CVT  ,DAVTMP,DAY  ,DAYL ,DDTMP ,DELT ,DEPTH ,
     &          DLV2 ,DRT2  ,DSINB ,DSINBE,DST2  ,DTEFF ,DTGA  ,
     &          DVR  ,DVS   ,EE   ,FGROS ,FL   ,FLT  ,FLV   ,
     &          FLVT ,FRT   ,FRTT ,FST   ,FSTT ,GLV  ,GPHOT ,
     &          GRT  ,GST   ,GTW  ,HAR   ,HARDAY,HARDEP,IKT  ,
     &          ILAMTM,ILFLT ,ILFLVT,ILFRTT,ILFSTT,ILRDRT,ILRDST,
     &          ILT  ,K     ,KT   ,L    ,LAT  ,LT   ,
     &          MAINRT,MAINT ,NGLV2 ,NGRT2 ,NGST2 ,RC   ,
     &          RCSHST,RDD   ,RDR  ,RDRIZ ,RDRT  ,RDST  ,REDAM ,
     &          REMOB1,REMOB2,ROC  ,SC    ,SINLD ,TBASE ,TEFF  ,
     &          TGRIZ ,TGW   ,TIME ,TL    ,TRAFAC,TRANS1,TRANS2,
     &          TREMOB,TW    ,TWLD1 ,TWLD2 ,TWLG1 ,TWLG2 ,TWRD1 ,
     &          TWRD2 ,TWRG1, TWRG2 ,TWGRIZ,TWRIZD,TWSD1 ,
     &          TWSD2 ,TWSG1, TWSG2 ,WLV  ,WST  ,IRS)

      IMPLICIT REAL (A-Z)

*-----Formal parameters
      INTEGER  IKT  ,ILAMTM,ILFLT ,ILFLVT,ILFRTT,ILFSTT
      INTEGER  ILRDRT,ILRDST,ILT
      LOGICAL  OUTPUT, TERMNL

      IF (DVS .LT. 1.0) GOTO 100

*----Call to SBRT ASTRO to introduce day length into MAIN for tentative
*    relationship REMOB2-DAYL; otherwise this call can be made at *ASTROOO
      CALL ASTRO
     $ (DAY,LAT,SC,DS0,SINLD,COSLD,DAYL,DSINB,DSINBE)

*-----Calculation of dry matter and its partitioning over the plant organs
            TW  = TGW + (TWLD1+TWSD1+TWRD1+TWLD2+TWSD2+TWRD2)
            FLV = LINT(FLVT ,ILFLVT,DVS)
            FST = LINT(FSTT ,ILFSTT,DVS)
            FRT = LINT(FRTT ,ILFRTT,DVS)
            FL  = LINT(FLT  ,ILFLT ,DVS)
```

```
*-----Growth of plant organs, maintenance respiration and translocation
*    Calculation assimilate requirement for plant organ formation.
      ASRQ   = 1.54
      MAINTS = 0.016*TWLG2+0.01*TWSG2+0.015*TWRG2
      MAINT  = MAINTS*TEFF
      MAINRT = 0.005 * TWGRIZ * TEFF

*-----Carbohydrate behavior: remobilization from rhizomes for plant formation at proper day length
*      and temperature conditions (presently related to DVS); translocation from plants to form
*      rhizomes, provided plants are present
    TRANS2 = 0.0
    TREMOB = 0.0

    TWGRIZ = AMAX1 (CRRIZ, TWGRIZ)
    TGRIZ  = TWGRIZ
    TWRIZD = INTGRL (TWRIZD, RDRIZ , DELT)

    IF (DVS.GE.1.0 .AND. DVS.LT.1.63) THEN
     IF (GPHOT .LT. MAINT) THEN
         IF (TWGRIZ .GT. CRRIZ) THEN
       TREMOB = INTGRL (TREMOB, REMOB2, DELT)
       REMOB2  = ROC * TWGRIZ
         ELSE
           WRITE(*,*)' Vegetation is dying '
      REMOB2 = 0.000001
         ENDIF

     ENDIF

    ELSE
      REMOB2 = 0.000001
    ENDIF

*-----If the carbohydrates fill the rhizomes by TRANS1 from cohort1, REMOB1 stays zero; TRANS2
*    remains zero, if the carbohydrates leave the rhizomes by REMOB2 to form the plants of cohort
*    but also if no plant biomass of cohort2 is present. The plants of cohort2 are formed by REMOB2
*    only at a certain DVS
    IF (TRANS1 .GT. 0.0)REMOB1 = 0.0
    IF (DVS .GE. 2.0)REMOB1 = 0.0
    IF (DVS .GE. 2.0)TRANS1 = 0.0
    IF (REMOB2 .GT. 0.000001)TRANS2 = 0.0

*-----Relative death rates
      RDR = INSW (DVS-2.001,0., LINT(RDRT,ILRDRT,DDTMP))
      RDS = INSW (DVS-2.001,0., LINT(RDST,ILRDST,DDTMP))

*-----Development rates
    IF(DAVTMP .LT. 3.0) THEN
         DVR = 0.0
    ELSE IF (DVS.LE.1.) THEN
      DVR = 0.022*DAVTMP/30
    ELSE IF (DVS.LE.6.0) THEN
      DVR = 0.015*DAVTMP/30
    ENDIF
```

```
*-----Calculation of effective daytime temperature
          DTEFF = AMAX1(0.,DAVTMP-TBASE)

*-----Calculation of dead plant material per organ
          DLV2  = TWLG2 * RDR
          DST2  = TWSG2 * RDR
          DRT2  = TWRG2 * 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,WLV,WST,
   $   DAY,HAR,HARDAY,HARDEP,DTGA,IRS)

*-----If harvesting takes place, weights various plant organs must be recalculated
*       (TWLVG,TWSTG,TWRTG,TW)
          IF(HAR .EQ. 1. AND. DAY .EQ. HARDAY) THEN
            TWLG2 = FLV * TGW
            TWSG2 = FST * TGW
            TWRG2 = FRT * TGW
            TW    = TGW + (TWLD1+TWSD1+TWRD1+TWLD2+TWSD2+TWRD2)
          ENDIF

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

*-----Induction of flowering at DVS=2; flowering occurs 10 days after induction.
*     Induction of flowering, translocation and senescence occur simultaneously .
    IF (DVS .GE. 1.63)THEN
    IF ((TWLG2+TWSG2+TWRG2) .GT. 0.0)THEN

            IF (TGW .GE. TWGRIZ) THEN
             IF (TRANS1 .EQ. 0.0) THEN
      TRANS2 = CVT * GPHOT*((TWLG2+TWSG2+TWRG2)/
   $ (TWLG1+TWSG1+TWRG1+TWLG2+TWSG2+TWRG2)) * TRAFAC

            ENDIF
           ENDIF
      ENDIF

*-----If there is no plant biomass REMOB2 must stay at zero
          IF ((TWLG2+TWSG2+TWRG2) .EQ. 0.0)REMOB2 = 0.0

    ENDIF
```

```
*-----When TRANS2 gets a value set REMOB2 to 0
      If (TRANS2 .GT. 0.0)REMOB2 = 0.0

*-----The total weight of the green rhizomes increases by translocation (TRANS2 from CHORT2)
*       and decreases by remobilization and rhizome maintenance respiration
        TWGRIZ = INTGRL (TWGRIZ, -(((-TRANS2 +REMOB2+ MAINRT)/1.242)
     $          +(RDRIZ*TGRIZ)), DELT)

*-----Total and net growth rates
        GTW = ((REMOB2*CVT) + GPHOT - TRANS2 - MAINT) / ASRQ
            GRT = FRT * GTW
            GST = FST * GTW
            GLV = FLV * GTW

            NGLV2 = GLV - DLV2
            NGST2 = GST - DST2
            NGRT2 = GRT - DRT2

  100 RETURN
      END

************************************************************************************
***                                  3.5 CHORT3                                  ***
*-----------------------------------------------------------------------------------*
*                                                                                   *
* Authors: Elly Best & Will Boyd                                                    *
* Date   : 18 August 1997                                                           *
* Purpose: This subroutine describes the behavior of the third plant cohort         *
*-----------------------------------------------------------------------------------*

      SUBROUTINE CHORT3(AMAX ,AMTMP ,AMTMPT,AMX   ,ASRQ  ,COSLD,CRRIZ,
     &          CVT  ,DAVTMP,DAY  ,DAYL  ,DDTMP ,DELT  ,DEPTH ,
     &          DLV3 ,DRT3  ,DSINB ,DSINBE,DST3  ,DTEFF ,DTGA  ,
     &          DVR  ,DVS   ,EE   ,FGROS ,FL    ,FLT   ,FLV   ,
     &          FLVT ,FRT   ,FRTT ,FST   ,FSTT  ,GLV   ,GPHOT ,
     &          GRT  ,GST   ,GTW  ,HAR   ,HARDAY,HARDEP,IKT   ,
     &          ILAMTM,ILFLT ,ILFLVT,ILFRTT,ILFSTT,ILRDRT,ILRDST,
     &          ILT  ,K     ,KT   ,L     ,LAT   ,LT    ,
     &          MAINRT,MAINT ,NGLV3 ,NGRT3 ,NGST3 ,RC    ,
     &          RCSHST,RDD   ,RDR  ,RDRIZ ,RDRT  ,RDST  ,REDAM ,
     &          REMOB1,REMOB3,ROC  ,SC    ,SINLD ,TBASE ,TEFF  ,
     &          TGRIZ ,TGW   ,TIME ,TL    ,TRAFAC,TRANS1,TRANS2,
     &          TRANS3,TREMOB,TW   ,TWLD1 ,TWLD2 ,TWLD3 ,TWLG1 ,
     &          TWLG2 ,TWLG3 ,TWRD1 ,TWRD2 ,TWRD3 ,TWRG1 ,TWRG2 ,
     &          TWRG3 ,TWGRIZ,TWRIZD,TWSD1 ,TWSD2 ,TWSD3 ,
     &          TWSG1, TWSG2 ,TWSG3 ,WLV   ,WST   ,IRS)

      IMPLICIT REAL (A-Z)

*-----Formal parameters
      INTEGER  IKT   ,ILAMTM,ILFLT ,ILFLVT,ILFRTT,ILFSTT
      INTEGER  ILRDRT,ILRDST,ILT
      LOGICAL  OUTPUT, TERMNL
```

```
      IF (DVS .LT. 2.0) GOTO 100
*----Call to SBRT ASTRO to introduce day length into MAIN for tentative
*     relationship REMOB3-DAYL; otherwise this call can be made at *ASTROOO

      CALL ASTRO
     $ (DAY,LAT,SC,DS0,SINLD,COSLD,DAYL,DSINB,DSINBE)

*-----Calculation of dry matter and its partitioning over the plant organs
      TW = TGW+(TWLD1+TWSD1+TWRD1+TWLD2+TWSD2+TWRD2+TWLD3+TWSD3+TWRD3)
           FLV = LINT(FLVT ,ILFLVT,DVS)
           FST = LINT(FSTT ,ILFSTT,DVS)
           FRT = LINT(FRTT ,ILFRTT,DVS)
           FL  = LINT(FLT  ,ILFLT ,DVS)

*-----Growth of plant organs, maintenance respiration and translocation
*     Calculation assimilate requirement for plant organ formation.
        ASRQ   = 1.54
        MAINTS = 0.016*TWLG3+0.01*TWSG3+0.015*TWRG3
           MAINT  = MAINTS*TEFF
        MAINRT = 0.005 * TWGRIZ * TEFF

*-----Carbohydrate behavior: remobilization from rhizomes for plant formation at proper day length and
*      temperature conditions (presently related to DVS); translocation from plants to form  rhizomes,
*      provided plants are present
      TRANS3 = 0.0
      TREMOB = 0.0

      TWGRIZ = AMAX1 (CRRIZ, TWGRIZ)
      TGRIZ  = TWGRIZ
      TWRIZD = INTGRL (TWRIZD, RDRIZ , DELT)

      IF (DVS.GE.2.0 .AND. DVS.LT.2.447) THEN
       IF (GPHOT .LT. MAINT) THEN
          IF (TWGRIZ .GT. CRRIZ) THEN
         TREMOB = INTGRL (TREMOB, REMOB3, DELT)
         REMOB3  = ROC * TWGRIZ
           ELSE
             WRITE(*,*)' Vegetation is dying '
        REMOB3 = 0.000001
           ENDIF

       ENDIF

      ELSE
        REMOB3 = 0.000001
      ENDIF

*-----If the carbohydrates fill the rhizomes by TRANS1 from cohort1, REMOB1 stays zero; TRANS2
*      remains zero, if the carbohydrates leave the rhizomes by REMOB3 to form the plants of cohort3,
*      but also if no plant biomass of cohort2 is present. The plants of cohort2 are formed by REMOB3
*      only at a certain DVS
      IF (TRANS1 .GT. 0.0)REMOB1 = 0.0
      IF (DVS .GE. 2.0)REMOB1 = 0.0
```

```
      IF (DVS .GE. 2.0)TRANS1 = 0.0
      IF (DVS .GE.2.3)TRANS2 = 0.0
      IF (REMOB3 .GT. 0.000001)TRANS3 = 0.0

*-----Relative death rates
        RDR = INSW (DVS-3.5001,0., LINT(RDRT,ILRDRT,DDTMP))
        RDS = INSW (DVS-3.5001,0., LINT(RDST,ILRDST,DDTMP))

*-----Development rates
      IF(DAVTMP .LT. 3.0) THEN
            DVR = 0.0
      ELSE IF (DVS.LE.1.) THEN
        DVR = 0.022*DAVTMP/30
      ELSE IF (DVS.LE.6.0) THEN
        DVR = 0.015*DAVTMP/30
      ENDIF

*-----ASTROOO
*-----Calculation of effective daytime temperature
            DTEFF = AMAX1(0.,DAVTMP-TBASE)

*-----Calculation of dead plant material per organ
        DLV3  = TWLG3 * RDR
        DST3  = TWSG3 * RDR
        DRT3  = TWRG3 * 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,WLV,WST,
     $   DAY,HAR,HARDAY,HARDEP,DTGA,IRS)

*-----If harvesting takes place, weights various plant organs must be recalculated
*       (TWLVG,TWSTG,TWRTG,TW)
            IF(HAR .EQ. 1. AND. DAY .EQ. HARDAY) THEN
          TWLG3 = FLV * TGW
          TWSG3 = FST * TGW
          TWRG3 = FRT * TGW
      TW = TGW+(TWLD1+TWSD1+TWRD1+TWLD2+TWSD2+TWRD2+TWLD3+TWSD3+TWRD3)
            ENDIF

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

*-----Induction of flowering at DVS=2.447; flowering occurs 10 days after induction
```

```
*    Induction of flowering, translocation and senescence occur simultaneously
     IF (DVS .GE. 2.447)THEN
     IF ((TWLG3+TWSG3+TWRG3) .GT. 0.0)THEN

           IF (TGW .GE. TWGRIZ) THEN
         IF (TRANS2 .EQ. 0.0) THEN
       TRANS3 = CVT * GPHOT *((TWLG3+TWSG3+TWRG3)/
    $ (TWLG1+TWSG1+TWRG1+TWLG2+TWSG2+TWRG2+TWLG3+TWSG3+TWRG3))
    $ * TRAFAC

            ENDIF
           ENDIF
       ENDIF

*-----If there is no plant biomass REMOB3 must stay at zero
       IF ((TWLG3+TWSG3+TWRG3) .EQ. 0.0)REMOB3 = 0.0

     ENDIF

*-----When TRANS3 gets a value set REMOB3 to 0
     If (TRANS3 .GT. 0.0)REMOB3 = 0.0

*-----The total weight of the green rhizomes increases by translocation (TRANS3 from CHORT3)
*       and decreases by remobilization and rhizome maintenance respiration
       TWGRIZ = INTGRL (TWGRIZ, -(((-TRANS3 +REMOB3+ MAINRT)/1.242)
    $          +(RDRIZ*TGRIZ)), DELT)

*-----Total and net growth rates
       GTW = ((REMOB3*CVT) + GPHOT - TRANS3 - MAINT) / ASRQ
           GRT = FRT * GTW
           GST = FST * GTW
           GLV = FLV * GTW
       NGLV3 = GLV - DLV3
       NGST3 = GST - DST3
       NGRT3 = GRT - DRT3

  100 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: MDELMW70.DAT; to be used as input file for MILFO.FOR                                                      *
* Contains data on biomass and water temperatures from Lake Wingra, WI, 1970                                      *
* Date: 10-10-97                                                                                                  *
* Time: 10:00:06                                                                                                  *
*-----------------------------------------------------------------------------------------------------------------*
* Initial constants
* -----------------
 CRRIZ  = 12.
 IWGRIZ = 50.
 IWRIZD = 0.
 IWLD1  = 0.
 IWLD2  = 0.
 IWLD3  = 0.
 IWLG1  = 23.5
 IWLG2  = 0.
 IWLG3  = 0.
 IWRD1  = 0.
 IWRD2  = 0.
 IWRD3  = 0.
 IWRG1  = 3.
 IWRG2  = 0.
 IWRG3  = 0.
 IWSD1  = 0.
 IWSD2  = 0.
 IWSD3  = 0.
 IWSG1  = 23.5
 IWSG2  = 0.
 IWSG3  = 0.
 NUL    = 0.
 REMOB1 = 0.

* Model parameters
* ----------------
 YRNUM  = 1.
 AMX    = 0.0165
 CVT    = 1.05
 DAYEM  = 1.
 DELAY  = 7.
 DEPTH  = 1.5
 EE     = 0.000011
 HAR    = 0.
 HARDAY = 212.
 HARDEP = 0.8
 NPL    = 11.
 RC     = 0.06
 RCSHST = 12.0
```

```
 RDRIZ  = 0.00042
 REDAM  = 0.5
 ROC    = 0.0576
 TBASE  = 3.
 TL     = 0.1
 TRAFAC = 0.35

* AFGEN functions
* ----------------------
* AMDVST =
*   0.001, 1.,
*   3.5, 1.,
*   5.0, 1.
 AMTMPT =
   -30., 0.00001,
   0., 0.00001,
   5., 0.18,
   10., 0.23,
   15., 0.40,
   20., 0.63,
   25., 0.78,
   30., 0.95,
   35., 1.0,
   40., 0.78,
   45., 0.38,
   50., 0.00001
 DMPCT  =
   1.0, .10,
   2.0, .16,
   3.0, .17,
   4.0, .10,
   5.0, .08
* DVRVT  =
*   -15., 0.,
*    0., 0.,
*   30., 0.022
* DVRRT  =
*   -15., 0.,
*    0., 0.,
*   30., 0.015
 FLT    =
   0., 0.50,
   2.3, 0.50,
   6.0, 0.50
 FLVT   =
   0., 0.47,
   2.3, 0.47,
   6.0, 0.47
 FSTT   =
   0., 0.47,
   2.3, 0.47,
   6.0, 0.47
 FRTT   =
   0., 0.06,
```

```
   2.3, 0.06,
   6.0, 0.06
 KT    =
   0., 0.006,
   3.5, 0.006,
   6.0, 0.006
 LT    =
   0., 1.15,
   101., 1.6,
   117., 1.4,
   131., 1.85,
   156., 1.85,
   173., 1.8,
   187., 1.8,
   215., 1.8,
   243., 2.0,
   257., 1.4,
   271., 1.6,
   299., 1.4,
   327., 1.15,
   365., 1.15
 RDRT  =
  -30., 0.042,
   0., 0.042,
   50.,0.042
 RDST  =
  -30., 0.042,
   0., 0.042,
  50., 0.042
 REDFT =
   0.0, 1.0,
   1.0, 1.0,
   6.0, 1.0
 TEFFT =
  -30., 0.0001,
    0., 0.0001,
    5., 1.0,
    20.,1.0,
    30., 2.0,
    40., 4.0,
    45., 8.0,
    50., 12.0
 TGWMT =
   1.,   50.,
   141., 50.,
   162., 120.,
   172., 106.,
   192., 105.,
   202., 130.,
   223., 160.,
   233., 180.,
   254., 220.,
   264., 150.,
   365., 50.7
```

```
WTMPT =
  1.,  3.5,
 60.,  3.5,
100.,  9.0,
150., 22.0,
190., 25.0,
220., 25.0,
250., 19.0,
300.,  9.0,
340.,  1.6,
365.,  1.6
```

```
*-------------------------------------------------------------------------------------------------------------*
* 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: MILFO.FOR                                                                                             *
* Date: 10-10-97                                                                                              *
* Time: 10:55:06                                                                                              *

* 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 ',
* 'DTEFF ',
* 'DTGA  ',
* 'DVS   ',
* 'FGROS ',
* 'GPHOT',
* 'IRS   ',
* 'MAINRT',
* 'MAINT ',
* 'REMOB1',
* 'REMOB2',
* 'REMOB3',
 'TGW',
* 'TGWM',
* 'TMPSUM',
* 'TRANS1',
* 'TRANS2',
* 'TRANS3',
* 'TW    ',
 'TWGRIZ',
* 'TWLD1 ',
* 'TWLD2 ',
* 'TWLD3 ',
```

```
* 'TWLG2 ',
* 'TWLG3 ',
* 'TWLVD ',
* 'TWLVG ',
* 'TWRD1 ',
* 'TWRD2 ',
* 'TWRD3 ',
* 'TWRG1 ',
* 'TWRG2 ',
* 'TWRG3 ',
* 'TWRIZ ',
* 'TWRIZD',
* 'TWRTD ',
* 'TWRTG ',
* 'TWSD1 ',
* 'TWSD2 ',
* 'TWSD3 ',
* 'TWSG1 ',
* 'TWSG2 ',
* 'TWSG3 ',
* 'TWSTD ',
* 'TWSTG ',
* 'WTMP ',

      '<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   = 'WIS'          ! Country code
 ISTN   = 1              ! Station code
 IYEAR  = 1970           ! Year
```

```
*-------------------------------------------------------------------------------------------------------------*
* CONTROL.DAT 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)
```

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	g CO_2.gDW^{-1}.h^{-1}
AMDVST	Developmental phase effect on AMX (relative)	-, -
AMTMP	Daytime temperature effect on AMX (relative)	-
AMTMPT	Table of AMX as function of DDTMP	-, -
AMX	Potential CO_2 assimilation rate at light saturation for shoot tips	g CO_2.gDW^{-1}.h^{-1}
ASRQ	Assimilate requirement for plant dry matter production	g CH_2O.g DW^{-1}
ATMTR	Atmospheric transmission coefficient	-
COSLD	Intermediate variable in calculating solar height	-
CRRIZ	Critical weight of the rhizome/root crown system	g DW.m^{-2}
CVT	Conversion factor of translocated dry matter into CH_2O	-
DAVTMP	Daily average temperature	°C
DAY	Day number (January 1=1)	d
DAYEM	First Julian day number	d
DAYL	Day length	h
DDELAY	Integer value of DELAY	-
DDTMP	Daily average daytime temperature	°C
DEC	Declination of the sun	radians
DELAY	Lag period chosen to relate water temperature to air temp., in cases where water temp. has not been measured	d
DEPTH	Water depth	m
DLV	Death rate of leaves	g DW. m^{-2}.d^{-1}
DMPC(i)	Dry matter allocation to each plant layer (relative)	-
DMPCT	Table of DMPC as function of water depth (relative)	-
DSINB	Integral of SINB over the day	s.d^{-1}
DSINBE	Daily total of effective solar height	s.d^{-1}
DRT	Death rate of roots	g DW. m^{-2}.d^{-1}
DSO	Daily extraterrestrial radiation	J.m^{-2} .d^{-1}
DST	Death rate of stems	g DW.m^{-2}.d^{-1}
DTEFF	Daily effective temperature	°C
DTGA	Daily total gross CO_2 assimilation of the plant	g CO_2.m^{-2}.d^{-1}

(Sheet 1 of 5)

Abbreviation	Explanation	Dimension
DTR	Measured daily total global radiation	$J.m^{-2}.d^{-1}$
DVR	Development rate as function of daily average temperature sum	d^{-1}, °C
DVRRT	Table of postanthesis development rate as function of daily average temperature sum (used for calibration; not read from MODEL.DAT)	d^{-1}, °C
DVRVT	Table of preanthesis development rate as function of daily average temperature sum (used for calibration; not read from MODEL.DAT)	d^{-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 $CO_2.m^{-2}.h^{-1}$
FGL	Instantaneous CO_2 assimilation rate per depth layer	g $CO_2.m^{-2}.h^{-1}$
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	-, -
FST	Fraction of total dry matter increase allocated to stems	-
FSTT	Table to read FST as function of DVS	-, -
GLV	Dry matter growth rate of leaves	g $DW.m^{-2}.d^{-1}$
GPHOT	Daily total gross assimilation rate of the community	g $CH_2O.m^{-2}.d^{-1}$
GRT	Dry matter growth rate of roots	g $DW.m^{-2}.d^{-1}$
GST	Dry matter growth rate of stems	g $DW.m^{-2}.d^{-1}$
GTW	Dry matter growth rate of vegetation (plant excluding rhizome/root crown system)	g $DW.m^{-2}.d^{-1}$
HAR	Harvesting (0=no harvesting, 1=harvesting)	-
HARDAY	Harvesting day number	d
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	h
I	Counter in DO LOOP	-
IABS(i)	Total irradiance absorbed per plant layer	$J.m^{-2}.s^{-1}$

(Sheet 2 of 5)

Abbreviation	Explanation	Dimension
IABSL(i)	Total irradiance absorbed by plant shoots	$J.m^{-2}.s^{-1}$
IDAY	Integer equivalent of variable DAY	d
IRS	Total irradiance just under the water surface	$J.m^{-2}.s^{-1}$
IRZ(i)	Total irradiance on top of depth layer I	$J.m^{-2}.s^{-1}$
IWGRIZ	Initial weight of live rhizome/root crown system	g $DW.m^{-2}$
IWLD1,2,3	Initial dry matter of dead leaves cohort 1,2,3	g $DW.m^{-2}$
IWLG1,2,3	Initial dry matter of green (live) leaves cohort 1,2,3	g $DW.m^{-2}$
IWRIZD	Initial weight of dead rhizome/root crown system	g $DW.m^{-2}$
IWRD1,2,3	Initial dry matter of dead roots cohort 1,2,3	g $DW.m^{-2}$
IWRG1,2,3	Initial dry matter of green (live) roots cohort 1,2,3	g $DW.m^{-2}$
IWSD1,2,3	Initial dry matter of dead stems cohort 1,2,3	g $DW.m^{-2}$
IWSG1,2,3	Initial dry matter of green (live) stems cohort 1,2,3	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	m^{-1}, d
MAINT	Maintenance respiration rate of the plant	g $CH_2O.m^{-2}.d^{-1}$
MAINRT	Maintenance respiration rate of the rhizome/root crown system	g $CH_2O.m^{-2}.d^{-1}$
MAINTS	Maintenance respiration rate of the plant at reference temperature	g $CH_2O.m^{-2}.d^{-1}$
NGLV	Net growth rate of leaves	g $DW.m^{-2}.d^{-1}$
NGRT	Net growth rate of roots	g $DW.m^{-2}.d^{-1}$
NGST	Net growth rate of stems	g $DW.m^{-2}.d^{-1}$
NPL	Plant density	plants $.m^{-2}$
NUL	Zero (0)	-
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	-
RAD	Factor to convert degrees to radians	radians.$degree^{-1}$

(Sheet 3 of 5)

Abbreviation	Explanation	Dimension
RC	Reflection coefficient of irradiation at water surface (relative)	-
RCSHST	Relation coefficient rhizome/root crown weight-stem length	m. g DW $^{-1}$
RDR	Relative death rate of leaves (on DW basis)	d^{-1}
RDRIZ	Relative death rate of rhizome/root crown system (on DW basis)	d^{-1}
RDRT	Table to read RDR as function of DAVTMP	d^{-1}, ^{o}C
RDS	Relative death rate of stems and roots (on DW basis)	d^{-1}
RDST	Table to read RDS as function of DAVTMP	d^{-1}, ^{o}C
REDAM	Reduction factor to relate AMX to pH and oxygen levels of the water as function of DVS (relative)	-
REDF(i)	Reduction factor for AMX to account for senescence plant parts over vertical axis of vegetation (relative)	-
REDFT	Table to read factor to reduce AMX over vertical axis of vegetation (relative)	-
REMOB1,2,3	Remobilization rate of carbohydrates cohort 1,2,3	g $CH_2O.m^{-2}.d^{-1}$
ROC	Relative conversion rate of rhizome/root crown into plant material	$gCH_2O.gDW^{-1}.d^{-1}$
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 daily average daytime temperature on maintenance respiration	-
TEFFT	Table to read TEFF as function of DDTMP	-, °C
TGRIZ	Total live rhizome/root crown system weight of the previous day	g $DW.m^{-2}$
TGW	Total live plant dry weight (excluding rhizome/root crown system)	g $DW.m^{-2}$
TGWM	Total live plant dry weight measured (field site)	g $DW.m^{-2}$
TGWMT	Table to read TGWM as function of day number	g $DW.m^{-2}$, d
TL	Thickness each plant layer	m
TMAX	Daily maximum temperature	°C
TMIN	Daily minimum temperature	°C
TMPSUM	Temperature sum after 1 January	°C

(Sheet 4 of 5)

Abbreviation	Explanation	Dimension
TRAFAC	Translocation factor (relative)	-
TRANS1,2,3	Translocation rate of carbohydrates cohort 1,2,3	g $CH_2O.m^{-2}.d^{-1}$
TREMOB	Total remobilization	g $CH_2O.m^{-2}$
TW	Total live + dead plant dry weight (excluding rhizome/root crown system)	g $DW.m^{-2}$
TWGRIZ	Total live rhizome/root crown dry weight of the current day	g $DW.m^{-2}$
TWLD1,2,3	Total dead leaf dry weight cohort 1,2,3	g $DW.m^{-2}$
TWLG1,2,3	Total live leaf dry weight cohort 1,2,3	g $DW.m^{-2}$
TWLVD	Total dry weight of dead leaves 2 or 3 cohorts	g $DW.m^{-2}$
TWLVG	Total dry weight of live leaves 2 or 3 cohorts	g $DW.m^{-2}$
TWRD1,2,3	Total dead root dry weight cohort 1,2,3	g $DW.m^{-2}$
TWRG1,2,3	Total live root dry weight cohort 1,2,3	g $DW.m^{-2}$
TWRIZ	Total live + dead rhizome/root crown system weight	g $DW.m^{-2}$
TWRIZD	Total dead rhizome/root crown system weight	g $DW.m^{-2}$
TWRTD	Total dry weight of dead roots 2 or 3 cohorts	g $DW.m^{-2}$
TWRTG	Total dry weight of live roots 2 or 3 cohorts	g $DW.m^{-2}$
TWSD1,2,3	Total dry weight of dead stems 2 or 3 cohorts	g $DW.m^{-2}$
TWSG1,2,3	Total live stem dry weight cohort 1,2,3	g $DW.m^{-2}$
TWSTD	Total dry weight of dead stems 2 or 3 cohorts	g $DW.m^{-2}$
TWSTG	Total dry weight of live stems 2 or 3 cohorts	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,d
YRNUM	Year number simulation (1-5)	Y

(Sheet 5 of 5)

Appendix C
Manipulation of Literature Data Used for the Model Equations

Photosynthesis

Effect of daytime temperature on photosynthesis (AMTMP)

To calibrate the relationship between temperature and photosynthetic activity, the photosynthetic rates compared with the photosynthetic rate at 35 ºC published by Titus and Adams (1979a,b) were used.[1]

Table C1
Relative Photosynthetic Activity of Milfoil Shoots in Response to Temperature (Conditions were light saturating and water was in equilibrium with atmospheric CO_2)

Temperature, °C	Relative Photosynthetic Rate
0	0.00001
5	0.18
10	0.23
15	0.40
20	0.63
25	0.78
30	0.95
35	1.00
40	0.78
45	0.38
50	0.05
55	0.00001

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

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 nonstructural carbohydrates, proteins, fats, cellulose, organic acids, and minerals (Table C2). This conversion factor indicates the amount of glucose consumed to produce each g of plant biomass (g CH_2O g DW^{-1}). This method has been employed to calculate assimilate requirement of milfoil shoots for biomass production.

Table C2
Estimated Chemical Composition of Milfoil Shoots (this study) and Typical Conversion Efficiencies 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 percent	Conversion Factor g CH_2O g DW^{-1}
Nonstructural carbohydrates	14	1.242
Proteins	17	1.704
Fats	8	3.106
Cellulose	33	2.174
Organic acids	11.2	0.929
Minerals	16.8	0.050
Milfoil shoot	100	1.539

Note: As the conversion factor for cellulose was not known, that for lignin has been used.

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 1.1-1.8 mmol (alkalinity Lake Wingra 1.1-1.8 mmol; Lee and Kluesener 1972). pH affecting potential photosynthetic rate at light saturation through REDAM can be modified by the user.

The model is calibrated for a light-extinction coefficient range of the water of 1.15 - 2.0 m^{-1} (Lee and Kluesener 1972); 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 Wingra at several points in time in 1970.[1] For Days 1 and 365, the same temperatures as those measured on the nearest dates in Lake Wingra, Wisconsin, have been taken.

Table C3
Seasonally Measured Daytime Temperatures in the Surface Water of Lake Wingra, Wisconsin, during 1970

Day, number	Temperature, °C	Day, number	Temperature, °C
1	3.5	216	25.3
62	3.5	223	25.3
69	4.0	230	24.4
76	5.3	237	23.2
84	6.3	244	22.5
90	6.5	246	22.9
97	5.7	251	23.0
98	7.0	258	16.5
104	6.7	265	20.0
111	6.9	272	15.8
118	15.2	278	15.1
125	15.3	286	14.3
132	17.6	293	11.8
139	17.0	300	12.8
146	19.1	307	8.2
153	19.1	321	4.1
160	22.7	328	0.3
167	23.9	335	1.7
174	22.7	342	0.9
181	24.8	349	0.1
188	23.5	355	1.2
195	26.8	363	1.6
202	22.4	365	1.6
209	26.7		

[1] Personal Communication, 1995, J. E. Titus, Univeristy of Binghamton, New York.

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13.ABSTRACT ***(Maximum 200 words)***

A simulation model for biomass dynamics of the submersed macrophyte *Myriophyllum spicatum* is presented. The model (MILFO) is based on carbon flow through the vegetation in meter-squared (m^2) water columns. It includes descriptions of several factors that affect biomass dynamics, such as site-characteristic changes in climate, water temperature, water transparency, pH and oxygen effects on CO_2 assimilation rate at light saturation, wintering strategies, grazing and mechanical control (removal of shoot biomass), and of latitude. The characteristics of the community and of the site can be easily modified by the user.

MILFO incorporates insights into the processes affecting the dynamics of an Eurasian watermilfoil community in relatively shallow, hard water (0.5-6 m depth; DIC concentration > 0.8 mmol and pH ranging from 7.6 to 9.4) under ample supply of nitrogen and phosphorus in a pest-, disease-, and competitor-free environment under the prevailing weather conditions. It has been calibrated on data pertaining to a milfoil community in Lake Wingra, Wisconsin, USA. At that site, growth starts from the basal rhizome/root crown system, alone or with wintering shoot biomass present. Shoot biomass usually peaks twice a year, in June originating from the first plant cohort and in August from the second cohort, and intensive

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downward transport of soluble carbohydrates occurs after anthesis of each cohort, replenishing the rhizome/root crown system. In a tropical climate, a third plant cohort is active.

MILFO simulated the dynamics of plant and rhizome/root crown biomass at Lake Wingra well over a period of 1 to 5 years. It has been used to calculate plant and rhizome/root crown biomass for the same latitude in a different year and for other latitudes in temperature (Alabama, USA) and tropical (India) areas, where it simulated biomass ranges similar to those measured in the field.

Sensitivity analysis showed that maximum plant biomass of a Eurasian watermilfoil community is most sensitive to a change in photosynthetic activity at light saturation and very sensitive to a change in light-use efficiency, and that end-of-year rhizome/root crown biomass was often more sensitive than maximum plant biomass. The latter illustrates the utmost importance of the rhizome/root crown system for local survival and biomass production in milfoil.

Environmental factor analysis indicated that changes in climate can greatly affect simulated end-of-year rhizome/root crown biomass. Maximum plant biomass proved far more sensitive to changes in water transparency than to changes in water depth.

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

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