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**The Response of Plants to Interacting Stresses:**

# TREGRO

**Model Version 3.0**

**For simulating the carbon, water, and nutrient dynamics of a plant-soil system using Macintosh® computers**

# Description and Parameter Requirements

July 1996

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# ABSTRACT

The simulation model TREGRO has been developed at the Boyce Thompson Institute from funds supplied by the Electric Power Research Institute to analyze the response of trees to multiple environmental stresses. TREGRO simulates the plant's ability to utilize resources to fix carbon in photosynthesis, the allocation patterns used to maintain carbon fixation and nutrient and water uptake, and the plant's ability to repair pollution damage. The TREGRO model can aid in evaluating long term effects of pollution on resource availability, potential for gradual deterioration of tree health under long periods of pollution exposure, and imbalances in growth accompanying shifts in carbon allocation.

TREGRO predicts growth and patterns of carbon allocation expected for an isolated tree exposed to various levels of ozone, nutrient stress, and water availability. The tree is divided into the following compartments: vegetative buds, a canopy consisting of up to ten leaf year classes, branches, stem, and coarse roots in two soil layers and fine roots in three soil layers. The model calculates the photosynthesis of the entire tree each hour as a function of ambient environmental conditions and the availability of light, water, and nutrients. To accomplish this task, the model keeps track of the the availability of light, water, and nutrient resources needed for the fixation process; the quantity of essential nutrients and water available in each soil horizon and the amount of these resources taken up by the tree; the amounts of these nutrient resources and fixed carbon available and used to build the component tissues of the plant; and the flow of carbon used to manufacture leaf tissue. The model predicts the growth of the tree over periods ranging from one hour (the basic model time step) to many years. The model was designed to be readily applicable to predicting the

growth dynamics of most tree species, and has been used to simulate both coniferous and deciduous trees.

This document describes the release of TREGRO (version 3.0). When used in conjunction with YASE, the soil solution chemistry and decomposition model, the complete soil-plant-atmosphere system of an individual tree's environment can be simulated.

# ACKNOWLEDGEMENTS

Funds for the development of this model were provided by the Electric Power Research Institute and the Boyce Thompson Institute, which also provided facilities, equipment, and technical support. Technical expertise was supplied by R. G. Amundson, T. J. Fahey, R. J. Kohut, and J. A. Laurence, without whose contributions this effort would not have succeeded. Additional support was provided by U.S. Environmental Protection Agency.

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# 1

# ABOUT THIS MANUAL

This manual replaces an earlier description of the TREGRO model, (Weinstein et al., 1991), which documented the first released version of the model (TREGRO 1.74). This document is intended to fully describe the processes in the TREGRO model and does not require reference to that earlier version.

# GETTING STARTED

The TREGRO computer model has been designed to take full advantage of the intuitive, user-friendly operations of the Macintosh® computer. Nevertheless, it is highly recommended that first time users read this document, especially this "Getting Started" section, before attempting to operate the model.

Using the TREGRO model requires a basic familiarity with Macintosh personal computer operations. In particular, this document assumes that the user knows how to perform the following simple tasks: copying files, using pull-down and pop-up menus, positioning the cursor and selecting text, and opening and naming files. If you are a new Macintosh user, these operations are fully described in the Macintosh user guide and demonstrated on the tutorial diskette that is shipped with all Macintosh computers.

## Hardware and Software Requirements

Running TREGRO requires either a 68K Macintosh with a floating point processor (FPU) or a Power Macintosh, and at least 4 MB of free RAM (2.5 MB for the interface and 1.5 MB for the model itself). If you have a Power Macintosh, use the XXXX version

included with this package. Before installing TREGRO on your computer, make sure you have a minimum of 2 MB of hard disk space available for storing the model, the model interface, and parameter files. An additional 1.3 MB is required for the included optional files. Also, each year of model simulation requires approximately 0.75 MB of hard disk space for storing output. A black and white monitor is sufficient, but if you are using a color monitor you should set it to 256 colors (using the "Control Panel" desk accessory, as described in the Macintosh users guide).

If you are unsure whether your hardware configuration meets these minimum requirements, consult your Macintosh user guide or computer support technician.

Your Macintosh must be equipped with System version 7.0 or later to run the model. In addition, TREGRO employs a HyperCard® interface that requires HyperCard version 2.1 or later.

## Model Installation

From the Finder, create a new folder by choosing "New" from the File menu and assign it a unique name (e.g., TREGRO FOLDER). It is important to avoid file names that are identical to any of the file names listed below. Next, for each of the enclosed 3.5" TREGRO diskettes: insert the diskette into your floppy drive, select all of the files on the diskette, and copy them onto your hard drive by dragging them over to the newly created folder on your desk top; do *not* copy the diskettes by selecting and dragging the diskette icon over to the folder. Double-click on any files ending in ".sea" to uncompress these self-expanding compressed archives. Be sure to select the current folder that you just created when prompted for where to put the uncompressed files from each archive. After uncompression, the original ".sea" file can be discarded.

As discussed above under Hardware and Software Requirements, a proper version of HyperCard and a Home stack (supplied with HyperCard) should also be located together somewhere on your hard disk (see your HyperCard manual for help).

The following files are part of the TREGRO model package and should now reside in your new TREGRO file folder:

- TREGRO: The compiled model.
- TREGRO.stk: The HyperCard stack that is the interface to the model.
- Ithaca88.0: Hourly meteorological data for Ithaca, NY, 1988.
- sample.params: A sample input parameter file for red spruce.
- sample.params.Dout: A sample binary output file.
- sample.params.Hout: A sample output file of selected hourly variables.
- sample.params.ERRORS: A sample error file.
- tregro.defaults: A small run configuration file that includes such information as the name of the input parameter file and the day range of the model run.

The three sample output files (*sample.params.Dout*, *sample.params.Hout and sample.params.ERRORS*) are provided to illustrate the output analysis features of TREGRO. They can be discarded to save space once you have done a model run and generated your own output files.

Once you have successfully copied all the files from your TREGRO diskettes to your hard disk folder, store the diskettes in a safe place as a backup copy in case you ever need to reinstall any files. Never attempt to run the model directly from the original diskettes, as you may inadvertently damage or alter the original copy.

## Starting the TREGRO Model Interface

Locate the file "TREGRO.stk" in your new folder. This is a HyperCard stack which serves as the model interface and communicates with the model by modifying the two input files and reading the output file.

The inputs for TREGRO are contained in two text files, *tregro.defaults* and *sample.params*. *Tregro.defaults* can not be renamed and must always be in the same folder as the TREGRO interface. This file contains basic information needed for initiating the model run, such as the name of the input parameter file to use and the start and end days for the model run. The input parameter file, here

named*sample.params*, can have any name determined by the user. Typically, input parameter files are created by modifying this *sample.params* file and saving the changed file under a new file name. Both of these input text files may also be viewed and edited outside of the TREGRO interface using commercial spreadsheet or word processor software (e.g., Microsoft's Excel® or Word®).

The general output file is a binary file that contains the daily model output variables generated by the model; its name is assigned by adding the suffix ".Dout" to the end of the corresponding input parameter file name (e.g., *sample.params.*Dout). Likewise, the other files that are produced by a model run are named using the appropriate suffix (".Hout" or ".ERRORS"). The interface is able to extract subsets of output variables from the binary file and graph the data or make a text table that can be imported to other Macintosh applications, such as spreadsheet or graphing programs.

To start the model interface, either select "TREGRO.stk" by clicking on it and choosing "Open" from the file menu, or by double-clicking on the icon. You should see an opening title screen and then the Main Menu. The buttons in the Main Menu and throughout the interface are operated by clicking on them once. On all screens, a button (usually in the upper right corner) will allow you to backtrack to other screens or to the beginning.

Note that you may encounter a message prompting you to "Convert the HyperCard stack"during your first TREGRO session. This is because your version of HyperCard is different from that used to write the model interface. If this occurs, simply click on the button to proceed with stack conversion to your HyperCard version; nothing will be lost in the process.

## Setting up a Model Run

To set up a run, click on "Change Model Parameters". First, you will see a screen on which you set the beginning day number of a model run (1 is recommended) and the ending day number (e.g., for a 2 year run, you might enter 730). To change any value,

select the text and type over it. Selecting text is done by clicking at the beginning or end of the text and dragging over it. (Note: The tab key will usually move from field to field, selecting text as it goes.) Ignore the other fields on this screen for now. When you are finished, click on "Continue".

The name of the input parameter file is entered on the Input Parameter Files screen (Fig. XX). If you are not automatically prompted for a New or Existing file, click in the field to bring up the dialog box that will enable you to create a new file or to specify an existing one. It is suggested that you make a new file and preserve the *sample.params* file. To do this, type in a file name that does not currently belong to any file, and click "Save". File names should not have any spaces or colons. In addition, the complete file path should be no more than 55 characters, including the colons used as path delimiters.

The interface will then ask you to pick a file on which the new file will be based. For this initial run, select *sample.params* as the base file and click "Open". After the cursor changes back to the "pointing finger", click on the "Modify Parameters" button change.

The Input Parameter Menu screen (Fig. XX) is the main "control panel" for setting up a model run. For this initial run with the sample parameters, you will make only one change from this screen. Go to the Meteorological Data screen by clicking on the "Meteorological Data" button. Make sure that the "Use Met Data Files" radio button is selected; click it, if it is not. Then, click on the "Change Met File" button to bring up a dialog box in which you can select the desired meteorological data file. Find the *Ithaca88.0* meteorological file in your TREGRO folder and select it in the dialog box. For now, ignore the other areas of this screen and click on the "Model Inputs" button to return to the Input Parameter Menu screen. Clicking the "Input Parameter Files" button brings up a dialog box asking you whether you want to save or discard the changes you've made to your input parameter file. If you want to return to the Input Parameter Files or Main Menu screens without altering your input file, click "Discard

Chgs". If you change your mind and decide to not stop browsing or changing inputs, click "Cancel". In this case, click "Save Chgs". You are then returned to the Input Parameter Files screen with your changes saved to your designated input file. You can then click the Main Menu button to return to the Main Menu and run the model.

To summarize what you have just done: You selected an input file, or parameterized tree, to simulate; the meteorological conditions under which you want the tree to "grow"; and the length of time it will "grow".

## Running the Model

Click on the "Start a Model Run" button. The Modify Parameters screen will appear on your monitor followed by a smaller window that shows the progress of the model run. There will be a delay of 1-2 minutes as the model reads the large meteorology data files. Don't worry about messages you may see flash by during model execution; this is normal unless a Macintosh system error window opens and prompts you to take some action. If you have to abort the run for some reason, type "cmd-period" (hold down the Command, or Apple, key in conjunction with the "period" key), wait for a beep, and then choose "Quit" from the File menu or type "cmd-Q". Note that TREGRO will run in the background, allowing you to use another application, but this will significantly slow down the model on all but the fastest computers.

When beginning a model run, the interface may ask "Where is TREGRO?" and prompt you with a file dialog box. If this occurs, locate TREGRO in the file dialog, click on it to highlight it, and click "OK". This tells the interface the correct directory pathway for locating the program; occasionally this may need to be reset.

If the model does not begin execution (i.e., the TREGRO Main Menu screen does not respond when you click the "Run Model" button), check the available memory by going to the Finder and choosing "About This Macintosh" in the Apple menu (see your Macintosh user manual). At least 1.5 MB of free memory are required to run TREGRO,

in addition to the HyperCard interface. If you do not have enough memory, quit other applications that are open.

If the model still does not run, check again to make sure your hardware setup is equipped with sufficient memory (see Hardware and Software Requirements, above). If it is, you may somehow have damaged the TREGRO interface or the model itself. To correct this, reinstall "TREGRO.stk" and "TREGRO" by copying them again to your hard disk folder (with the replace option) from the original backup diskettes. If all this fails, your Macintosh might be damaged and need service. Consult your support technician for advice.

## Viewing Model Output

After the model run is finished, you will find yourself back at the Main Menu of the interface. It is strongly suggested that you check the error file, designated as "*yourinputfile*.ERRORS". To do so, click on the button labelled "Check Error File For Each Model Run". You will be asked to select an application to use in reading this text file. Under most circumstances, there should be only the date of the model run and the names (with the full paths) of the input parameter and meteorological files used. Other messages may be due to the parameters used or may indicate problems with the model's operation. One common problem occurs when the user neglects to correctly specify the location of the desired meteorological file prior to starting a run. If the model cannot locate the file, it will use simulated weather data, indicated by the default file name, *zznoMetFile.0*. Only by checking the error file can the user be assured of noticing this error.

TREGRO offers two ways of viewing your model results: QuickGraph, for generating standard time series and XY plots of a limited number of outputs and days, and a Custom method for viewing an unlimited number of outputs or days in a spreadsheet or more sophisticated graphing program. QuickGraph is briefly described here. Both methods are described fully in the Model Outputs section.

To view your results, click on the button "Quick Graphs or Tables" under Data Analysis Tools on the Main Menu screen. The built-in graphing is fast, but limited. The interface will take you to the "Select Output Values" screen to choose different output parameters to view. It will ask if you want to graph over time. Answer "Yes" for a time series plot of up to four variables. Answer "No" if you want an *xy* plot of any single variable against up to four other variables (e.g., to see correlations).

The buttons on the "Select Output Values" screen are pop-up menus. Click and hold the mouse button down until the menu appears, then drag to an item to highlight it and let the button up. For example, try clicking on the button labeled "Biomass" and select the item "total tree mass". That item should now appear on the parameter list on the screen. Select another output from another pop-up menu. Now click the "Continue" button above the parameter list to go to a screen where you will specify the output file from which you want the interface to extract the data.

On the first line on this screen you will notice that the interface has automatically entered the name of the output file for the last model run that you did. If this line is blank or needs to be changed, click on the button just above it to select one of the available output files. The next line is the name of the text file that will be created. This file is labelled *yourinputfile*.qg# by default; click the "Change QuickGraph file name" button to choose another. Below this name field you can select the start and end days for extracting data, as well as the number of days to skip (i.e., plotting interval). QuickGraph can plot 249 days. If you have selected a range greater than this, the interface will warn you and indicate the number of days it will skip. When you are ready, click on the "QuickGraph" button on the lower right. The interface will ask for a label for the ordinate axis, which you can leave blank, and then create the graph on your screen. Clicking the "YAxis General (or Exponential)" button toggles between two methods of displaying the *y* axis values. Buttons on the bottom of the graph enable you to plot the same variables for a different output file or day range, plot different

variables from the same output file, or to print the graph. The arrow buttons allow you to position the legend. Click on the "Help" button for a shortcut method for moving the legend. When you are done, click on the "Main Menu" button to return to the main screen.

## Next Steps

TREGRO allows great flexibility in parameterizing tree species. This flexibility, however, requires a large number of input parameters. Although the interface provides easy access to these parameters, it is suggested that the user be systematic in checking and changing parameter values when setting up a TREGRO run, to prevent the use of unintended values. The order in which the parameters are discussed in Section 4: Parameter Descriptions and Instructions is a good sequence to follow.

A few things to keep in mind when parameterizing TREGRO:

(1) Be sure to read all notes and directions provided on the interface screens.

(2) Input is by fields designated by dotted underlines, pop-up menus that present a list of possible choices, radio buttons, or check boxes. Shadowed boxes or rounded rectangles are either pop-up menus or buttons that progress to another input level.

(3) Do not leave fields blank or enter letters instead of numbers. Most input fields do not do error-checking. It is left up to the user to check inputs for accuracy.

(4) Worksheets are provided in some places in the interface to aid in parameterization. Values entered in these worksheets are not automatically written to the input parameter file. Be sure to enter the desired values in the proper fields.

(5) Some fields, such as those in worksheets, are calculated fields based on input fields. These calculations may not update after entering new input values until you click outside the input field or hit <enter>.

You are now ready to start using TREGRO. Although the interface is highly intuitive for an experienced Macintosh user, it is strongly recommended that you read the following sections, which cover model functions and operation in greater detail.

This is the second release of TREGRO. If you discover any bugs, experience any difficulties in your specific applications, or require other assistance, contact the developer:

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# PHILOSOPHY BEHIND THE TREGRO MODEL

## Simulating the Availability of Carbon Supplies to Determine Interacting Stress Response

The size of the available carbon pools in relationship to the demands for carbon can play a major role in determining whether stress leads to plant damage. Plants survive because they have response systems that can mitigate the detrimental effects of a stress. They decline if the limits of this mitigation system are exceeded. The response systems of trees depend on mobilizing carbon to rebuild injured tissue or to increase resource collecting area. The limits of the mitigation system are reached when carbon is unavailable to construct new tissue or to meet increased respiratory needs associated with injury repair.

For example, consider a tree exposed to levels of ozone sufficiently high to suppress the rate of photosynthesis. The reduced rate of photosynthesis leads to a decrease in the amount of carbon available for basic plant maintenance and growth. A possible response by the plant would be to mitigate ozone damage by increasing the quantity of new leaf surface. This would be accomplished by preferentially increasing the proportion of carbon being allocated to leaf and branch growth. If carbon reserves are sufficiently plentiful, enough new leaf area may be added through this process to recover to pre-stressed rates of photosynthesis.

Mitigation is not achieved without a cost, however. Insufficient carbon may be available for allocation to root growth. Even in sites without severe deficiencies of water or nutrients, this loss of root biomass could render the plant more susceptible to

limitations caused by periodic fluctuations in the availability of these resources. When there is insufficient root surface area for water and nutrient uptake to meet the needs of new tissue production, carbon fixation will decline. Thus, the mitigation of stress from one source may indirectly increase susceptibility to stress from another source by reducing the plant's carbon resources.

Trees can provide a large supply of available carbon by rapid rates of photosynthesis. However, since photosynthesis rates vary daily and seasonally, the rate of new fixation is often insufficient to meet all the carbon demands of the plant. At such times, the plant meets its needs by drawing on carbon reserves accumulated during periods of more rapid fixation. Under conditions of extended or severe stress, there may be insufficient carbon from the sum of photosynthesis and reserve carbon to satisfy plant requirements.

Therefore, the capability of trees to withstand stress may be closely related to the amount of available carbon in the plant. In plants with low carbon supplies and reserves, changes in carbon allocation can occur only at the expense of reduced allocation to other tissues. The principal focus of this modeling effort has been to estimate the status and dynamics of the carbon balance of a tree under a variety of stress scenarios and to predict the implications of a given carbon status on tree survival. To understand the chain of events between the initial stress, the demands on plant carbon reserves, and the eventual plant response, TREGRO can be used to track the level of available carbon (including newly fixed photosynthate and carbon reserves), predict the pattern of growth that will occur given changes in available carbon, and estimate the effect of a wide range of stresses on this growth.

## Brief Description of TREGRO

TREGRO is a simulation model of the carbon, water, and nutrient flows of an individual plant. It was developed to analyze the response of trees to multiple stresses. TREGRO was designed to evaluate the ways that one stress, such as temperature,

drought, or nutrient deficiency, affects the response of the tree to another stress, such as exposure to atmospheric ozone. It performs this analysis through a simulation of the flux of carbon into the plant, the use of carbon to build and maintain tissues within the plant, and the manner in which these processes are altered by exposure to stress. Finally, and perhaps most importantly, TREGRO gives the user a tool to evaluate the degree to which a tree is capable of mobilizing carbon resources to minimize injury from stress.

The model code is written in FORTRAN and consists of a series of difference equations used to deterministically calculate rates, such as photosynthetic fixation and respiration, and solutions to mass balances used to calculate carbon, nutrient, and water pool sizes and fluxes between pools at each iteration time step.

In the model, the tree is divided into the following compartments: vegetative buds, a canopy of leaves grouped by age class, branches, stem, coarse roots in two soil horizons, and fine roots in three soil horizons. In each of these compartments the model keeps track of three carbon pools: living structure; dead structure, or wood; and total non-structural carbohydrate (TNC). As used here, wood is the same as what is considered heartwood or non-living tissue in the literature, while structure is the living tissue. Sapwood plus TNC is equal to what is considered sapwood in the literature. The model calculates the photosynthesis of the entire tree each hour as a function of ambient environmental conditions and the availability of light in the canopy, water, and nutrients, using equations published by either Farquhar (Farquhar et al. 1980) or Lohammer (as implemented by Running) (Lohammer et al. 1980; Running 1984). TREGRO also provides an hourly estimate of ozone uptake under changing conditions of water vapor and other environmental conditions. Uptake of water and nutrients are calculated daily based on the nutrient status of the three soil horizons. An associated model, YASE, (Yanai, ) can be used to calculate daily soil equilibrium nutrient concentrations.

In TREGRO, direct ozone injury suppresses the rate of photosynthesis through either a cumulative effect on photosynthesis, an instantaneous respiration cost or both, depending on the choice of the user. The reduced rate of photosynthesis leads to a decrease in the amount of carbon available for basic plant maintenance and growth. Carbon is redistributed within the plant daily for growth, storage, respiration and senescence. TREGRO calculates how the plant is likely to shift its carbon allocation as a result of the lowered supply of carbon.

TREGRO contains no explicit control of carbon partitioning as a function of environmental stress. Instead, carbon and nutrients are allocated to the various growing tissues according to priorities of tissue type. Typically, aboveground portions of the plant are assigned by the user to have first access to newly fixed carbon, while belowground portions have first access to nutrients for growth. The user can change the order of these priorities. The user also assigns maximum growth rates of tissues in each of five different growth periods throughout the year. Tissues can grow at maximum rates only if carbon and nutrients are abundant; insufficient carbon or nutrients limit growth. This simple scheme can be used to produce commonly observed changes in root-to-shoot ratio under carbon limitation, such as that caused by ozone stress.

The model predicts the stress response of a tree growing in isolation; it ignores the influences of adjacent trees on the light regime, the availability of water and nutrients, and the dynamics of the litter layer. However, by manipulation of the light environment, TREGRO can simulate a tree in any portion of a forested canopy.

Of the list of parameters required for operation of the model, most are easily measured or are obtainable from the literature, including rates of photosynthesis, rates of tissue growth, and periods of phenological development. For some species, the estimates of respiration for most tissues are not well-known even though they can greatly influence the estimates of carbon balance.

Every effort was made to construct the model from first principles of tree response to the environment in order to create a tool that was generic, applicable to a wide variety of tree species, and not calibrated to a specific experimental set of trees. However, many parameters are best estimated from a specific data set produced for this purpose.

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# DESCRIPTIONS OF MODELED PROCESSES

The model simulates the processes by which carbon is fixed in the leaves, the processes of carbon redistribution and utilization throughout the plant, and the processes by which water and nutrients are taken up for use in photosynthesis, transpiration, and growth. To do so, the model follows the flow of the three plant materials: carbon, water, and each of six major nutrients. These flows are linked through representations of the mechanisms by which they influence one another. The ability of the plant to utilize each of these materials depends in part on the availability of the other two. Detailed functional flow diagrams depicting the model structure and integration of process subroutines can be found in Appendix A.

The tree is represented by a number of compartments: vegetative buds, leaves by age class, branches, stem, coarse roots in two soil horizons and fine roots in three soil horizons (Table 3-1). Carbon stored in these compartments may be divided into three types: living structure; dead structure, or wood; and total non-structural carbon (TNC), which includes both soluble sugars and starch. Only branch, stem, and coarse root compartments have wood. Although in reality fine roots contain their own pool of TNC, fine root TNC in TREGRO is added into the coarse root pools for convenience. This approximation should have no significant ramifications unless the life span of a root is proportional to its initial TNC, as some speculate; however, such a mechanism is unsupported at present.

Soluble nutrients (i.e., those contained within the plant, but not bound in living or dead structure) are not assigned to specific tissues. However, the concentrations of key

tissues, such as leaves, are calculated when needed. TREGRO adds nutrients taken up by the roots to a single pool of labile (non-structurally bound) nutrients for the plant as a whole. As tissues grow, nutrients are removed from this single labile pool to become structurally bound in the newly grown tissue. Since each tissue maintains a fixed ratio of bound nutrient to structural carbon, the quantity of nutrients structurally bound in any tissue can be easily calculated by multiplying this ratio to the structural biomass at the time. The total nutrient content of a plant is equal to its structurally bound nutrient content plus the non-structurally bound nutrient in the plant's labile pool. Photosynthetic processes are assumed to have access to all non-bound nitrogen and magnesium.

The simulated processes in TREGRO are calculated on one of two time steps. Photosynthesis and soil and plant water potentials are computed hourly, while nutrient uptake, allocation and growth are simulated on a daily time step.

Table 3-1. Carbon distribution in the simulated tree.

| Compartments | | Carbon pools within Compartments | | |
|---|---|---|---|---|
| | | TNC | Living Structure | Dead Structure (Wood) |
| Buds | | | • | |
| Leaves: | current (= flush 0) | • | • | |
| | flush 1 | • | • | |
| | flush 2 | • | • | |
| | ⋮ | | | |
| | flush *n* | • | • | |
| Branch | | • | • | • |
| Stem | | • | • | • |
| Coarse root | upper | • | • | • |
| | middle | • | • | • |
| Fine root | upper | * | • | |
| | middle | * | • | |
| | lower | * | • | |

* = Fine root TNC is added to the coarse root pools.

## Carbon Balance

Simulating the carbon balance of the tree requires calculating gross photosynthesis, growth and maintenance respiration, and senescence. The size of the simulated carbon pool at every time step is equal to the accumulated total amount of carbon fixed into plant structure plus that available as non-structural carbon (TNC) reserves. The daily change in carbon in the whole plant is the sum of photosynthesis of all leaf classes minus the sum of the maintenance respiration and the growth respiration

of each tissue type, each calculated hourly and summed over the entire day, and minus the tissue lost to senescence:

$$\frac{dC}{dt} = \sum_{i=1}^{n} P_{g_i} - \sum_{j=1}^{(n+7)} R_{m_j} - \sum_{j=1}^{(n+7)} R_{g_j} - \sum_{j=1}^{(n+7)} L_j$$

where:

$C$ = sum of carbon in all plant tissue pools

$\frac{dC}{dt}$ = change in whole plant carbon per unit time

$P_g$ = gross photosynthesis

$R_m$ = maintenance respiration

$R_g$ = growth respiration

$L$ = tissue loss through senescence

$i$ = leaf class

$j$ = compartment (leaf classes, branch, stem, coarse roots in 2 soil layers, fine roots in 3 soil layers)

$n$ = number of leaf classes

Allocation to growth and storage moves carbon within the plant, not directly affecting the total carbon balance, but indirectly influencing photosynthetic capacity and respiration losses. The more structure contained in a tissue, the larger will be its maintenance respiration.

### Carbon Budgets and Inaccessible Carbon

An annual carbon budget for the total carbon in the modeled system can be calculated:

$$\begin{aligned} Total\ carbon = {} & cumulative\ gross\ P_s - cumulative\ respiration \\ & - cumulative\ senescence - total\ inaccessible\ carbon \end{aligned}$$

where "cumulative" outputs are annual cumulations, zeroed at the start of each new year, and total inaccessible carbon is the total cumulative amount of carbon that was daily in excess of what was needed to grow tissues at their maximum rate and to fill the TNC pools throughout the plant. Trees most likely employ a negative feedback mechanism to slow photosynthesis during times when production exceeds demand. However, since this mechanism has not been determined to date, TREGRO places this carbon in a pool which is unavailable to the plant for future growth, essentially accomplishing the same purpose. The accumulated quantity that is placed into this unavailable pool is kept track of for budgetary purposes. To use the equation above, one must first calculate the yearly increment in the inaccessible pool, since the output "inaccessible carbon" from the model is zeroed at the start of the run and then cumulates for the duration of the run.

### Photosynthesis

Two methods are available for calculating photosynthesis, the Lohammer method and the Farquhar method. These methods are described more fully in the following sections. The Lohammer method gives a more empirical approximation of photosynthesis because it contains a parameter, the maximum mesophyll conductance, which cannot be measured directly from field observations. This parameter must be adjusted so that the photosynthesis rate produced by this module under conditions of high moisture availability, high light, low vapor pressure deficit (VPD), high nutrient availability, and optimal temperatures matches that observed under similar conditions in the field.

The Farquhar routine uses parameters that more closely match quantities commonly measured by physiologists. Further, it calculates photosynthesis by solving the energy balance budget for a representative leaf, a more widely accepted calculation. This calculation requires much more computing time, however, and consequently

causes simulations to run at a slower pace. It is important to note that if the user wishes to calculate evapotranspiration and to move water through the soil, the Farquhar routine must be used.

If available light is not provided with the hourly environmental input data, it can be calculated from the time of day, time of year, and probability of cloudiness; the model also estimates other missing environmental data automatically, as described in Section 4: Parameter Descriptions and Instructions: Meteorological Data.

**The Lohammer method.** The Lohammer photosynthesis module is based on concepts developed in the models of Lohammer et al. (1980) and Running (1984). The module uses environmental input data (daily rainfall and hourly light, temperature, humidity, and ozone) to calculate gross photosynthesis each hour by each age class of leaf tissue. The rate of fixation is proportional to the resistance to carbon dioxide flow into the leaf at the stomate (stomatal conductance) and at the cell membrane (mesophyll conductance):

$$Photosynthesis = \frac{k_s * k_m}{k_s + k_m} * \Delta CO_2$$

where:

$k_s$ = stomatal conductance

$k_m$ = mesophyll conductance to $CO_2$

$\Delta CO_2$ = gradient from atmosphere to carboxylation site

The calculated stomatal conductance, $k_s$, of a leaf class during each hour depends on the maximum stomatal conductance possible under optimal growing conditions, and the water vapor pressure deficit (VPD):

$$k_s = Max\left[0, k_{s_{\max}} * \left(1 - VPDSLP * Max\left[0, VPD_t - VPDTHSH\right]\right)\right]$$

where:

$k_{s_{\max}}$ = maximum stomatal conductance

$VPDSLP$ = absolute value of slope of relationship between stomatal conductance and VPD

$VPD_t$ = vapor pressure deficit at hour $t$

$VPDTHSH$ = minimum VPD at which a reduction in $k_{s_{\max}}$ occurs.

Increases in VPD above a user-defined threshold cause decreases in stomatal conductance at a linear rate also defined by the user.

Simulated mesophyll conductance depends on a maximum possible conductance (measured under light-saturated conditions), the available light, temperature (a user-definable curve from which a modifier is calculated), the age class of the leaves, and a minimum nitrogen or magnesium concentration. The relationship between available light and mesophyll conductance reflects the half saturation and compensation point levels (measured from trials of assimilation under different light levels):

$$k_m = \frac{I - I_0}{I + I_{1/2}} * k_{\max} * f(T) * A * U$$

where:

$I$ = incident shortwave radiation (µE/m$^2$ s)

$I_0$ = light compensation point (µE/m$^2$ s)

$I_{1/2}$ = irradiance at which $k_m$ is half its maximum value (µE/m$^2$ s)

$k_{\max}$ = maximum mesophyll conductance (cm $CO_2$/s)

$T$ = air temperature (°C)

$f(T)$ = user-definable curve relating $k_{\max}$ to air temperature

$A$ = leaf age modifier

$U$ = nutrient modifier based on N and Mg concentrations (see Stresses: Nutrient Stress section)

**The The Farquhar method.** Following the method defined and described by Farquhar et al (1990) and Kirschbaum and Farquhar (1987) and modified by Collatz et al (1992), the model calculates the photosynthetic assimilation of a representative leaf as the minimum of three potential rates: the light-limited rate, $J_e$; the RuBP regeneration-limited rate, $J_c$; or the capacity for the export or utilization of the products of photosynthesis, $J_s$ ( approximately, the maximum value of assimilation at saturating light and $CO_2$).

To calculate $J_e$:

$$c_i = c_a - \left( A_n * \frac{1.6 g_s + 1.4 g_b}{2.24 g_s * g_b} \right)$$

where:

$c_i$ = internal partial pressure of $CO_2$

$c_a$ = atmospheric partial pressure of $CO_2$

$A_n$ = assimilation of $CO_2$

$g_s$ = stomatal conductance

$g_b$ = boundary-layer conductance

(2) $T_0 = \frac{O_2}{tau}$

where:

$O_2$ = the oxygen concentration

$tau$ = a ratio of the kinetic parameters describing the partitioning of RuBP to the carboxylase or oxygenase reactions of Rubisco.

(3) $J_e = a * \alpha * Q_p * \frac{c_i - T_0}{c_i + T_0}$

where:

$a$ = leaf absorbance to photosynthetically active radiation

$\alpha$ = intrinsic quantum efficiency for $CO_2$ uptake

$Q_p$ =

$J_c$ is calculated as:

$$J_c = \frac{V_{\max} * (c_i - T_0)}{c_i + K_c * \left(1 + \frac{O_2}{K_0}\right)}$$

where:

$V_{\max}$ = the maximum catalytic capacity of Rubisco per unit leaf area;

$K_c$ = the Michaelis constant for $CO_2$

$K_0$ = the competitive inhibition constant for $O_2$ with respect to $CO_2$ in the Rubisco reaction.

$J_s$ is calculated as:

$$J_s = \frac{V_{\max}}{2}$$

When using this model, leaf respiration is a function of $V_{m.ax}$. The kinetic parameters of the model: $V_{max}$ , $K_{c,}$ $K_o$ and tau, are themselves functions of temperature, with exponential increases in their rates of activity with increases in the surface temperature of the leaf. This temperature is approximated by solving the energy budget of the leaf. Both photosynthesis and respiration are inhibited at high temperatures, with this inhibition increasing rapidly once temperatures climb above 40°C.

Photosynthesis is also reduced from a maximum value as a function of soil water potential (see "Stresses: Water Stress" section).

### Age and Light Distribution Effects on Photosynthesis

TREGRO allows for the parameterization of different photosynthetic efficiencies for each leaf age class. Depending on the method chosen, leaf classes can differ in their values for $k_{max}$ (Lohammer) or $V_{max}$ (Farquhar).

The fraction of leaves in each leaf class that are exposed to full light must be set by the user for each of two periods: during the early morning and late afternoon hours and during the hours of 10 AM until 3 PM. The remaining leaves are considered to be in shade, which is a user-definable fraction of full light. The model assumes that these proportions do not change over the course of a simulation.

### Respiration

TREGRO uses two types of respiration: growth respiration, defined as the carbon cost of growing new structure, and maintenance respiration, defined as the carbon cost of maintaining that structure.

Growth respiration can be set for each tissue as a fraction of the carbon that is allocated to that tissue for growth. For example, setting this fraction to 0.2 means that only 0.8 g of every 1 g of allocatable carbon will be converted into structure. This respiration is temperature-independent.

Maintenance respiration of each tissue depends on the the mass of tissue structure, its base respiration rate at 20°C, the temperature increase at which this rate doubles (Q function), and the air temperature.

$$R_m = Mass_{str} * r * 2^{\left(\frac{T-20.0}{Q}\right)}$$

where:

$Mass_{str}$ = Mass of tissue structure (g C)

$r$ = respiration rate (leaves: fraction of structure/hr; other tissues: fraction of structure/day)

$T$ = air temperature (°C)

$Q$ = doubling function

Rates of maintenance respiration at 20°C can be specified separately for each tissue, as can the rates of increase.

## Allocation and Growth

### Phenology of Growth

The simulated pattern of growth is restricted by tree phenology, or the timing during the year when growth of a particular tissue type is permitted  The user can choose which growth events occur in each of five growth periods, as well as when one-time events (annual leaf drop and dormancy), occur.  The duration of the growth periods are determined by the environment (i.e., accumulated growing degree days), by tree status (i.e., TNC content), or by calendar day.

Dormancy in TREGRO is a period of no plant activity, including respiration.  The physiological calculations of photosynthesis, respiration, allocation, and soil water movement are turned off during this period.  No dormant period need be established. Alternatively, dormancy can be simulated as a period when only respiration occurs.

### Choices for Actions in Each of the Growth Periods

Table XX lists the actions possible in each growth period, with a description of each.  The user selects from this list, instructing the model in any given growth period to perform some or all of these actions.  The order in which the actions are listed determines their priority for allocation of the carbon left after first replenishing the deficit caused by daily maintenance respiration and the filling of the leaf TNC pools.

An event may be selected more than once in a growth period; each occurrence of this event will be executed daily.  Note that, with one exception, each tissue-growing

event (e.g., Grow Stem from Photosynthate) will grow up to the maximum allowed daily growth for that tissue at that temperature. Thus, the model could be set to grow stem structure three times daily during growth period 4. In the presence of adequate nutrients and allocatable carbon, this would result in actual daily growth that was three times the calculated maximum daily growth. The one exception to this is when growing branches from TNC. In this case, no more than the calculated maximum daily growth can be attained.

Table XX. Description of actions possible in each growth period.

| **Choice** | **Description of action when choice is selected** |
|---|---|
| Drop leaves | Drop leaves if the tree is stressed due to low TNC levels. This stressed leaf drop cannot occur before growth period four. On the first day in growth period four, the degree day after which leaves can drop is calculated as the sum of the current degree days and the user-input value for degree days to delay this drop. When the accumulated degree days exceed this calculated drop-degree-day value and the model is still in growth period four, leaves will be dropped when TNC levels are less than the minimum and the structure is above a minimum. If the model is in growth period five, leaves will be dropped any time these two cases are true. |
| Grow vegetative buds | Vegetative buds are grown based on the user-input growth rate. The user can choose whether they will be used or not on the "Growth Switches" card. |
| Grow leaves | If the leaves are not fully grown, check if it's the first day of the leaf flush. If it is, transfer the vegetative bud structure to the current leaf class structure or try to grow a user-input fraction of the leaf goal. Grow leaves from photosynthate, branch TNC, stem TNC, all other leaf class's TNC, coarse root A TNC, and coarse root B1 TNC. Note that leaves can only be grown normally in growth period 3. They cannot be grown in growth periods 1 and 2. They can be grown in growth periods 4 or 5; they will not form a new leaf class, but will continue to increase the last leaf class grown in growth period 3. |

| | |
|---|---|
| Grow branch from photosynthate and TNC | Grow branch from photosynthate and branch TNC, stem TNC, coarse root A TNC, and coarse root B1 TNC. The user can choose whether to grow branches from photosynthate only on the "Growth Switches" card. |
| Grow stem from photosynthate | Grow stem from photosynthate. |
| Grow coarse roots A from photosynthate | Grow coarse roots A from photosynthate. |
| Grow coarse roots B1 from photosynthate | Grow coarse roots B1 from photosynthate. |
| Grow branch wood | Grow branch wood from branch structure. |
| Grow stem wood | Grow stem wood from stem structure. |
| Grow coarse roots A wood | Grow coarse roots A wood from coarse roots A structure. |
| Grow coarse roots B1 wood | Grow coarse roots B1 wood from coarse roots B1 structure. |
| Update nutrient pools | Calculate the nutrient concentration in the throughfall, calculate the nutrient uptake, and adjust the pools accordingly. The pools will not exceed their maximum size. |
| Grow and senesce fine roots | Grow fine roots from either photosynthate and coarse root A and B1 TNC or photosynthate only, according to the user input switch on the "Growth Switches" card. Each layer of fine roots (A, B1, B2) is grown from a third of the available photosynthate and all of the available coarse root A and B1 TNC. Kill off specified amount of fine roots in layers A, B1, and B2. |

| | |
|---|---|
| Convert photosynthate to starch | If there is available photosynthate, allocate the photosynthate to various TNC pools in the plant. The actual compartment depends on the current growth period. For growth period one, all photosynthate is stored as branch TNC. For growth periods two, three, and four, the photosynthate is divided among the branch, stem, and coarse root compartments in proportion to their deficits. For growth period five, the photosynthate is divided between coarse roots A and B1. If there is still photosynthate left over after this, coarse root A is filled to capacity, followed by coarse root B1. Any remaining photosynthate goes into an inaccessible carbon pool. The implication of this is that no further growth from photosynthate can occur after this so this action should be the last growth action performed. Also, think about always including this so that an accounting of all photosynthate can be accounted made. |
| Do nothing | No action is performed. |

### Transitions between Growth Periods

The timing of the transition from one growth period to the next is determined by reaching either a user-defined calendar day (growth periods 1 and 5), a user-defined number of growing degree days (growth period 2), or by a combination of degree days, leaf mass, and available tree TNC (growth periods 3 and 4). Calendar days are used for growth periods 1 and 5 to facilitate a more predictable transition, because these periods are frequently used as dormant periods. Entry into growth periods 3 and 4 is complex due to TREGRO's flexibility in growing leaves. This is discussed further in the Section on "Leaf Growth" below.

### Typical Growth Patterns

Figure XX shows a set of growth events chosen in each growth period for an example tree in a typical simulation The model performs each action once a day within

a given growth period in the order in which they appear in this list, from top to bottom. The user assigns this order.

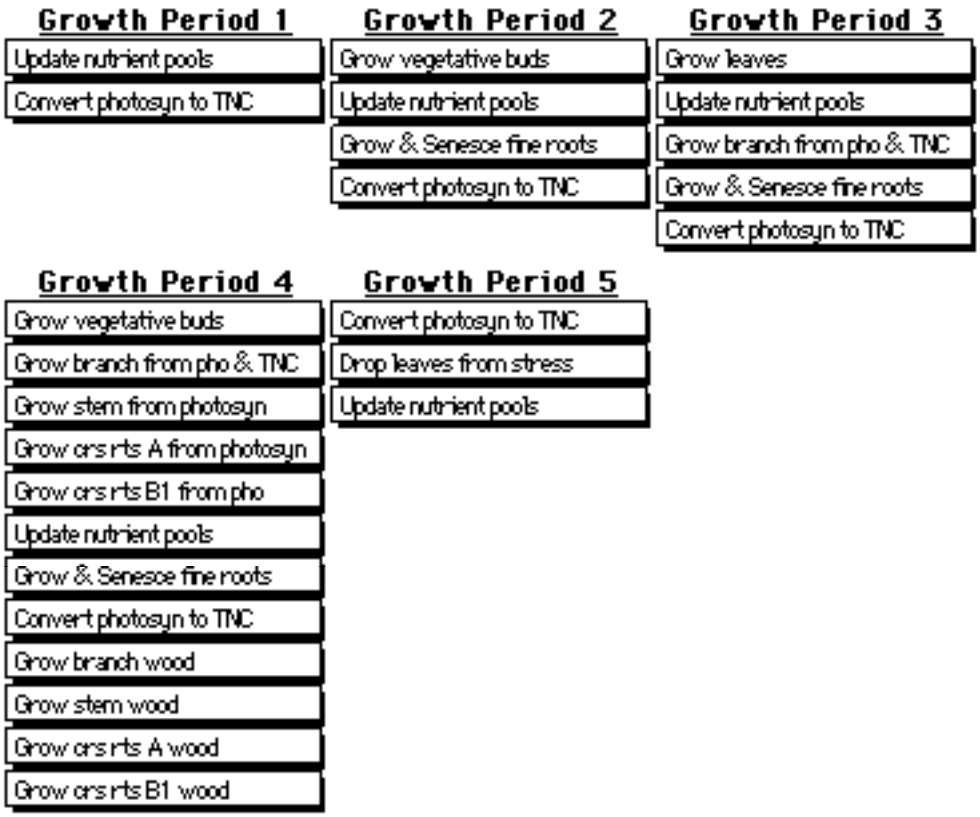



**Figure XX. Example actions in each growth period.**

Figure XX shows an example of the carbon allocation that will occur as a consequence of these choices. Before growth begins in the spring, newly fixed carbon that is not respired can only be used to increase TNC stores (Period 1). An early spring period of root growth and bud swelling (Period 2) is followed in late spring by leaf flushing and branch elongation (Period 3). Carbon fixed in midsummer (Period 4) is used to increase branch, stem, and coarse roots. In the winter (Period 5), plant growth is dormant and only respiration is allowed.

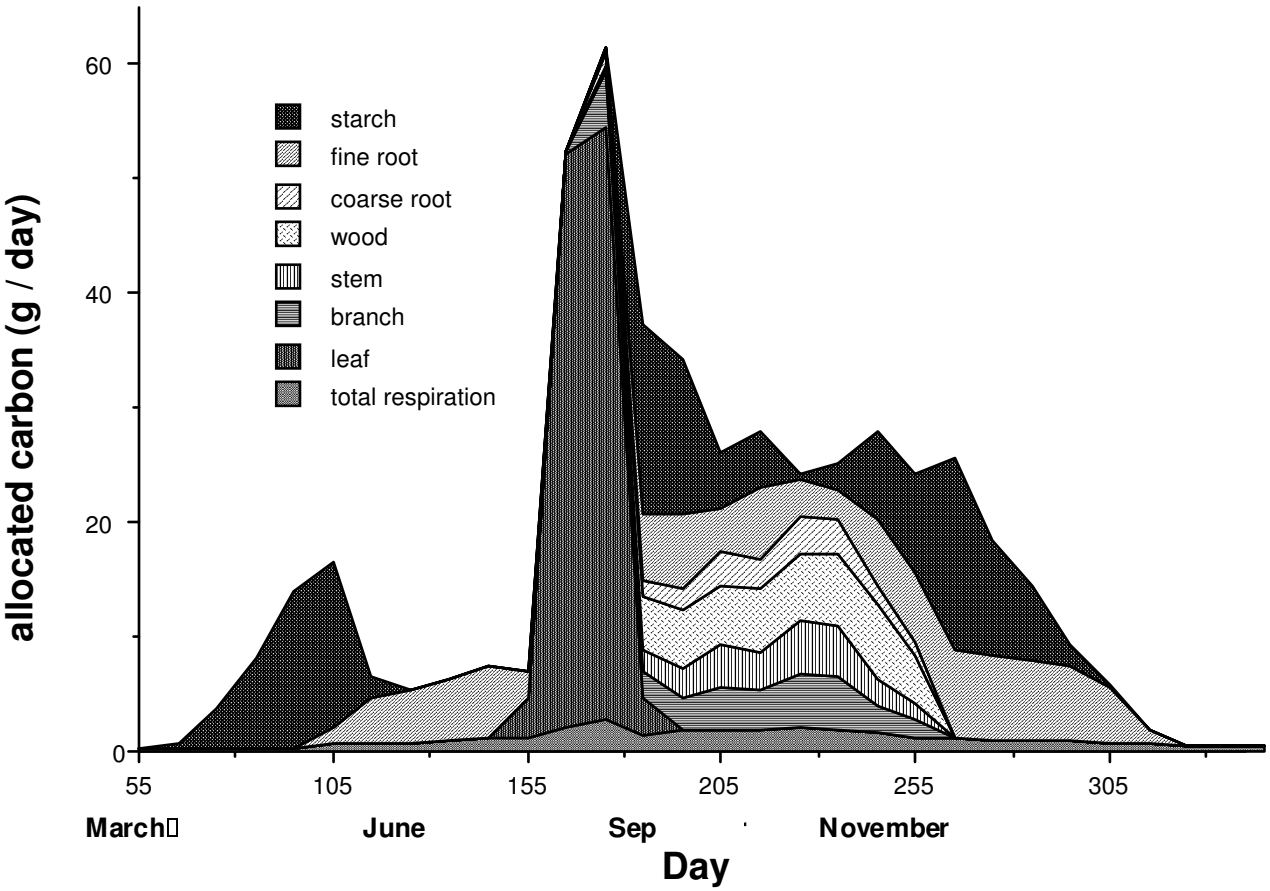



**Figure XX. Pattern of annual carbon allocation produced by a sample run of TREGRO.**

The following is a detailed description of the consequence of these choices. Note that this is only an example of the sequence of actions that can be chosen and the user can choose a different sequence.

**Growth period 1:** Dormancy and Pre-Growth Storage (late Oct/early Nov until mid April). The only actions chosen are to update the nutrient pools (adding the new uptake) and to use any available newly fixed carbon to convert this photosynthesis product to total non-structural carbohydrate (TNC), filling the carbon storage reserve pools within the plant. New photosynthate is available to be stored as TNC for evergreen species; naturally, deciduous species would not produce and store photosynthate at this time. Within this event, the model will first fill the TNC storage of

the leaves to saturation. Leaf TNC is restored to maximum using photosynthate generated within that leaf class only; leaves cannot import TNC from other tissues or leaf classes to fill their own TNC pools.

Next, the model sends photosynthate to the branches, stem, and coarse roots in proportion to the TNC deficit for each tissue. The deficit is calculated as the difference between the TNC content of a tissue and its TNC saturation level, which in turn is a function of the structural mass of the tissue.

**Growth period 2:** Bud Formation and Root Growth (mid-April until mid-May). During this period, new photosynthate is first used to grow vegetative buds for next year's leaves. As with all other structural tissue construction, this growth rate is dependent on available carbon, temperature and nutrient stores. Nutrient pools are then updated with new uptake and fine roots are grown and senesced. Photosynthate not used in vegetative bud growth is available for root growth. Any photosynthate available after meeting the fine root growth demand will then be used to fill TNC pools in various non-leaf tissues, as described in the previous growth period.

**Growth period 3:** Leaf Elongation and Branch and Root Growth (mid-May until late June). When this growth period begins, carbon is transferred to a new leaf class compartment, referred to as the "current leaf class". As discussed later under Parameter Descriptions, this carbon can be either the carbon stored in the vegetative buds compartment or a user-selected amount. The new current leaf class then continues to increase from this initial mass throughout the growth period. Growth period 3 ends when one of the following occurs: the leaf goal weight is attained, tree TNC (excluding the current leaf class) drops below a user-defined minimum, or a set number of growing degree days is exceeded. Carbon for this growth comes from current photosynthate and from TNC drawn from branches, stem, other leaf classes, and coarse roots, in that order (a general discussion of the order of carbon sources is presented below). In the case of species capable of having multiple leaf flushes during one growing season,

growth period 3 can be re-entered on two conditions: tree TNC is replenished to a user-defined value and a critical number of growing degree days has not been exceeded.

Following the updating of nutrient pools, newly fixed carbon, as well as TNC, will be used to elongate branches. Although conceptually the branches are increasing in length during this time, the model does not distinguish increasing length from adding diameter. Both are merely increases in structural weight.

If any remaining carbon is available, fine roots will then be grown from both photosynthate and reserve TNC pools or photosynthate only, depending on the user's choice. In practice, because leaf growth demands so much carbon during this growth period little is left for fine root growth and little growth occurs. Such suspensions in root growth in mid-growing season are commonly observed.

**Growth period 4:** Vegetative Bud Formation, Structural and Wood Formation, and TNC Buildup (July and to late September). Vegetative buds for next year's leaves are constructed first. Carbon is then allocated, in order of priority, to branch structure, stem structure, and coarse root structure. During this period nutrient pools are updated only after this structural growth to ensure that the growth of these tissues will not have access to the new uptake. Fine roots can then be grown with first access to the new nutrient taken up this day.

Excess carbon is then stored as TNC in branches, stem, and coarse roots based on their relative demand, as discussed previously. Finally, structural carbon is converted to wood in stem, branches, and coarse roots during this period, each at its own user-defined rate.

**Growth period 5:** TNC Reserve Formation and Leaf Loss (late September until late October or early November). TNC storage continues during this period if photosynthate continues to be in excess of respiration needs. Allocation to branch and stem structural growth is stopped, as is conversion of structure to wood. Leaves are dropped when leaf TNC in that class falls below a specified minimum (see Senescence

below). Note that this stressed leaf drop is different than the one-time user-defined percentage of each leaf class that can be configured as an autumnal leaf drop. The last action on each day of this growth period is to update nutrient pools with the new uptake.

As should be clear by now, unlike the previous versions of TREGRO version 3.0 allows the user to make their own assumptions about the order of priority of these actions. This change was made because of the speculative nature of evidence supporting the priority order predetermined in previous versions, and because it was observed that the model's predictions of the response to stress were very sensitive to this order. Therefore, it was deemed important to give the user the ability to design their own priority order.

### Leaf Growth

TREGRO can grow one or more flushes of leaf mass in a given year. For each flush, a target mass is calculated based on user inputs. This goal mass calculation is discussed in detail below. Growth period 3 is used for fully-functional leaf growth; leaf growth can also occur in growth periods 4 and 5, but it is generally not recommended due to the lack of programmable control of this growth.

The leaf compartment in TREGRO is divided into up to 10 leaf age classes, numbered 0 to 9, in order of increasing age. Leaf class 0 is also referred to as the "current" leaf class. On entering growth period 3 for the first time in a leaf flush, a shuffling of leaf classes occurs in which the leaf mass in each class is reassigned to the next older class (e.g., leaf class 3 to leaf class 4). Leaf mass in leaf class 9, the last leaf class, accumulates unless leaf senescence occurs.

Normally, leaf growth is initiated on entry into growth period 3. Entry into this growth period is determined by a combination of conditions: the accumulated degree days must be between the entry thresholds for growth periods 3 and 4, the ratio of total

tree TNC to total tree structure (excluding current leaves) must be above a user-defined threshold, and the tree must not have already grown its maximum number of leaf classes for that year. On the first day of leaf growth, the leaf class is initialized with either of two options, the mass of vegetative buds or a fraction of the goal mass (see Parameter Descriptions and Instructions: Growth Priorities: Growth Options for details). The model will then remain in growth period 3 on subsequent days as long as the leaf flush goal mass has not been reached, a certain minimum total tree TNC ratio is maintained, and the degree day entry threshold for growth period 4 is not reached.

When the tree reaches the leaf mass goal or no longer has sufficient available carbon (photosynthate and TNC) to grow leaves, the model will move to growth period 4 and that leaf class is completed. In the case of species capable of having multiple leaf flushes during one growing season, growth period 3 can be re-entered if total tree TNC is replenished to the critical entry value and the degree day threshold for entry into growth period 4 has not been reached.

**Leaf mass goal calculation**

The size of the leaf class that TREGRO attempts to be grow in each leaf growth period is calculated in one of two ways. In the simplest, Fractional Increase, the new leaf mass goal is calculated at the start of the growth period as the increase in size over the largest previous leaf class by some defined fraction. Calculating the goal based on the largest leaf mass grown previously, rather than restricting the base mass to the last leaf mass grown, enables the tree to try to grow increasingly large primary flushes in a year following a year with a parameterized small secondary flush or a small flush due to poor conditions.

While easier to parameterize, the disadvantage of the Fractional Increase method of leaf growth is that it has little direct connection to the status of the tree. Thus, despite such characteristics as maturity or relatively small branch mass, a simulated tree will

continue to try to grow an increasingly large leaf flush, dependent only on the availability of sufficient amounts of carbon for growth.

The second method, Sapwood-based Leaf Increase, is perhaps more realistic biologically. It is based on the concept that the amount of sapwood determines the amount of leaves that can be supported by the tree. Unlike the Fractional Increase method, the sapwood-based leaf mass goal is calculated daily and is therefore closely tied to the status of the tree. ~~This~~The calculation requires that the user supply the density of sapwood ($D_{SAP}$), overall density of wood ($D_{ST}$), ratio of leaf area to sapwood area (R), and two constants for calculating stem diameter at breast height (dbh).

First, we calculate stem diameter at breast height (dbh) in cm using the following equation (Clark III, A. and J. G. Schroeder, XXXX):

$$dbh = \left(\frac{Mass_{ST}}{a}\right)^{-2b}$$

where:

$Mass_{ST}$ = total stem mass (g C; from model)

$a$ = constant (input parameter)

$b$ = constant (input parameter)

Π

Next, we calculate cross-sectional stem area ($cm^2$) at dbh as:

$$Area_{ST} = \pi * \left(\frac{dbh}{2}\right)^2$$

Next, we calculate sapwood area ($cm^2$) as:

$$Area_{SAP} = \left[\frac{\left(\frac{Mass_{SAP}}{D_{SAP}}\right)}{\left(\frac{Mass_{ST}}{D_{ST}}\right)}\right] * Area_{ST}$$

[Note: same as $\left(\frac{Volume_{SAP}}{Volume_{ST}}\right) * Area_{ST}$]

where:

$Mass_{SAP}$ = mass of sapwood = $Mass_{STRUCTURE_{STEM}} + Mass_{TNC_{STEM}}$

(g C; from model)

$Mass_{ST}$ = total stem mass (from model)

$D_{SAP}$ = density of sapwood (g C/cm$^3$; input parameter)

$D_{ST}$ = overall density of wood (g C/cm$^3$; input parameter)

Next, we calculate area of total leaves (m$^2$) that can be supported by a given amount of sapwood:

$Area_{LF=}R * Area_{SAP}$

where:

$R$ = ratio of projected leaf area to sapwood cross-sectional area (m$^2$/cm$^2$; input parameter)

In the next step, we calculate the total leaf mass (g C) that can be supported by the given amount of sapwood:

$$Mass_{LF} = \frac{Area_{LF}}{PRLFAR * CONV}$$

where:

$Area_{LF}$ = area of total leaves (m$^2$)

$PRLFAR$ = projected specific leaf area (m$^2$/g dry wt; input parameter)

$CONV$ = g dry wt to g C conversion factor

Finally, we calculate the mass (g C) of leaves needed to grow to fill the leaf carrying capacity of the tree:

$$Mass_{TARGET} = Mass_{LF} - Mass_{CURRENT}$$

where:

$Mass_{LF}$ = total leaf mass allowed (g C)

$Mass_{CURRENT}$ = total leaf mass now present on tree (g C)

### Allocation of Newly Fixed Carbon

Each simulation day, the model calculates the allocation of newly synthesized carbohydrate to various tree compartments for respiration, growth, and TNC storage. Maintenance respiration needs are met first, followed by refilling of the leaf storage pools that may have been partially exhausted to meet growth needs during the previous day. Photosynthate is then available for growth, which includes growth respiration. The rate at which carbon can be used for growth is limited by the amount of carbon available, the amount of nutrients available, or the maximum possible growth rate. When carbon or nutrients are insufficient to permit all tissues to grow at their maximum possible rates, the priority of the various tissues for carbon and nutrients becomes important, as described below. Growth partitioning in this model is mechanistically, not empirically, defined. There is no explicit ratio in the model used to partition carbon among different tissues. Instead, carbon for growth is allocated on a daily time step according to simple rules of priority and the limits of maximum growth rates and nutrient availability.

Allocation of newly fixed carbon occurs once at the end of each day according to a priority list of tissues, shown in Table XX, subject to limitations imposed by the availability of nutrients and maximum possible growth rates.

Table XX. Sink Priorities for allocation of newly fixed photosynthate for the previous example, table 3-3.*

| Allocation to existing tissues | Allocation to new tissues** |
|---|---|

| Growth period | Respir-ation | Leaf TNC | Other TNC | Buds | Leaf | Branch | Stem | Coarse root | Fine root |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 2 | 3 | • | • | • | • | • | • |
| 2 | 1 | 2 | 5 | 3 | • | • | • | • | 4 |
| 3 | 1 | 2 | 6 | • | 3 | 4 | • | • | 5 |
| 4 | 1 | 2 | 8 | 3 | • | 4 | 5 | 6 | 7 |
| 5 | 1 | 2 | 3 | • | • | • | • | • | • |

* Numbers represent the order in which each sink will receive newly fixed photosynthate. A sink with a lower number will receive photosynthate before one with a higher number. After the needs of a sink are fully satisfied and if newly fixed photosynthate remains, carbon will be given to fill the needs of the next highest priority sink. If the rate at which high priority sinks use photosynthate is low, more carbon may actually be given to low priority tissues during a time step.

** Allocation to new tissues for growth includes carbon losses due to associated growth respiration.

• Indicates growth periods in which the respective tissue is not permitted to grow.

The numbers in the table represent the order in which each tissue will receive newly fixed photosynthate. Respiration always has first priority for carbon use. Leaf TNC stores have second priority. When phenology permits them to grow, the remaining tissues have the following priority for newly fixed carbon: buds, leaves, branches, stem, coarse roots, and finally fine roots, in order of their proximity to leaves, the source of the new photosynthate. This order of priority never changes once the user has established it. Further, the user defines that some tissues are not allowed to grow during certain growth periods or times of year, as indicated in Table 3-3 and described above in "Phenology of Growth". After the growth of all tissues is satisfied, any remaining carbon is allocated to the other TNC pools, as described below in "Carbon Sinks".

For example, in growth period 1 new photosynthate will first be given to meet respiration needs of all tissues. After these needs are fully satisfied, if newly fixed photosynthate remains, carbon will be given to fill the needs of leaf TNC pools. Once these TNC pools are filled buds will be given carbon. If the bud growth rate is low

because of low temperature conditions, etc., the amount of carbon buds can use may be small, and carbon may remain to be given to fine roots and then, after meeting the root demand, to other TNC pools.

It may seem peculiar to fill existing leaf TNC stores during this period before growth of new leaf structure. However, TNC storage in existing leaves is only temporary, as this carbon source will be tapped to grow leaves once all the newly fixed carbon is allocated, as explained later in this section.

The order of priority changes depending upon the phenological stage of the tree. This allocation scheme causes the relative growth rate of different tissues to remain approximately constant throughout a given growth period when resources needed for growth are in abundant supply, but deviates from this pattern when essential resources become limiting. Thus, environmental conditions influence carbon partitioning whenever a resource is in short supply. This method of simulating allocation is more environmentally responsive than a fixed proportional scheme such as those employed by Dixon et al. (1978), Ågren and Axelsson (1980), and Mohren et al. (1984). The method is more mechanistic than using a ratio of available resources as a signal to alter allocation, such as in the models of Borchert, (1973), Reynolds and Thornley (1982), and Schulze et al. (1983).

Although a tissue higher on the priority list is given the first opportunity to use available carbon, its growth rate is limited by a maximum daily growth rate obtained from measured allometric relationships (see Section 4 for a description of the method by which these rates are set). Therefore, it is rare in practice that a tissue will use all the carbon fixed in the one-day time step. In fact, when resources are abundant, the tissue that will garner the largest supply of available carbon will be the one with the fastest possible growth rate, i.e., the one representing the greatest carbon sink, even if it is low on the priority list. However, when carbon is in short supply, a tissue with a high maximum growth rate that is low on the priority list may not grow as fast as those

above it on the list even though it represents a potentially larger sink. In essence, carbon will be used by other growth processes before it reaches this sink. Of course, even under low carbon availability, it is possible for a low priority tissue to grow more than tissues higher on the list if the higher priority tissues have very low growth rates.

Furthermore, since tissue can only grow as fast as the rate at which nutrients are supplied as raw materials to build structure, low levels in the plant nutrient pool can restrict carbon use and growth even if ample carbon is available, thereby preventing maximum growth rates of high priority tissues from being achieved. Indeed, growth of above ground tissues may be particularly restricted while below ground tissues are permitted to grow, even though below ground tissues always have lowest priority for carbon regardless of growth period. This can occur because the model allocates carbon to roots immediately after nutrient uptake has been calculated near the end of the daily time step (figure XX), allowing root growth first access to a plant nutrient pool that has just been replenished; this depletes the nutrient pool available for above ground growth during the next time step. By replenishing the plant nutrient pool after above ground growth but before below ground growth, the model simulates (but without tracking separate nutrient pools for each tissue) how in reality nutrients are allocated with highest priority to tissues closest to the location of uptake; i.e., having obtained the nutrients, the fine roots have first priority at nutrient utilization. Under nutrient limited conditions root growth can draw down the plant's nutrient pool before above ground tissue growth can occur the following day, causing some tissues to be limited by low nutrient supplies even if plenty of carbon is available from new photosynthesis or from TNC reserves. Therefore, if nutrient resources are in short supply, the simulated roots will grow faster than above ground tissues because they are the most likely to have adequate nutrients for growth, and shoot growth will be limited by the lack of nutrient. Carbon not used by the shoot then becomes available to roots, permitting their continued growth. Increased carbon allocation to roots should result, until such time as

the increased root mass is sufficient for nutrient uptake to support shoot growth again. In this way root growth is likely to be limited by carbon availability and above ground tissue growth is likely to be limited by nutrient availability.

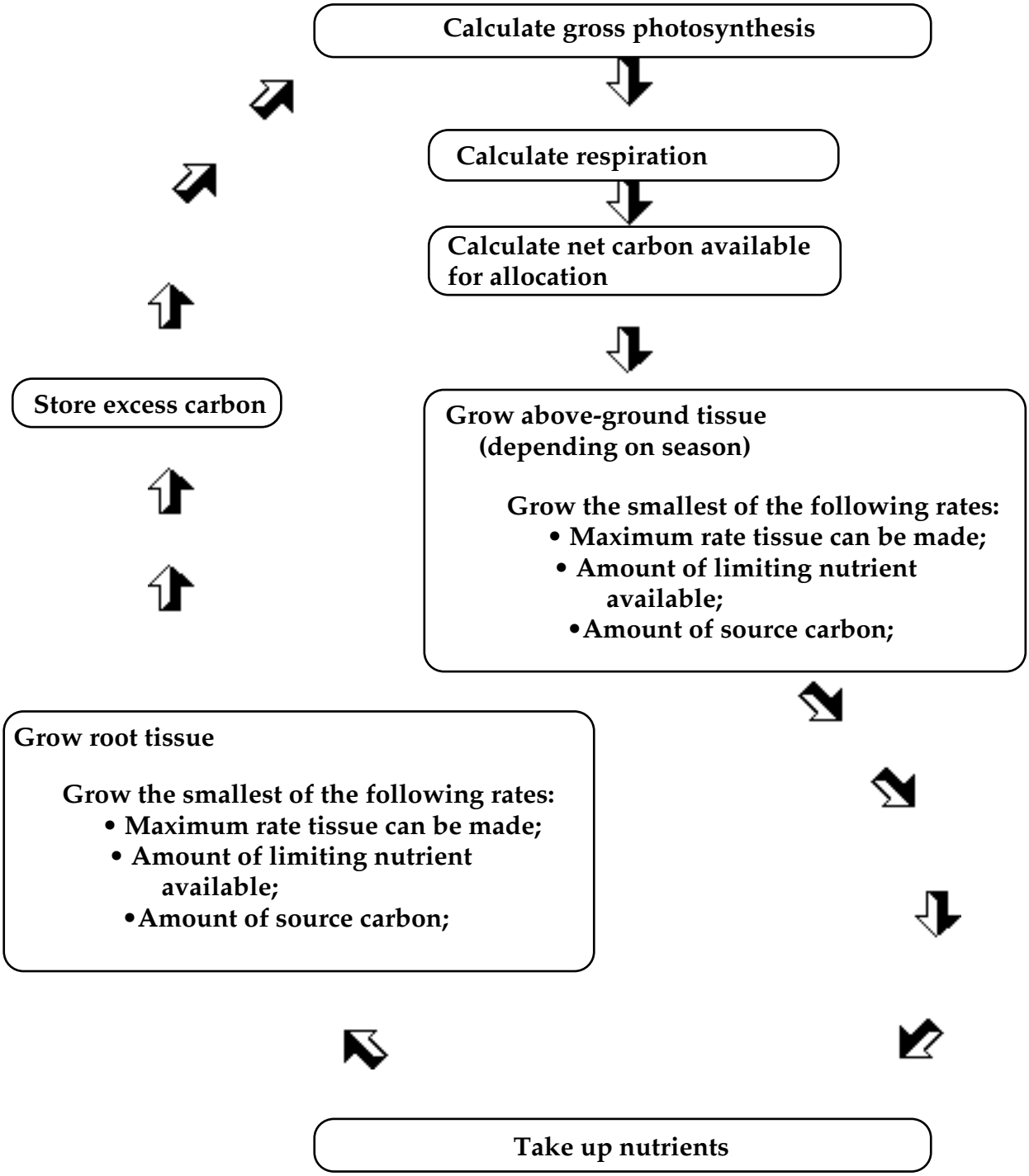


**Figure XX. Sequence of events simulated during a day in TREGRO using the priority order shown in table 3-3.**

Structural tissue is constructed in any plant part only if all the necessary resources of carbon and nutrients are available to that plant part in the required stochiometric relationships. Only living structural tissue requires nutrients for formation. Since wood in the model is formed at a variable rate by converting living structural tissue, TNC and wood construction are not directly limited by nutrient availability; however, they are indirectly influenced by nutrient affects on living stem growth.

If the day's supply of photosynthate exceeds the demand for respiration and growth, excess carbon will be stored as TNC among the TNC pools. First the TNC storage of the leaves are filled to saturation. The excess carbon is distributed to branch, stem, and coarse root TNC pools in proportion to the TNC deficit for each tissue. The deficit is calculated as the difference between the TNC content of a tissue and its TNC saturation level.

This method of simulating carbon allocation requires that empirical data be used to set the maximum growth rate allowed for each tissue and to establish the order of priority in allocation during each growth period. However, the realized growth rate of tissues is not predetermined by empirical data, but reflects the pattern of available resources.

### Stored Carbon Sources

Daily carbon sinks are created through the dynamics of structural and storage pools for each leaf age class, branches, stem, coarse roots and fine roots, and by the respiration costs of maintaining and growing structural tissues. These sinks may demand more carbon than can be provided by newly fixed photosynthate. In this event, carbon will be drawn from TNC storage sources as indicated in Table XX.

Table XX. Total nonstructural carbohydrate (TNC) source priorities for growth of different tissues.*

| Tissue type to be grown | Source of carbon: Newly fixed photosynthate | Leaf TNC | Branch TNC | Stem TNC | Root TNC |
|---|---|---|---|---|---|
| Buds | 1 | • | • | • | • |
| Leaves | 1 | 4** | 2 | 3 | 5 |
| Branches | 1 | • | 2*** | 3*** | 4*** |
| Stem | 1 | • | • | • | • |
| Coarse roots | 1 | • | • | • | • |
| Fine roots | 1 | • | • | • | 2 |

• Carbon cannot be obtained for this tissue from this source.

* Priorities of sources from which carbon is drawn to meet each tissue's growth needs during a time period. The carbon for growth of each tissue is drawn first from the source indicated as "1", next from "2", etc.

** This does not include TNC in the current leaf class, which cannot be used to meet growth needs.

*** Branches can use branch, stem, or root TNC only during growth period 2.

Maintenance respiration needs must be satisfied before carbon can be allocated to growth or TNC storage; growth respiration needs are met during growth allocation for each tissue. The maintenance respiration needs of each leaf class are always met first, from the carbon fixed by that class during the day, from new net fixation by other leaf classes, or from TNC stores, in that order. Daily maintenance respiration needs of non-leaf living structural tissue are met from daily excess of newly fixed carbon over leaf respiration needs or, if more is needed, from TNC stores. Some net photosynthate is typically available during most of the year to meet the maintenance respiration needs of other tissues. If the supply of net photosynthate fixed during the day is exhausted and

TNC is needed to satisfy respiration, carbon is extracted from the tissues with TNC proportionately closest to saturation. The TNC saturation level of each tissue is a function of the structural mass of the tissue. More saturated compartments will donate proportionately more TNC.

Each tissue type draws carbon for growth in a different order of priority from other tissues. These orders of priority for each tissue are listed in Table XX. Although all tissues preferentially draw carbon from newly fixed photosynthate, once this source is exhausted different tissues satisfy their needs from different alternative sources of stored TNC. For example, in the growth periods when branches can grow, they meet their growth demand for carbon by obtaining carbon first from newly fixed photosynthate, next from branch TNC (if all newly fixed photosynthate supplies have been exhausted before branches have grown at their maximum allowable rate for the time interval), next from stem TNC, and finally from root TNC. Only roots can draw on TNC for growth in more than one growth period; branches can use TNC only in growth period 2 and leaves grow only in growth period 1. Stem and coarse roots can grow only using new photosynthate.

### Senescence

The only tissues allowed to senesce in TREGRO are fine roots and leaves. This senescence is temperature-independent.

Fine roots die at a constant rate defined separately in each of three soil layers. The rate parameter determines the fraction of the existing fine root structure to subtract each day. Root senescence will therefore be higher in a plant with more fine root biomass.

Leaf senescence can be either stress-induced, based on the condition of the tree, or planned, based on the calendar day. Stress-induced senescence occurs due to a low TNC pool in a leaf class. When TNC falls below a minimum TNC level of XX (as a fraction of leaf structure) due to stress or leaf age, a fraction of that leaf class is dropped each day. Since the TNC in the age class is retained in the remaining leaves, senescence

progresses only until the minimum TNC level is restored. A leaf class must be at least a certain size before it can be dropped. Thus, young leaves are not dropped before they have an opportunity to be filled with TNC. The user can also set a degree day-based senescence delay in growth period 4 to allow the current leaves to attempt to fill their TNC pool, before possible stress-induced senescence.

In a planned, or autumn-like, senescence, leaves are dropped on a given calendar day each year. As with stress-induced senescence, the percentage of leaf structure dropped can be set individually for each leaf age class. Resorption of the nutrients contained in senesced tissue is possible. The user has complete control over the degree of this resorption.

## Water Balance

TREGRO enables the user to select two alternative methods for calculating plant water uptake:

(1) Constant Water Model: a simple and relatively fast hydrologic simulation using a constant rate of water uptake per gram of fine root per day for saturated soils.

(2)Transpiration Water Model: a more complicated, but more accurate, forward differencing version of the Richards equation (Buttler and Riha, 1988).

### Constant Water Model

The advantages of this module are that a single parameter is required and a greater speed of calculation realized in comparison to the Transpiration Water Model. However, the user should be aware of the consequent reduction in accuracy and realism. For example, there is no canopy evaporation. Thus, after the canopy is filled initially, all rainfall is considered to be throughfall. This method is perhaps best used as a shortcut to an initial parameterization of a tree species, or where further data is not available.

## Transpiration Water Model

This module accepts precipitation as an input and calculates the following on an hourly time step: canopy retention and evaporation, soil evaporation and infiltration (but not runoff), vertical water movement through the soil profile, soil water contents and potentials by layer, root water potential, a feedback factor for photosynthesis, water uptake, and leaching below the root zone. The module also maintains a mass balance of water.

Hourly precipitation values are used to calculate canopy water retention, which is a function of leaf mass. When the canopy is saturated, water is applied to the soil surface. If the canopy is holding water, the photosynthesis module assumes a humidity of 100%. Canopy evaporation is a function of temperature, solar radiation, and humidity.

**Evapotranspiration/Water uptake**

We make the simplifying assumption that canopy evapotranspiration equals root water uptake, i.e., the amount of water in the plant is constant and there is no resistance to water movement through the plant. As part of the energy balance calculations of the Farquhar photosynthesis module, a potential evapotranspiration is calculated for all leaf classes in both full sun and shade. This total evapotranspirative demand is used by the water module as a potential water uptake amount. If soil water contents and root masses are adequate, this potential will be realized.

If, however, soil water contents are low and/or root mass is inadequate, only a portion of the evapotranspirative demand can be met. This leaves the energy balance calculations slightly in error. To compensate for the error, a correction factor is applied in the next time step in order to reduce $V_{max}$ and indirectly reduce the evapotranspirative demand. If the correction applied was too large, it will correct itself in the next time step. In this way, the coupling between the water and photosynthesis

modules constantly seeks the appropriate amount of evapotranspiration and, therefore, root water uptake.

Once the total water uptake is known, it is distributed among soil layers according to the water potential and fine root mass of each root-containing layer.

Evaporation occurs from the upper soil layer only. This upper layer is a litter layer that functions only in the water model. It is in addition to the main layers, A, B1 and B2, used throughout TREGRO for root growth, and water and nutrient uptake. A potential soil evaporation is calculated as a function of temperature, solar radiation, and humidity. Actual evaporation is usually lower than the potential because of low water content of the ~~upper~~ litter layer and limitations of water movement through the soil. It is calculated, using the Penman-Monteith equation, as follows:

$$actual\ soil\ evaporation = potential\ soil\ evaporation * \left( \frac{RH_{soil} - RH_{air}}{1 - RH_{air}} \right)$$

where: $RH$ = relative humidity.

$$RH_{soil} = e^{\left( \frac{MW_{H_2O} * \Psi_{soil}}{R * T_{soil}} \right)}$$

where:

$MW_{H_2O}$ = molecular weight of water

$\Psi_{soil}$ = soil water potential

$R$ = gas constant = 8.31

$T_{soil}$ = soil temperature (°K)

**Soil water distribution and drainage**

Water moves as a result of gravity forces and water potential gradients. For example, a high root density in one layer of soil can deplete water in that layer, causing a flux of water into it from adjacent layers.

The Richards equation is used to calculate the water fluxes between soil layers. To avoid having to solve this equation iteratively, the forward difference method is used in TREGRO. In this method, water fluxes are calculated from the potential differences and conductivity of the soil layers at the beginning of the time step; the solutions are explicit and readily calculated.

The current water potentials are used to determine how much water should move. These water potentials are calculated according to Campbell as:

$$WC_i = WC_{s_i} * \frac{A}{WP_i^{\left(\frac{1}{N}\right)}}$$

where:

$WC$ = water content

$WC_s$ = saturated water content

$A$ = air entry potential

$N$ = slope of soil release curve

$$WC_i = WC_{s_i} * \frac{A}{\Psi_i^{\left(\frac{1}{N}\right)}}$$

where:

$WC_i$ = water content

$WC_{s_i}$ = saturated water content

$A$ = air entry potential

$\Psi_i$ = water potential

$N$ = slope of soil release curve

Water flux is then determined by the Richards equation as:

$$WF = \frac{-\left(K_{i+1} * WP_{i+1} - K_i * WP_i\right)}{Sd_{i+1} + Sd_i}$$

where:

$WF$ = water flux

$K$ = soil hydraulic conductivity

$WP$ = water potential

$Sd$ = soil layer depth

$i$ = soil layer number

The change in the mass of water in each layer each hour is then calculated as:

$$\frac{dV_i}{dt} = WF_{i-1} - WF_i - T$$

where:

$V_i$ = volumetric water content of layer $i$

$WF_{i-1}$ = water flux into layer $i$

$WF_i$ = water flux from layer $i$

$T$ = evapotranspiration

$i$ = soil layer

The forward difference calculation will generally overestimate water flux each time step, since the calculated flux rate is correct at the beginning of the time step but the actual potential gradient tends to be lessened by water movement during the time step. We deal with this overestimation in two ways:

1. Using a small time step (10 min) helps minimize the size of the errors and allows quick compensation in the next time step.
2. Control through parameters. A damping coefficient can be set to reduce the propensity for this calculation to overshoot its goal and send water oscillating in opposite directions in alternate time steps. In the extreme case, calculated water fluxes may exceed the water content of a soil layer. A second parameter sets the maximum fraction of soil water in a layer that can move each time step. Ideally, if a problem arises, the soil layer thickness or the time step should be changed to give more realistic flux rates.

Under saturating conditions, the water content of each soil layer is allowed to reach the Saturation Point, calculated as:

$$SatPt_i = 0.75 * \left( \frac{1 - BulkDens_i}{PartDens_i} \right)$$

where:

*BulkDens* = Soil bulk density, defined as the mass of dry soil per unit volume ($g/cm^3$) (Brady, 1974)

*PartDens* = Soil particle density, defined as the mass of a unit volume of soil solids ($g/cm^3$) (Brady, 1974)

*i* = soil layer

Any water in excess of saturation is removed as drainage. When the bottom layer is saturated, it is drained to Field Capacity. This occurs at least once a day, either during the time step in which saturation occurs or, in the occurrence of rain, at the next rain-free time step, but no later than midnight of that day. This then allows water from other saturated layers to move down to the bottom layer and out of the system.

## Nutrients

### Uptake/Loss

Nutrient uptake in TREGRO can occur by two pathways: active uptake by fine roots (the primary mechanism) and adsorbtion from throughfall. Nutrients may also be lost to throughfall.

Uptake by the roots involves a sequence of processes: active solute uptake by roots, mass flow of solutes towards the root, diffusion of solutes along the concentration gradient maintained by active uptake, and the depletion of solutes, both in solution and on exchange surfaces, in a zone around the root. This depletion zone is assumed to reach a steady state, with an unchanging concentration profile, which can be calculated as a function of root absorbing power, water uptake rate, soil buffer capacity, and the diffusion coefficient (Nye and Spiers 1964). Change over time is accommodated by recalculating the solution on each day that the Update Nutrient Pools growth event is called. The advantage of the steady-state approach lies in the independence of the solution to the previous conditions. Uptake thus calculated can accommodate unpredictable changes in root growth and mortality, root density, and water uptake rates, as required in simulating plant growth for multiple seasons in a dynamic environment.

Plant uptake is the sum of contributions by old and new roots:

$$Uptake = U_{old} + U_{new}$$

Solute uptake by established roots, $U_{old}$ (in moles), is the product of root surface area, solute concentration at the root surface, the root absorbing power and the time interval:

$$U_{old} = L * 2\pi * r_0 * \alpha * C_0 * \Delta t$$

where:

$L$ = root length (cm)

$r_0$ = radius of the root (cm)

$\alpha$ = root absorbing power (cm/s)

$C_0$ = concentration of substance at the root surface (mol/cm$^3$)

$\Delta t$ = the model time step (s).

$C_0$ can be calculated from $C_{av}$, the average solution concentration, by the proportion $P$:

$$P = \frac{C_0}{C_{av}} = \frac{v_0}{\alpha + (v_0 - \alpha)\left(\frac{2}{2-\gamma}\right)\left(\frac{\left(\frac{r_x}{r_0}\right)^{2-\gamma} - 1}{\left(\frac{r_x}{r_0}\right)^{2} - 1}\right)}$$

where:

$v_0$ = inward radial velocity of water at the root surface (cm/s$^2$)

$\gamma = \frac{r_0 v_0}{D * b}$ (dimensionless), where $D$ = diffusion coefficient (cm$^2$/s) and $b$ = buffer capacity of the soil, or the ratio between exchangeable and dissolved nutrient

$r_x$ = average radial distance to the next root's zone of influence (cm):

$$r_x = \frac{1}{\sqrt{\pi * L_v}}$$

where $L_v$ = root density as length per unit volume (cm root/cm$^3$ soil).

Solute uptake by new root growth, $U_{new}$ (in moles), is calculated as the amount of solute mined from the depletion zone as this zone attains the steady state:

$$U_{new} = A * \Delta L$$

where:

$\Delta L$ = root growth since the last iteration (cm)

$A$ = the amount of solute removed from the depletion zone per unit length of root (mol/cm):

$$A = \pi * b * C_{av} * \left\{ \left( 1 - \frac{P * \alpha}{v_0} \right) \left( r_{av}^2 - r_0^2 \right) - \frac{2P}{v_0} * \left( \frac{v_0 - \alpha}{2 - \gamma} \right) * r_0^2 * \left[ \left( \frac{r_{av}}{r_0} \right)^{2-\gamma} - 1 \right] \right\}$$

where $r_{av}$ equals the radius at which the nutrient concentration, $C$, equals $C_{av}$:

$$r_{av} = r_0 * \left[ \left( \frac{2}{2 - \gamma} \right) * \frac{\left( \frac{r_x}{r_0} \right)^{2-\gamma} - 1}{\left( \frac{r_x}{r_0} \right)^2 - 1} \right]^{\frac{-1}{\gamma}}$$

Yanai (XXXX) gives a more complete explanation of this method of simulating solute uptake.

### Tissue Concentrations

The maximum nutrient concentrations of each tissue in TREGRO are composed of two compartments: the amount of nutrients that was needed to grow the existing tissue (the construction cost) and a soluble pool of nutrients that is available for further growth. Both construction cost and the maximum nutrient concentration are user-configurable for each tissue and each nutrient. The soluble pool of a nutrient is calculated as the sum across tissues of the difference between the maximum

concentration and the construction cost times the mass of tissue structure. Thus, the tree has one soluble pool for each nutrient.

For a particular nutrient, $X$:

$$PotAvailPool_X = \sum_{i=1}^{n} \left[ \left( MaxConc_{X,i} - ConCost_{X,i} \right) * Struct_{X,i} \right]$$

where:

$i$ = 1 to $n$ tissues

$Struct$ = structural mass

TREGRO first calculates the total uptake of each nutrient from the uptake by fine roots and the uptake or loss from throughfall. The amount of nutrient needed to fill the tree's soluble pool is then calculated and the uptake is allocated. Uptake is not allowed to exceed the amount needed to fill the soluble pool to its maximum.

At senescence, nutrients will be lost according to a user-definable fraction of the dropped tissue structure. Setting this fraction to a number less than 1.0 allows for the simulation of nutrient resorption. The amount of nutrient that is passed to the soil is the construction cost of the tissue dropped plus that tissue's share of the soluble pool, adjusted for any resorption.

## Stresses

### Ozone Effects

Because of the strong diurnal pattern in ozone concentration, calculation at an hourly time step was essential for simulating ozone damage. In the Ithaca area, ozone concentrations were commonly highest at mid-day or early in the afternoon when light levels are also high. During this time of day, the vapor pressure deficit can be high enough to reduce stomatal conductance. Consequently, the model calculates the actual ozone dose by adjusting ambient ozone for stomatal conductance during each hour,

after first converting the ozone concentration from ppb to grams of ozone per gram of leaf carbon.

TREGRO includes two hypothesized mechanisms of ozone damage: (1) an instantaneous effect on respiration and (2) a reduction in mesophyll conductance (Lohammer photosynthesis module) or $V_{max}$ (Farquhar photosynthesis module), based on the cumulative ozone dose. Both mechanisms are linear relations defining a threshold below which no damage occurs. The modification of each leaf class is calculated separately based on the leaf area, leaf mass, and stomatal conductance of that age class. Either or both of these mechanisms can be invoked in a simulation.

**Respiration Effect**

Respiration can be tied to instantaneous ozone dose to simulate the cost of repairing tissue damage. According to this hypothesized mechanism, growth reductions under ozone are caused by compounded instantaneous carbon costs, rather than by cumulative damage to the leaf. The respiration modifier is calculated as follows:

$$OzExpR = 1 + Max\left[0, \left(\left(OzSlpR * \frac{OzLev}{LeafMass} * Stomat * LeafArea\right) - OzThR\right)\right]$$

where:

$OzExpR$ = respiration modifier

$OzSlpR$ = slope of the reduction curve

$OzLev$ = hourly ozone level (g $O_3$)

$LeafMass$ = mass of leaf class (g C)

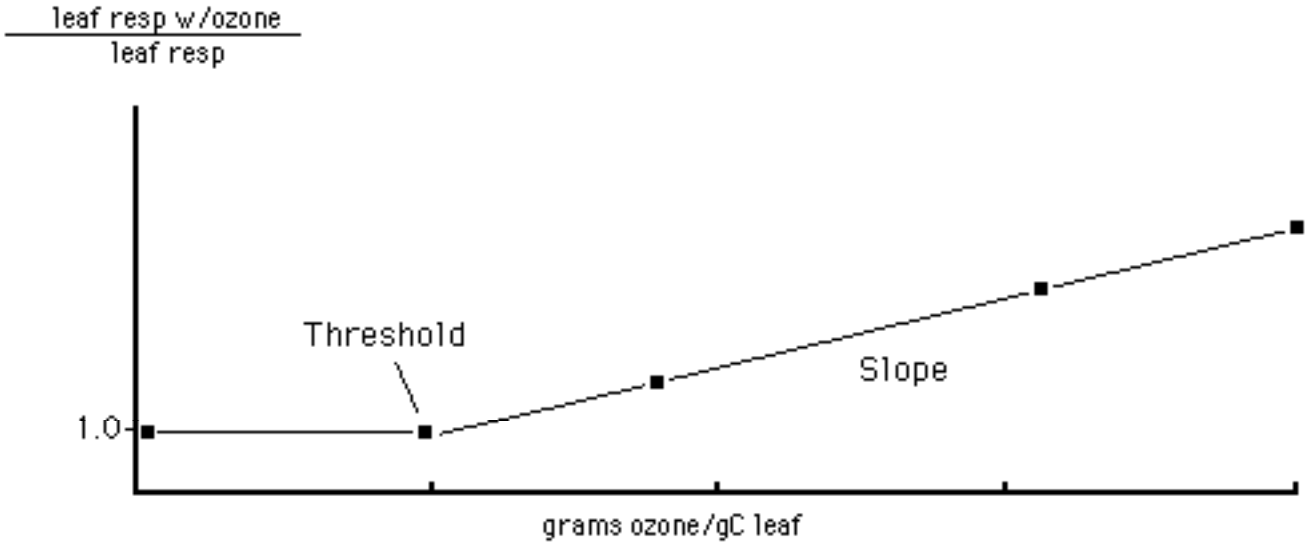
$Stomat$ = stomatal conductance (cm $H_20/s$)

$LeafArea$ = leaf area ($m^2$)

$OzThR$ = threshold when effect starts (g $O_3$)

This relationship is shown in Fig. XX.

**Figure XX. Relationship between ozone uptake and leaf respiration**




**Mesophyll Conductance/$V_{max}$ Effect**

Mesophyll conductance or $V_{max}$ can be reduced according to the cumulative ozone dose. The modifier is calculated as follows:

$$OzExpM = 1 - Max\left[0, \left(OzSlpM * \left(\frac{OzLeaf}{LeafMass} - OzThM\right)\right)\right]$$

where:

$OzExpM$ = modifier

$OzSlpM$ = slope of the reduction curve

$LeafMass$ = mass of leaf class (g C)

$OzThM$ = threshold where reduction starts (g $O_3$)

$OzLeaf$ = cumulative leaf dose (g $O_3$) calculated as follows:

$$OzLeaf = OzLeaf + Max\left[0, \left((OzLev - OzAccTh) * Stomat * LeafArea\right)\right]$$

where:

$OzLev$ = hourly ozone level (g $O_3$)

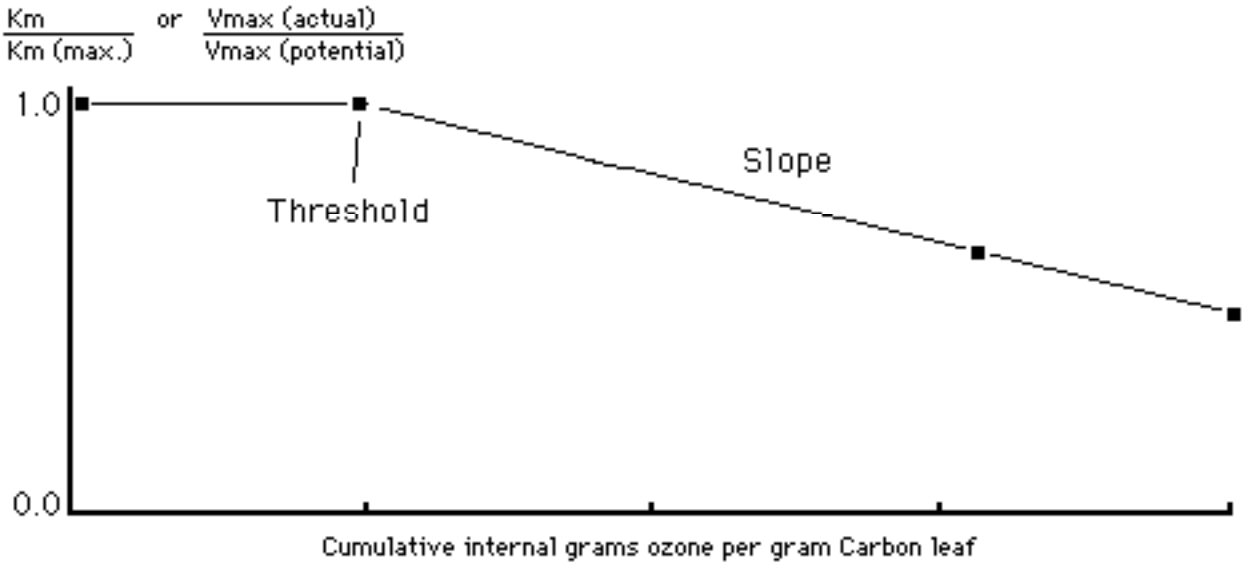
*OzAccTh* = hourly accumulation threshold (g $O_3$) below which no accumulation occurs

*Stomat* = stomatal conductance (cm H2O/s)

*LeafArea* = leaf area ($m^2$)

This relationship is shown in Fig. XX.

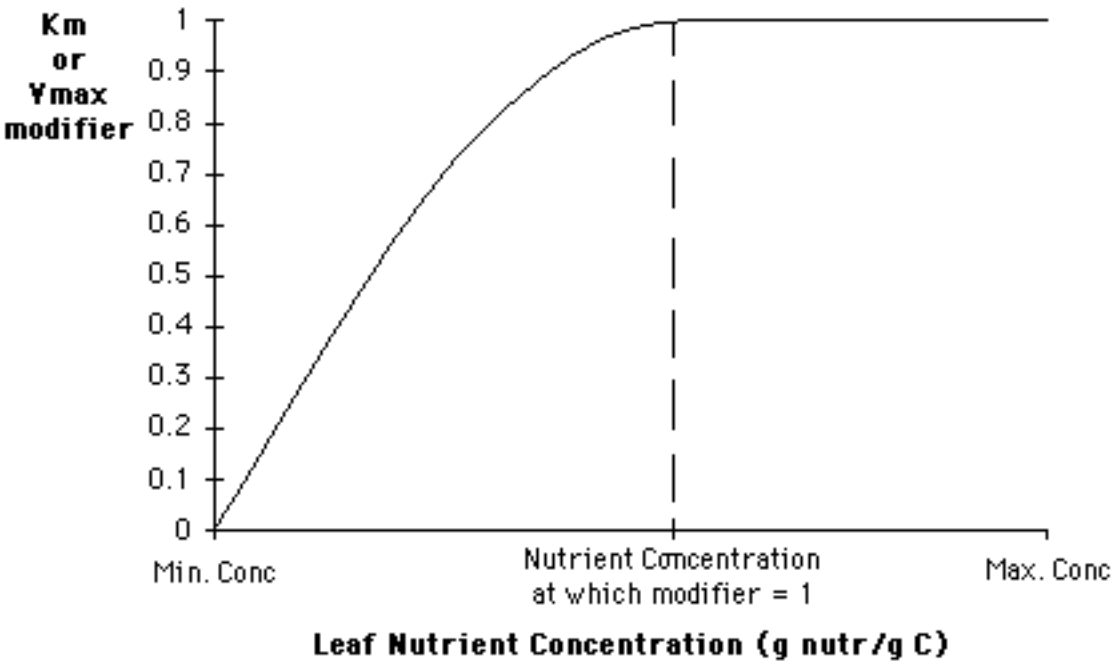
**Figure XX. Relationship between cumulative ozone uptake and mesophyll conductance (Lohammer) or $V_{max}$ (Farquhar).**



### Nutrient Stress

A reduction in the photosynthesis of each leaf age class due to low concentrations of nitrogen or magnesium can be simulated in TREGRO. Depending on the photosynthesis method chosen, either mesophyll conductance (Lohammer method) or $V_{max}$ (Farquhar method) is reduced for a given leaf class based on the nutrient concentration present in that class and the user-configurable threshold concentration and minimum modifier values. The photosynthesis modifier used is the smaller of the two modifiers calculated from the nitrogen and magnesium concentrations.

**Figure XX. Relationship between N or Mg concentrations in the leaves and mesophyll conductance (Lohammer) or $V_{max}$ (Farquhar).**




### Acid Rain

Acidic precipitation can lead to reduced soil nutrient availability. Hydrogen ions displace nutrient cations on exchange sites; the cations are then carried out of the rooted

zone in the soil solution. As explained above, the mechanisms of cation depletion (solution equilibria, cation exchange, mineral dissolution, and leaching) are not represented in this version of the model. However, reduced nutrient availability can be simulated by specifying low concentrations of soil nutrients.

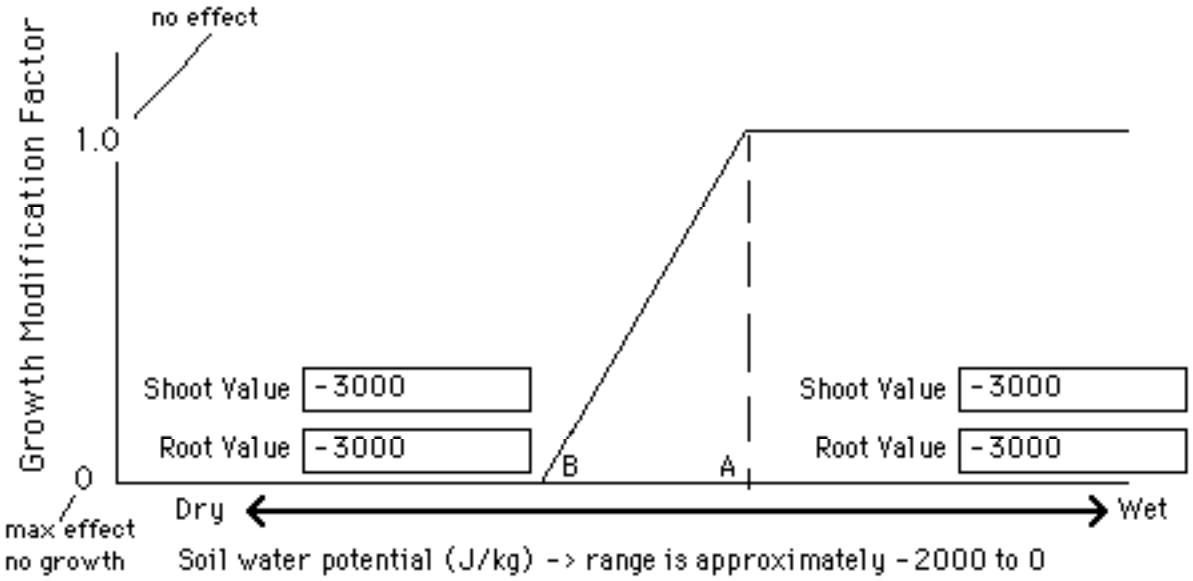
## Water Stress

There are two negative effects of low soil water potentials on tree growth in TREGRO: a direct reduction in growth and an indirect reduction through a decrease in photosynthesis. These effects occur only if the Farquhar method is used to calculate photosynthesis in conjunction with the Transpiration Water model.

### Growth reduction

Growth reduction through water stress occurs when the soil water potential drops below the threshold water potential (A in Fig. XX). Water potentials less than that at B cause a complete cessation of the growth of the specific tissue. Those falling between potentials A and B cause a linear reduction in this growth. The water potential values that define these two thresholds are set by the user. There are two sets of thresholds: those for fine roots and those for all other tissues. Fine roots function in water uptake; therefore, the critical water potential is the value for the particular soil layer of that fine root compartment. All other tissues, including coarse roots, rely on the water potential of the wettest soil layer.

**Fig. XX. Effect of soil water potential on growth using Farquhar method with Transpiration Water model.**




**Photosynthesis reduction**

Growth can also be modified as a result of reduced photosynthesis brought about by decreased root water uptake. In a relationship similar to that shown for the growth reduction of fine roots (Fig. XX), water uptake for each layer of fine roots is reduced when that layer's water potential drops below a threshold potential A. Uptake ceases completely when the potential drops below potential B. As discussed in section Water Balance: Transpiration Water Model above, there is a feedback mechanism between actual root water uptake and the potential transpiration calculated by the Farquhar photosynthesis method. When water uptake is less than that predicted by potential transpiration, $V_{max}$ is reduced in order to reduce potential transpiration in the next time step of the model. This reduction in photosynthesis results in a decrease in carbon fixation and a subsequent reduction in growth.

# 4

# PARAMETER DESCRIPTIONS AND INSTRUCTIONS

This section discusses the details of setting the many parameters available to the user in TREGRO. For ease of reference, subsection headings are the same as the button names on the Input Parameters Menu. See Section 3: Descriptions of Modeled Processes for details about the underlying equations and rationale of a model subsection. The basics of installing and setting up a model run are discussed in Section 1: Getting Started. The user should review this section before attempting to parameterize TREGRO for the first time.

## Run Duration and Output Options

After clicking "Change model parameters" on the Main Menu, the user must select the calendar days during which the simulation will run. While any start and end days can be chosen, bear in mind that any model processes that would have occurred before your start day will not now occur. For instance, a start day that occurs after leaf growth was scheduled means that the simulated tree will not have any leaves in that leaf age class. This can have severe consequences on the validity of the simulation. Therefore, start TREGRO runs on day one unless you are sure of the outcome of a shortened simulation year.

Other output files can be selected, in addition to the standard daily output file (*yourinputfile*.Dout). Entering start and end days other than zeroes for hourly output will activate the output of hourly data for a suite of variables related to photosynthesis, respiration and water uptake (*yourinputfile*.Hout). This data can be useful in such instances as when parameterizing photosynthesis. Clicking the "Zelig Outputs" button

will output a small file containing the few model data needed for running the Zelig stand model (*yourinputfile*.ZELOUT).

Because processing time and output file size increase with the length of the model run, it is best to set a simulation to run for the shortest period necessary to answer your scientific question. Often a two or three year run is sufficient. The daily output file averages ca. 786 KB per simulation year. An hourly output file averages ca. XX KB per day.

After setting the desired options and run duration, click "Continue".

## Input Parameter File(s)

This screen allows you to select or create the input parameter file to be used in your simulation. Note that it is also possible to set up several runs at one time. The procedure for doing this is discussed in Advanced Parameterization at the end of this Chapter. The button "Experiment Setup" will take you to a screen that allows you to automatically set up a series of input files for such a "multiple run" with a sequence of values for selected input parameters. This procedure is also discussed in the Advanced Parameterization section.

On entering this screen, you may find your desired input file already listed in the box to the right of the arrow. Alternatively, if no file is listed or you want to use a different file, click in the box to bring up a dialog box asking you whether you want to create a new file or use an existing one. Creating a new file allows you to make a copy of an existing file that can then be modified in some way. You will first be asked to name the new file and then to select the file you are copying. File names should not have any spaces or colons. In addition, the complete file path should be no more than 55 characters, including colons as path delimiters.After the input file has been designated, you can choose either to run a simulation using this unmodified file by clicking the "Main Menu" button to return to the top level, or to first modify some input parameters by clicking the "Modify Parameter(s)" button.

The input parameters used in TREGRO are listed in Tables XX through XX, and include the parameter values for simulating a red spruce.

As mentioned earlier, it is suggested that the user be systematic in checking and changing parameter values when setting up a TREGRO run, to prevent the use of unintended values. The names of the following sections correspond to the buttons found on the Input Parameter Menu. The order in which these sections are listed is a good sequence to follow. Note that these sections are not intended as an exhaustive description of all TREGRO parameters. The interface has been designed to offer much of the information needed to parameterize the model. This chapter is intended to offer guidance in understanding the specific parts of the interface and in setting certain parameters.

The Notes field on the Menu offers a convenient way of making brief notes regarding the current input file. Notes can be up to 255 characters; carriage returns are unnecessary in this field, since text will wrap. These notes are saved as part of the file itself.

## Model Setup

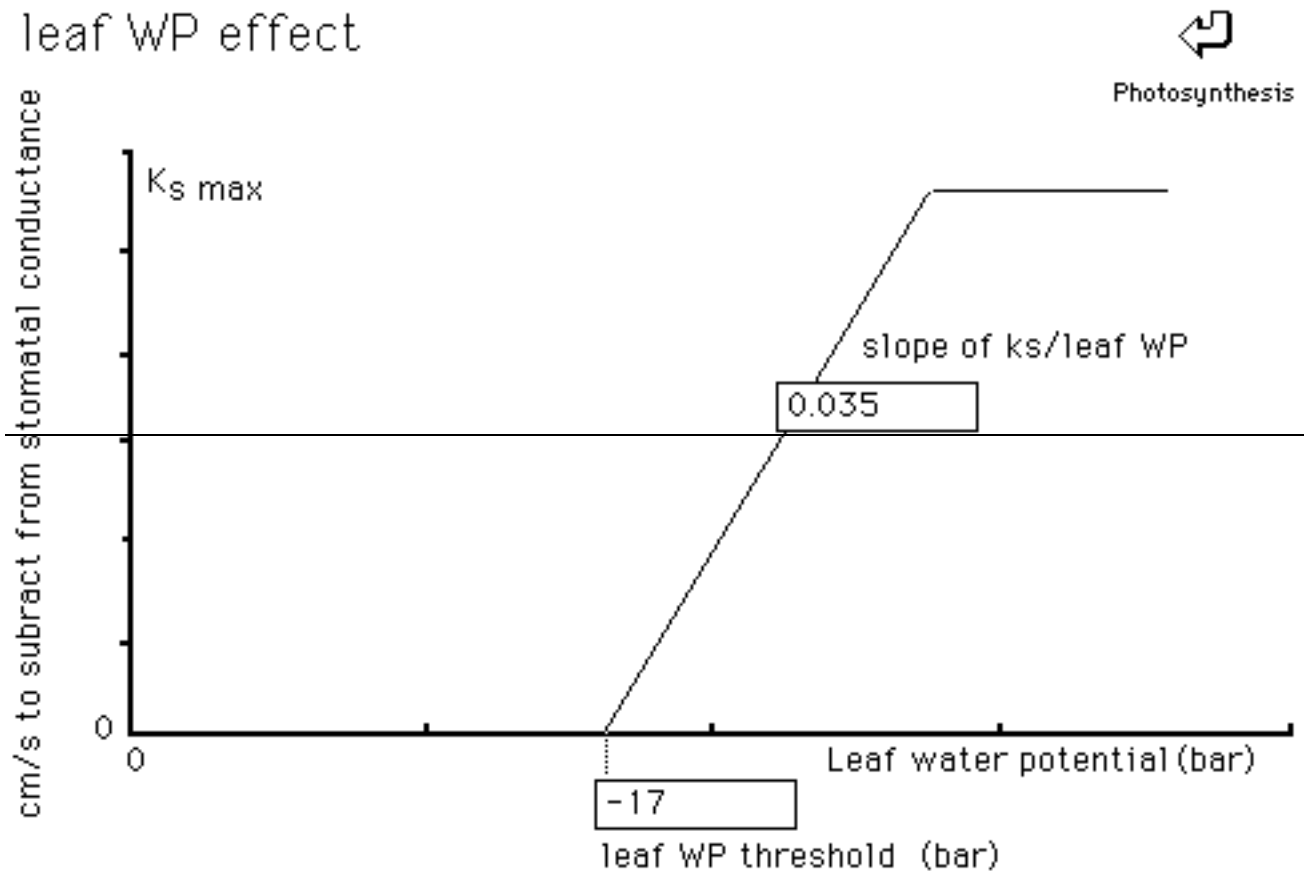
This screen selects the basic modules that will be used for photosynthesis, water and soil, and allows access to their parameters. Note that in TREGRO version 3.0, there is no direct connection to the external soil model, YASE.**Photosynthesis**

Select the photosynthesis model and click Parameterize Photosynthesis.**Lohammer method**

Parameterizing the Lohammer method involves setting $K_{Smax}$, the maximum possible stomatal conductance, and its modification by VPD; $K_{Mmax}$, the maximum mesophyll conductance, and its modifiers; and the CO2 gradient from atmosphere to carboxylation site.

In the VPD modification of $K_{Smax}$ (Fig. XX), the slope of is negative, but can be entered as either a positive or negative number; the result will be the same. ~~The first of these is the effect of leaf water potential on $K_S$, requiring the user to define a threshold (bars) above which there is no effect, and the slope of the stomatal conductance value to subtract from the maximum value with respect to leaf water potential (cm • $s^{-1}$ $bars^{-1}$) (Figure 4-1). The second function is the effect of vapor pressure deficit (VPD) on $K_S$, where the~~This modifier requires a no-effect threshold (bar) and slope of the stomatal conductance with respect to VPD (~~cm $H_20$/s bar) are entered (Figure 4-2).~~

Mesophyll conductance is a function of the maximum possible mesophyll conductance ~~(cm $CO_2$/s)~~, a light response curve, and several modifiers. The light response curve is a function of the current light level, the compensation light level, and the light level at half saturation (Figure XX). The current light level can be modified for the effect of shading by clicking the "Shading Effects" button. On this screen, shade can be defined by the user as a fraction of full light. The fraction of each leaf class that is in shade can be set for two different periods of the day, morning/evening and 10 AM to 3 PM.~~, which is described as the amount of light transmitted though shade as a fraction of full light and the fraction of each leaf class in the shade, both for midday and for morning or evening (see Section 3).~~




**~~Figure 4-1. Hypercard screen, used to change parameters, showing the effect of leaf water potential on reduction of stomatal conductance used in TREGRO.~~**

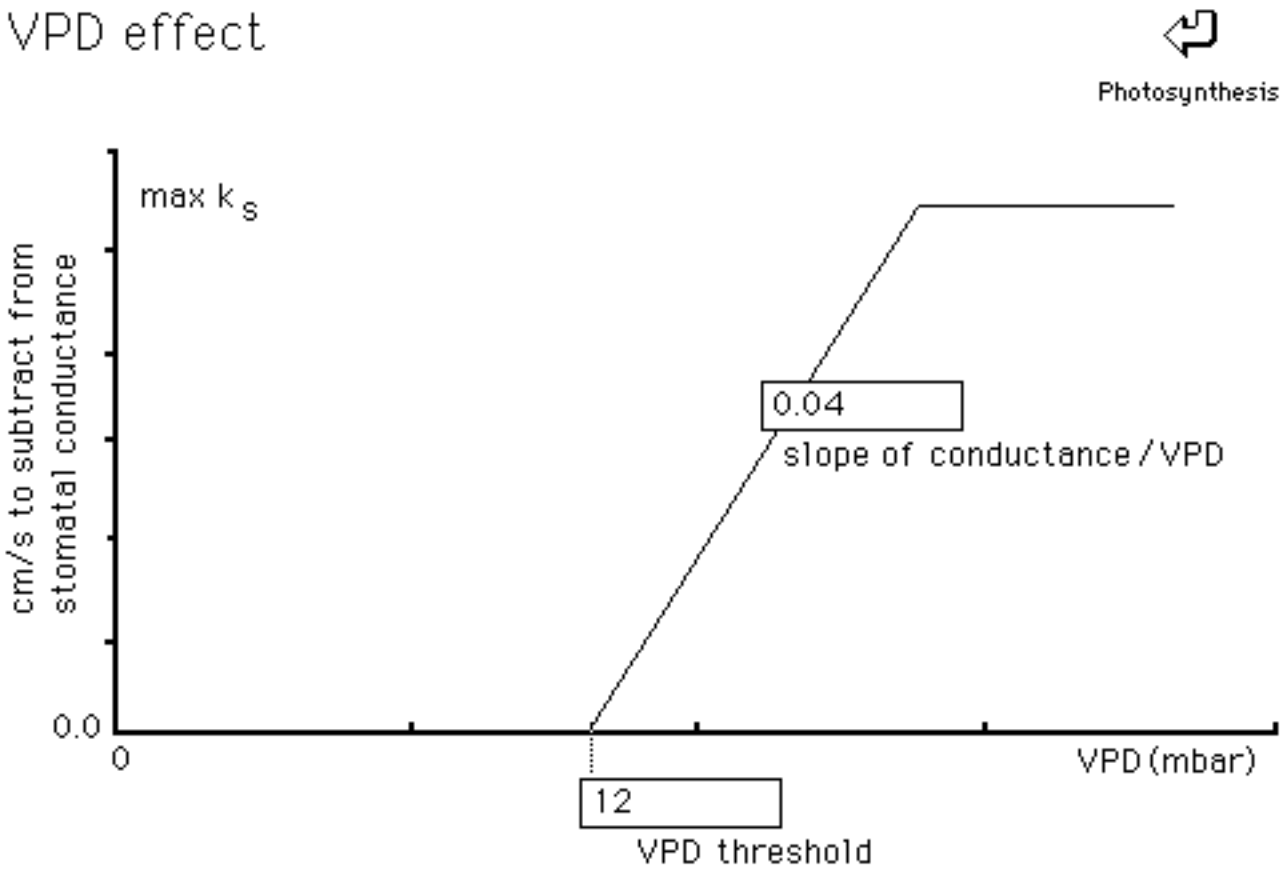



**Figure XX.** **Hypercard screen, used to change parameters, showing the effect of vapor pressure deficit (VPD) on reduction of stomatal conductance used in TREGRO.**

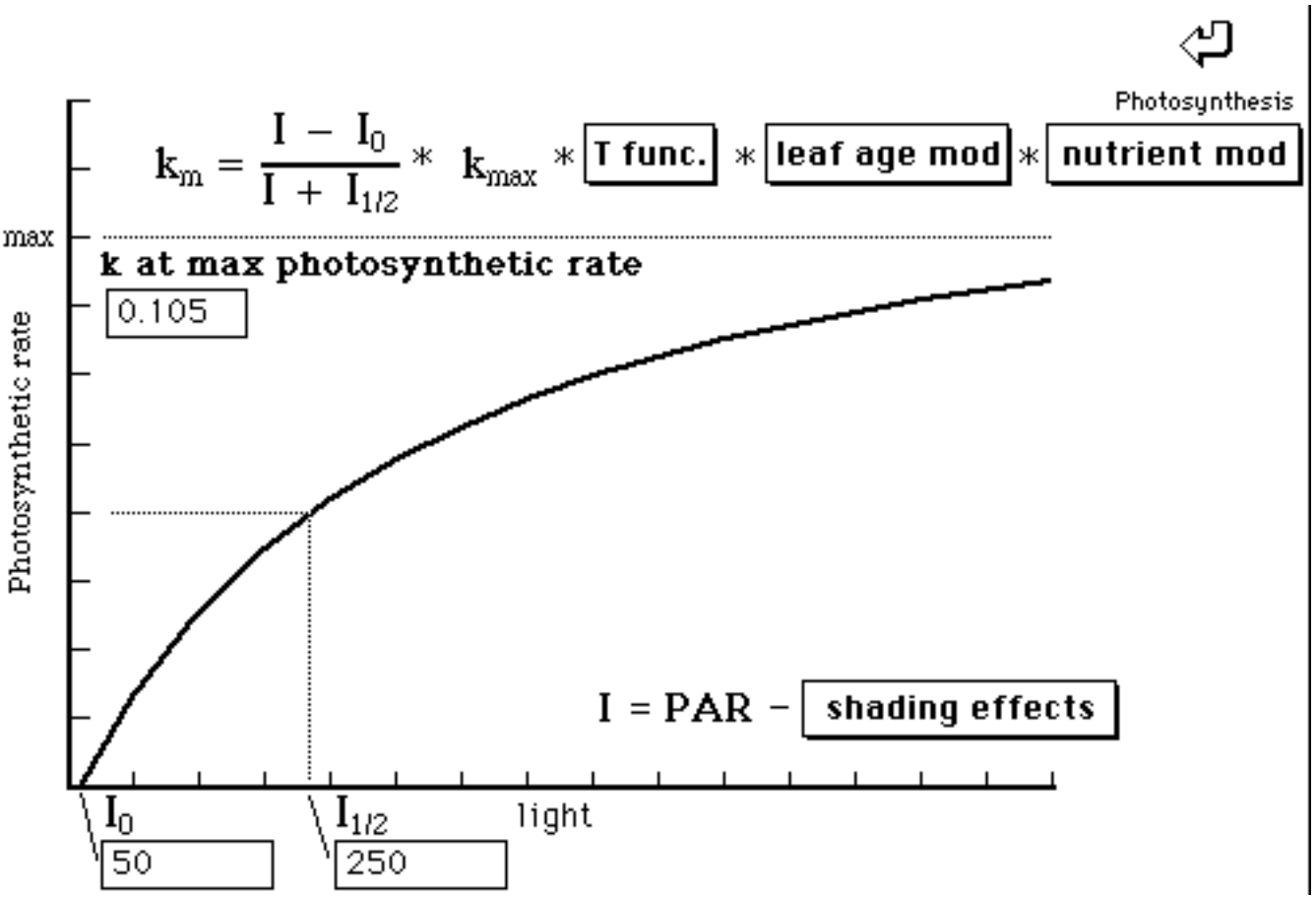



**Figure XX. Hypercard screen, used to change parameters, showing the effect of photosynthetically active light on the photosynthetic rate in TREGRO.**

The $K_m$ modifiers are user-configurable and accessible by clicking the buttons in the equation for $K_m$ . The temperature function ("T func.") allows the setting of a modification curve over a range of ten temperatures. Both the degree of modification and the temperature at which this modification occurs (the *x* axis) can be set. TREGRO interpolates between these temperatures. (Table XX and Figure XX). The photosynthetic efficiency of each age class ("Leaf Age Mod") is a fractional modifier that can be thought of as a fraction of the efficiency of the current leaves, when that leaf class is set to 1. Nutrient modification ("Nutrient Mod") is a decrease in photosynthetic efficiency due to a low nitrogen or magnesium concentration in tree. The user can set the concentration threshold below which this decrease occurs and the minimum modifier occurring when the soluble pool is zero.

The gradient from the atmosphere to the carboxylation site assumes a negligible concentration at the mesophyll and is given in kg $CO_2/m^3$.

**Farquhar method**

Parameterizing the Farquhar method involves setting values for $V_{max}$, convergence criteria, shading effects, $Q_{10}$ modification, modification by nitrogen and magnesium, and other miscellaneous parameters.

Convergence criteria are used in the iterative solution of the Farquhar equations. Values that are too large prevent adequate iteration and resolution of the equation. Values that are too small may result in a lack of convergence in the calculations within the prescribed number of iterations; this is reported in the .ERRORS file. We suggest values of ca. 0.01 Pa as a good compromise between these two extremes.

Shading Effects function in the same way as described in the Lohammer method; a certain fraction of each leaf class is simulated as growing in the user-defined shade, depending on the time of day.

The $Q_{10}$ parameters included with TREGRO are similar to those presented in Farquhar et al (1990). Note that this is function is preset to a $Q_{10}$, unlike other areas of TREGRO where the Q functions can be set.

Nutrient modification of $V_{max}$ by nitrogen and magnesium functions can be parameterized in the same way as in the Lohammer method.

Miscellaneous parameters are, generally, the values used in Farquhar et al (1990). Note that the degrees of latitude should be set to that of the simulated tree. Dark respiration is the fraction of $V_{max}$ used to fulfill the maintenance respiration of the leaves. The Farquhar calculations are very sensitive to this number and it should be changed only moderately, if at all.

### Water

Select the desired water module and click Parameterize Water. Note that if the Lohammer photosynthesis method is used, only Constant Water Uptake can be selected.

**Transpiration Water Model**

Inputs on the General Soil Parameters screen are discussed in the following section on Soil.

The Per Layer Values screen defines soil characteristics pertaining to water movement. Note that for convenience, all of the parameters found on the General Soil Parameters card, with the exception of soil surface area, can also be modified on this card. As discussed previously, a litter layer without roots is added in this water model to allow a reasonable simulation of soil evaporation. This layer will dry out quickly and control evaporation resulting in better agreement with field data. We suggest a thin layer of ca. 1.0 cm. As with all TREGRO parameters, care should be taken to insure that the units of values to be input coincide with those expected in the model.

It is essential that the relationship between the initial Water Content, Saturation Point and Field Capacity is properly parameterized. See the documentation on these

screens for help. Note that the Saturation Point is not input directly, but is calculated from Bulk Density and Particle Density.

Growth modification from water stress requires two thresholds: one above which no modification occurs (threshold A) and one below which no growth occurs (threshold B). This modification is parameterized separately for fine roots, which function in water uptake, and all other tissues. A suggested range of soil water potentials under which a gradual decrease in growth could be expected is 0 to -2000 J/kg. This modification can be effectively turned off by setting both the A and B threshold potentials to unrealistically low water potentials, such as $-1.0e^6$ J/kg.

$V_{m.ax}$ modification from water stress can be parameterized in the same way as the growth modification.

### Soil

There is no choice of soil modules in this version of TREGRO, so click Parameterize Soil and then General Soil Parameters to set the soil characteristics of the three general soil layers. Note that the interface insures that each layer has the same surface area.

Soil Bulk Density should always be less than Particle Density (definitions in Chapter 3). Initial Water Content is defined as the volume of water in a unit volume of soil ($m^3/m^3$)

As mentioned in the previous section, an additional litter layer is added in the Transpiration Water Model. When running that module, all parameters on the General Soil Parameters screen, with the exception of Soil Surface Area, can also be set on the Per Layer Values screen. Doing so is more convenient and gives a more comprehensive overview of both water and soil model parameters.

## Initial Biomass

Each of the tree compartments (vegetative buds, leaves, branches, stem, coarse roots, fine roots) must be given starting masses of one or more of the forms of carbon used in the model: structure, wood, and TNC (Table XX). As discussed previously, branches, stem, and coarse roots can contain all three forms; leaves can have structure and TNC; fine roots and vegetative buds contain only structure. Biomass amounts should be input in grams of carbon, which are assumed to be one-half of dry weight. Note that each of the Initial Biomass screens contain two navigation buttons: "Initial Biomass" which allows you to return to the main Initial Biomass screen in order to parameterize the biomass of another compartment, and "Model Inputs" which allows you to quickly jump out to the Input Parameter Menu when you are done setting biomasses. ~~The forms of carbon are living structure (respiring tissue), wood (dead or non-respiring structure), and TNC (total non-structural carbohydrate). In this model version, the carbon pool SUGAR is not considered separately, so that STARCH is equivalent to TNC.~~

### Leaves

Leaves can grow up to ten age classes, or flushes, each year and retain up to ten age classes over the length of the model run. On this screen, first set the maximum numbers of leaf classes and annual flushes. These numbers only set limits on the numbers of age classes; the actual amount of leaf growth is determined by how well the tree grows given its set of parameters and the meteorological data. ~~Setting the number of leaf classes stored does not determine when leaves will be dropped; leaf senescence is mechanistically modeled (see Section 3).~~ If the tree has attained the maximum number of leaf classes, the penultimate leaf class will be added to the last class when the next flush occurs.

The initial amount of structure and TNC for each leaf class is entered in the upper left of the screen. Scroll through each leaf class using the arrows. Note that the newest leaf class, leaf class 0, is also referred to as current leaves.

The Projected Specific Leaf Area must be entered on this screen. This is the leaf surface area in $m^2$ per gram *dry weight*,. Note that unlike most input parameters in TREGRO, the units are in g dry weight, since this more often coincides with empirical data. For reference, this input is also displayed in g C.

### Vegetative Buds

Vegetative bud structure is only required when using this method for initializing a new leaf class (see Growth Priorities and Rates: Growth Options below). Do not put structure in this compartment if this growth option is not selected. To do so will cause confusion in the analysis of biomass outputs, since total tree biomass and structure will include this initial structure. While TREGRO will assume an initial biomass of 1.0 g even if this input is set to zero, such a small mass will increase the time necessary to grow a desired amount of bud structure. Therefore, when vegetative buds are used in the simulation, be sure to start with a non-zero initial biomass.

### Root Dimensions

Two parameters are required to describe the fine roots for nutrient and water uptake. Root Radius is defined as the _____. Specific Root Length is the length (in m) per g C.The radii are length-weighted, which means (since most of the length is in the smallest size class) that the result depends on what radius is used to characterize each size class. The model uses the center of each size class. although this may not be the length-weighted mean of the size class. TREGRO uses a length-weighted estimate because the radii are used in the model only in the equations for nutrient uptake, and root length is the dominant factor in cases where diffusion and solution flux to the root surface limit uptake. Root surface area would be the dominant factor in cases where

Imax is limiting--in other words, two different weightings of radii would be appropriate in these two different circumstances.

## TNC Capacities

This screen sets TNC capacities as a percentage of structure for all tree compartments. Because structure is dynamic in a simulated tree, the actual TNC capacity of a tissue is calculated daily using these inputs.

Note that although all ten possible leaf classes are listed, only the capacities for the number of leaf classes displayed on the left are used.

## Leaf Turnover

Two types of leaf senescence can be parameterized here. For each leaf class, a percentage (not fraction) of the age class is specified to be dropped. For annual leaf drop, these percentages will be dropped on the day specified as the start of autumn. For stressed leaf drop, these percentages are dropped whenever the TNC pool of a class drops below a level of XXXX. In growth period 4, a delay can be set based on growing degree days. This is to allow any new leaf structure that was grown at the end of growth period 3 to fill with available TNC. As with the TNC Capacities screen, only the inputs for the selected number of leaf classes are used.

This screen allows the user to parameterize both deciduous and evergreen species. Deciduous leaves are simulated by specifying a 100% loss of leaves in the autumn, while evergreen trees can be set to have smaller rates of leaf loss from any or all leaf classes.

## Growth Priorities and Rates

This version of TREGRO allows the user control in defining the order and characteristics of growth events at different times of the year. Along with Model Setup, this series of Growth Priorities and Rates screens is fundamental in configuring a TREGRO simulation. Here you can define the growth events that occur in each growth

period, set the rates at which this growth or senescence occurs, set the degree of temperature-dependence of these rates, select some options to alter the ways in which some tissues grow, and translate an input file from a previous version of TREGRO to the format used in TREGRO 3.0. This last function, Input file translation, is discussed fully in Appendix B.

A normal parameterization would involve progressing through the Growth Options, Set Up Growth Periods, and Set Up Growth Rates screens. It is crucial that these screens be visited in this sequence to insure that all rates have been set properly. Before stepping through these screens, note that the number of growth periods is displayed as five. This number is fixed in TREGRO 3.0.

The Growth Options screen sets options for how a leaf class is initiated and which carbon sinks are used to grow branches and fine roots. Note that a description of these options is located at the bottom of this screen for reference.

The source of the initial structure for a new leaf class can be defined as either structure grown by the model as vegetative buds or an initial "deposit" toward the target leaf class structure, calculated from a user-defined fraction of this goal mass. The vegetative buds method, while more realistic in its process, requires the extra parameterization of an initial biomass of vegetative buds, scheduling this growth during a growth period, and assigning a growth rate. Because this growth is dependent on the temperature and the carbon and nutrient pools of the tree throughout bud growth, the ultimate structure that initiates a new leaf class is not easily predicted. The user-defined fraction provides a relatively predictable shortcut. Using this method, the maximum growth of the new leaves that is allowed on the first day of leaf growth is increased by the input fraction of the leaf class goal weight. Provided that the allocatable carbon pool from photosynthesis and TNC is sufficient on that day, the new leaf class will contain structure equal to the specified fraction of target leaf class structure plus the daily growth at that temperature.

The carbon sources for branch and fine root growth can also be altered on this screen. These switches are provided to enable the user to match the carbon allocation of these two compartments to the allocation pattern used in the previous release of TREGRO, version 1.7.4. Note that a reminder that one or both of these switches has been selected can be found at the top center of the main Growth Priorities and Rates screen.

### Growth Periods

Clicking the "Growth Periods" button takes you to the first of two Growth Periods screens. The interface is able to recognize whether the current input file was the also the last file viewed by the interface. If so, you will be taken directly to the first screen without delay. If you had previously viewed a different file, then there is a delay while the interface sets up the growth periods in the way they are configured in the current input file.

The five growth periods are distributed over two "Growth Periods" screens (Fig. XX). Use the buttons at the bottom center of the screen to navigate between these screens. Be sure to visit both screens when parameterizing. To add or change a growth event, click and drag down the pop-up menus in each slot under a growth period to select an event. Up to fourteen events can be specified in a growth period; they will occur in the order listed on each day of that period. For details of specific growth events, a Descriptions of Growth Choices screen is accessible from these screens (see also Descriptions of Modeled Processes: Choices for Actions in Each of the Growth Periods).

A few items of note when setting up growth periods:

(1) "Convert photosynthate to TNC", should always be included in each growth period after all other events. To do otherwise can waste excess photosynthate

and cause discrepancies in calculations of carbon balance and TNC pools under certain circumstances.

(2) As noted on these screens, leaves can not be grown during growth periods 1 and 2, and can only be grown with a leaf class shuffle in growth period 3.

(3) There is a reminder in the lower left to show you whether the code switches set on the Growth Options screen are on or off.

On completing your configuration of the growth periods, you can either click "Back" which will take you to the main Growth Priorities and Rates screen from either screen, or page backward to the main screen using the buttons at the bottom center. On doing this, you will note that a message box appears confirming that these changes are being "saved". These changes are not saved to the input file at this point, but are cached for later writing to the file if you choose to save all of your changes on exiting to the Main Menu.

### Growth Rates

After returning to the "Growth Priorities and Rates" screen, click on the "Set Up Growth Rates" button to go to the screens used to set growth rates (Fig. 5). After a slight delay for setting up these rates according to any changes you made in the growth period configuration, the first of two screens appears. Notice that only the events that you listed for a particular growth period have a box around their rate. Rates without boxes will not be used.

Active rates can generally be changed in the standard Macintosh manner by selecting the box contents and typing or pasting. In most cases, these are maximum potential growth rates in terms of g C/g C of structure per day at 20C. Wood growth and senescence of leaves and fine roots are temperature-independent. All rates are specific to the growth period in which they are entered. Some boxes do not require you to enter any numbers and will indicate this with a dialog box when you click on them. Click on the "Update Nutrient Pools" field to see an example of this. A few events,

such as "Grow and Senesce Fine Roots" require you to go to a different screen to input the rates. Clicking on those fields when the rate is active will automatically take you to the appropriate screen. Note that both growth and senescence rates of fine roots are entered on these screens.

In practice, these maximum growth rates are established by identifying the fastest daily growth per gram tissue carbon exhibited at any time during a growing season by trees in the field. This maximum is only achieved when all resources are abundant. During most periods of the year, carbon supplies will be inadequate to maintain this maximum growth rate, and the actual growth rate predicted by the model will be lower. This maximum growth rate can then be adjusted to simulate the annual weight increase of each tissue type observed in the test trees. For red spruce, maximum growth rates of roots were estimated from studies involving conifer root systems (Persson 1983). ~~Fine roots were set to turnover at a fixed daily rate corresponding to a residence time of approximately one year.~~

You may find it useful to zero unused rates using the button in the upper left corner. Clicking this button brings up a dialog box in which you can choose to zero unused rates on one or both cards. Since these changes will be made in the input file if you choose to save your parameter changes, be sure that you do not want to save currently unused rate values for future runs.

When you have entered the growth rates on both screens, return to the Growth Priorities and Rates screen by clicking "Back" in the upper right corner. You may now want to set the Q temperature modification functions for the growth rates. If so, click on the "Q Fcn for Growth & Respiration Rates" button. Otherwise, return to the Input Parameter Menu by clicking "Model Inputs".

### Q Fcn for Growth & Respiration Rates

This screen allows you to set the temperature differential over which a doubling in growth rate will occur. For instance, entering "10" in a field sets this doubling function

as a $Q_{10}$. This means that, at 30 C, the maximum growth rate of leaves will be double the rate that you entered on the Set Up Growth Rates screen. Generally, all tissues will have the same Q function. To facilitate this, enter a value in "Set All To" field and hit <enter> or click outside the field. All fields will then be set to this value.

## Phenology

The timeline at the bottom of the Phenology screen offers an easy way to visualize the progression through the growth periods of a simulated year of growth. Transitions between growth periods depend on either cumulative heat degree days or calendar day. The "Calendar day #s" button on the right is included as an aid to setting calendar day-based transitions.

In practice, entry into specific growth periods can be set using one or two characteristic growth events observed from field data (Fig. XX). ~~t~~The entry into the pre-growth, or storage, period (growth period 1) may be set ~~from field data~~ to the first day of significant photosynthetic activity; for growth period 2 (root growth), the time of soil thawing; for growth period 3 (leaf growth) the ~~entry is set to coincide with~~ start of bud break; for growth period 4, the degree-day threshold is less important -- it is typically entered as a result of full leaf expansion or TNC exhaustion; and for growth period 5 (root growth and storage), ~~should mark a~~ the time of translocation of carbon below ground.

In the case of growth period 3, the transition into and out of the growth period is also mediated by the status of the tree in terms of the amount of TNC present. The minimum fractions of total tree TNC that control this transition, as described in section XXXX, are set at the top of the Phenology screen. As discussed previously, these fractions are the ratio of the total tree TNC pool to total tree structure, excluding current leaf TNC and structure.

Dormancy, which is not explicitly shown on the timeline, is defined by the calendar day entered for starting growth period 1 and the day entered in the field

labelled “Calendar day that growth ends”. For instance, values of “2” and “365” for these fields, respectively, sets dormancy to a period of one day on calendar day 1.

Clicking the “Degree Day Calculations” button, accesses a screen for parameterizing the calculation of heat and cold degree days. Enter a threshold temperature and the day range over which to cumulate daily values. If the model run has been set to begin after the start day of either cumulation period, you can initialize either cumulation with some amount of degree days to offset the reduced number of calculated degree days. Note that although cold degree days are calculated by the model and can be output, they are not used in any part of the simulation. If desired, this calculation can be turned off by setting both days of the day range to “366”.

Returning to the Phenology card, note that both the day of autumnal leaf senescence and the degree-day delay in stressed leaf drop in growth period 4 can be set here, as well as on the Leaf Turnover screen. See Parameter Descriptions: Leaf Turnover for an explanation of these inputs.

## Leaf Mass Goal

The simplest of the two leaf mass goal calculation options, Fractional Increase, requires only two inputs. The Fractional Increase input is the fraction that the tree will try to increase each new leaf flush over the largest previous (not necessarily last) leaf flush. Thus, a fraction of 0.35 would result in a calculated goal weight that was 1.35 times the largest leaf flush ever grown by the tree. Bear in mind that this is just a goal. Whether the leaf flush will reach this goal and become the largest leaf mass against which the next goal is calculated depends on many factors discussed elsewhere. The Initial Weight Goal input is the goal weight for the first simulated leaf flush. This goal should first be calculated by the user as the fractional increase over some theoretical initial current leaf mass. Note that this base current leaf mass does not have to be the same as the actual initial current leaf mass parameterized in the Initial Biomass section

of TREGRO (see Parameter Descriptions and Instructions: Initial Biomass). In fact, in the case of a deciduous tree species, it could not be the same, since this type of tree would have no initial leaf mass. In this case, the base leaf mass for the calculation could be from field data on leaf flushes from actual trees that were one year younger than the tree to be simulated.

If Sapwood-Based Leaf Goal is chosen, click the "Set Input Parameters for Sapwood Calculation" button to go to the two input screens. Values for the required five parameters can be entered directly or, more commonly, entered by first using the worksheet which is accessed by clicking the Worksheet button on the first input screen. The worksheet enables you to see the result of your input values and to adjust them so that the model will have the exact sapwood/leaf mass relationship that you want. Values for the actual model inputs are entered in the leftmost column and the estimated mass components of the tree at the time of leaf flush are entered in the center column. If you want to use the initial biomasses of the different compartments here, click the button at the bottom center. The rightmost column presents the results of the different steps in the calculation. By adjusting inputs such as the constants*a* or *b*, a tree can be parameterized with a specific dbh and total leaf mass at a given stem mass. An input crucial to this calculation is the Projected Specific Leaf Area, entered on the Initial Biomass: Leaves screen.

Values of *a* and *b* for various tree species can be found in Clark and Schroeder (XXXX). For red oak (dry weight), *a* and *b* are typically 3.12 and 1.17, respectively. Waring and Schlesinger (XXXX) give typical values of *R* for several species. An *R* for white oak is 0.4, while a range for conifers and hardwoods is 0.1-0.75. A good source of density data is The Wood Handbook (XXXX).

When you are satisfied with the input values, click "Back". Answering "Yes" in the resultant dialog box will then display these values in the input fields on the two input screens. Answering "No" will leave the original values in the fields.

A few things should be noted about parameterizing the sapwood-based leaf goal. ~~It is important to b~~First, be careful to convert any input parameters from the literature (such as the constant *a* and the densities) to g C. Second, the model assumes that the TNC of the stem is at maximum capacity. Therefore, enter a TNC mass on the worksheet that is the TNC capacity of the stem according to the TNC Capacities screen. Third, in many cases stem growth is set to occur after leaf growth. If dbh is of interest as a parameterizing target, then constants *a* and *b* should be adjusted so that an end-of-the-year dbh is calculated from the pre-growth stem masses input on the worksheet, as if it was based on the end-of-the-year stem mass. Fourth, note that the leaf mass that is calculated on the worksheet is the total leaf mass that the tree can support. The actual target leaf mass is the difference between this total, which can change daily, and the previously grown leaf mass.

## Nutrients

Parameterization of nutrients in TREGRO can be viewed as having two sections: uptake and allocation. Six nutrients can be parameterized: N, P, S, Ca, Mg and K. Screens for each of these nutrients can be accessed individually from the main Nutrients screen or can be reached by paging through the nutrients in either section.

On the main screen, set the initial internal nutrient pool of each nutrient as a fraction of the maximum pool. This maximum pool is calculated for each nutrient and is a sum of the maximum pools of all plant compartments, as calculated from parameters entered in the Allocation series of screens. For example, an initial fraction of 0.5 means that each nutrient's pool is half full at the start of the simulation.

Now, progress through both the Uptake and Allocation sections. For now, ignore the two "Set All Nutrients to ..." buttons at the bottom of the Uptake section.

### Uptake

On entering a nutrient's uptake screen, you must first decide whether to include this nutrient in the simulation. Answer the "Nutrient used for growth?" question on

the upper right of the screen by clicking the box to select your answer. Generally, it is best to use all six nutrients in a TREGRO simulation. Next, enter the solution concentration for the nutrient by soil layer.

For each nutrient, three basic uptake parameters must always be set: alpha, the absorbing power of the root; b, the buffer capacity of the soil; and D, the soil diffusion coefficient. Two options are available for setting alpha in TREGRO. A value of alpha can be either input directly or calculated based on an iterative dynamic calculation. If the alpha calculation is selected, three more parameters must be set: $C_{min}$, nutrient concentration at the root surface; $I_{max}$, the maximum nutrient influx at high concentration; and $k_m$, the concentration at which influx is half of $I_{max}$. Select the desired option for alpha by clicking the correct radio button in the middle of the screen. Note that in an input file which has already been parameterized for both inputting and calculating alpha, this option can be quickly selected for all nutrients by clicking the appropriate button on the main Nutrients screen.Values for uptake parameters may be obtained from experimental data. In the *sample.params* input file provided with TREGRO, data from XXXX for xxxx was used. However, data was not available for some parameters. In this case, we used the convention of "9.999" to an estimated order of magnitude (e.g., 9.999E-13 for $I_{max}$).

### Tissue Nutrient Concentrations

Determining nutrient concentrations in the tree requires the following inputs, in grams nutrient/gram total dry weight, for each tissue and nutrient:

(1) Construction Cost. This is the amount of nutrient needed to grow 1 gram of total dry weight.

(2) Maximum Nutrient Concentration. This is the maximum allowable concentration, including both the construction cost of that tissue and the maximum soluble pool.

(3) Fraction In Senescence. The fraction of the nutrient pool in senescing tissue that is lost from the tree during senescence. In other words, this parameter controls the amount of nutrient resorption during senescence. A value of zero means that all of the nutrient in senescing tissue is retained by the tree, while a value of 1 means that none is retained. Note that this is a fraction, not a percentage.

(4) Fraction Of The Total Dry Weight that is TNC and wood combined.

Although TREGRO uses the first three parameters in terms of grams nutrient/gram structural Carbon, the interface has been designed to allow you to enter values in more readily available units of grams nutrient/gram total dry weight. It then converts the values to the proper units before saving them to the input file. Clicking the "Model Inputs" button in the lower right corner of a nutrient's allocation screen will display the actual values used as model inputs. These inputs are calculated by multiplying the user inputs by 2 to convert from grams dry weight to grams carbon and then dividing by the fraction that is structure (= 1 - Fraction that is TNC and wood) to obtain grams nutrient/gram structural Carbon.

~~The maximum amount of each nutrient that can be stored in the plant, in excess of that contained in plant structure, is expressed as a fraction of the total mass of structure (Table 4-5). The units for this fraction are grams of C equivalents, or the amount of structure that could be built with the given amount of nutrient. For example, if the maximum pool for N is set at 0.1, then the plant can store enough N to increase its structure by 10%. The initial amount of stored nutrient in the plant, above that contained in structure, is specified as a fraction of the maximum allowable storage. This second fraction applies equally to all nutrients, imposing a balanced internal nutrient pool at the start of a model run (i.e., all nutrients in the correct stochiometric ratios sufficient to increase the plant by the given fraction with no remaining nutrients).~~

## Throughfall

Parameters on the Throughfall screen are used in the calculation of the transfer of nutrients between the tree canopy and rainfall due to dry deposition and canopy exchange, resulting in a certain nutrient concentration in throughfall. The Exchange Coefficient can be negative or positive, with a positive value signifying a loss of nutrient through the leaves to the rainfall. The Dry Deposition Slope parameter must be positive. This is the amount of a nutrient that is deposited on the leaf surface per dry (i.e., non-rainfall) day. Both these parameters must be input on a per $m^2$ leaf area basis.

Note that the total canopy area is shown on this screen. This area is equal to the soil surface area that is input on the General Soil Parameters screen under Model Setup: Parameterize Soil and is, in fact, the same parameter. Although this area can be changed here, it is suggested that you change it as part of the soil parameterization procedure to avoid confusion.

## Meteorological Data

You have a choice of using either a defined meteorological data file or simulated data in a TREGRO simulation. On entering the Meteorological Data screen, select one of these options by clicking the "Use Met Data Files" button. When this button is turned on, a field will appear below it listing the meteorological data file to be used. If another file is desired, click on the "Change met file" button to bring up a file selection box. You may find that a file called *zznoMetFile.0* is listed in this field. This dummy file name used by TREGRO when the simulated data option is chosen. Simply choose a new file to replace this one. Note that the entire pathname is listed when a file is selected. This path is important; without it TREGRO can not find the meteorological file for a simulation. For this reason, it is very important that this screen is always checked before a model run to determine that the correct data file is selected. Remember that even though the correct file name is listed, if the file has been moved since it was selected, the path will be incorrect.

The name of a met file must end with a period and a single digit. By convention, the first file in a series should start with ".0". For example, the file called *Ithaca88.0* , which was provided with TREGRO, contains meteorological data collected near Ithaca, NY in 1988. For multiple year runs, the model looks for a file with the same name but increments the file number extension. In the second model year, TREGRO will look for a file called *Ithaca88.1* which contains 1989 data. If no file is found, the model will reuse the data from the last file read. Thus, if you want to insure that a multiple-year model run uses the same met data each year, make sure that there are no other files of that series in the same folder as the desired file.

TREGRO uses hourly meteorological data. The data file is a text file that can be viewed in a spreadsheet or word processing program. There is a specific format that must be followed. Use the file that was provided with TREGRO 3.0, *Ithaca88.0*, as a model. There are 3 header lines followed by 24 lines per day times 365 days for a total of 8763 lines. TREGRO uses a 365 day year; any extra days, such as in a leap year, are ignored. The first 3 lines are used for the start day of the meteorological data (line 1), the end day (line 2), and any notes about the file (line 3). There should not be any tabs in these header lines and line 3 should not start with a numeric character. Note that if Microsoft Excel is used to make changes in the file, tabs may be inadvertently added in these 3 lines when the file is saved. These will have to be removed in a word or text processing program. Also, there should not be any extra returns at the end of the file; the file should end at hour 24 of day 365 and not with an empty line.

Table XX shows the type and order of the meteorological variables in the meteorological file. The model reads, but ignores, the year, month, day, and hour; these are not needed for model input but are provided for the user's information and reference. TREGRO will compensate for whether air temperature is entered in Centigrade or Fahrenheit and if relative humidity is entered as a percentage or a fraction. The same units should be used for all hourly values of these variables in the

file. Vapor pressure data is not used in TREGRO 3.0, but serves as a placeholder; instead, relative humidity and air temperature are used to calculate VPD. Ozone should be entered in ppb; the model will do the calculations needed to convert to the necessary grams of ozone. Missing data should be entered as "9999". For air temperature and PAR, TREGRO will simulate the missing data using the parameters described in the next section. Missing rainfall, relative humidity, and ambient ozone data will be replaced with the defaults entered on the right side of the Meteorological Data screen.

**Table XX. Segment of sample meteorological data file.**

| Year | Month | Day | Hr | Air Temp < C or F> | Humidity <% or Frac.> | Vapor Pressure <mbars> | PAR <μE/m$^2$> | Rain <mm> | Ozone <ppb> |
|---|---|---|---|---|---|---|---|---|---|
| 88 | 1 | 1 | 100 | 35.3 | 84 | 0.588 | 9999 | 0.508 | 12 |
| 88 | 1 | 1 | 200 | 36 | 84 | 0.604 | 9999 | 0.508 | 12 |
| 88 | 1 | 1 | 300 | 36.6 | 84 | 0.615 | 9999 | 0.508 | 12 |

### Simulated Meteorological Data

Missing temperature and light data, whether for an hour or an entire year, can be simulated using parameters set on the screens accessed under "Set Defaults For Simulations Of:". These screens can be accessed individually from the main Meteorological Data screen or by paging through them. Parameter values should be derived from the meteorology of the site in which the simulated tree is to grow. Care should be taken in parameterizing these inputs, since incorrect values may cause serious perturbations in the tree's normal growth during hours where missing data is being simulated.

### Meteorological Modifiers

Users can add a positive or negative constant to all hourly air temperatures, whether they are actual data or simulated. Multipliers are provided for ozone levels

and rainfall, also applied hourly to either real or simulated data. Modification can be turned off by setting the temperature modifier to zero and the multipliers for ozone or rainfall to 1.

## Ozone Effects

Two hypothesized mechanisms of ozone effects on gross photosynthesis can be implemented in the model. By clicking a checkbox, either or both mechanisms can be selected, or ozone can have no effect. After selecting an ozone effect, click on the appropriate button to edit that function. Clicking the "Edit Mes. Cond. Curve" takes you to a screen with input fields for a threshold and the slope of the linear function. The threshold is the amount of accumulated ozone below which there is no effect on mesophyll conductance. Note that the value entered for the slope should be positive even though the actual function has a negative slope.

Included on this screen is a worksheet to aid in parameterizing this effect. First, enter values for the variables in the upper half of the worksheet. Note that the values for ozone and stomatal conductance are unrealistically, but necessarily, static; use good average values from the photosythetically active part of the day. The accumulation threshold is the ozone concentration above which ozone will begin to be accumulated. Hourly values at or below this threshold will be ignored. Second, enter values for the threshold and slope parameters. The calculated values for leaf mass, total cumulative ozone, cumulative ozone per gram leaf, and percentage decrease in mesophyll conductance are displayed in the bottom half of the worksheet. Adjust the threshold and slope until you get the desired reduction in mesophyll conductance. Remember to click outside an input field or to hit <enter> in order to update the calculated fields. The values on the worksheet portion of this screen are not saved to your input parameter file. Therefore, you must remember to go to the "Set Ozone Accumulation Threshold" button on the main Hypothesized Ozone Effects card and enter the value that was used on the worksheet.

Selecting the respiration effect and clicking the "Edit Resp. Curve" on the Hypothesized Ozone Effects screen takes you to the Respiration Effect screen. The parameter inputs and worksheet function in the same way as the Mesophyll Conductance Effect. Adjust the inputs until you get the desired increase in respiration.

A modifier that multiplies the amount of ambient ozone can be entered on the Hypothesized Ozone Effects screen. This is the same parameter as that found on the Meteorological Modifiers screen.

## Respiration Rates & Q Fcn

In the sample parameter file (*sample.params*), a default value of XX% of carbon mass lost per day is currently used for all tissues, a value at the low end of the range suggested by Waring and Schlesinger (1985).the current value in *sample.params* is XX g lost as respiration for every 1 g allocated to growth, leaving XX g available to build tissue structure.

Growth and maintenance respiration rates are set using the same units as growth rates: the fraction of compartment structure per day at 20°C, modified by a definable Q function for the current air or soil temperature. These Q function values are the same ones used for growth. Respiring compartments are: vegetative buds, leaves, stem, branches, coarse roots, and fine roots. Growth respiration is the respiration resulting from growing structure. It is set as a fraction of the carbon that is allocated to the compartment; the remainder is then available for growth. Depending on the Photosynthesis module chosen, leaf respiration may or may not be set from this screen; the Farquhar method has an internal parameter for this, Dark Respiration (see Model Setup: Farquhar: Miscellaneous Parameters).

Each screen contains a button for the rapid setting of all compartments to the same respiration rate. Remember that leaf respiration is on an hourly basis, unlike other tissues. Therefore, the value entered here is first divided by 24 before filling the fields.

In the red spruce parameter file, rates of maintenance respiration at 20°C were initially assumed to be the same for all tissue, XX% of carbon mass lost per day. The actual amount of respired $CO_2$ given off by each tissue will vary because of differences in weight and environmental temperature. Respiration rates can then be adjusted to simulate the actual annual carbon gain achieved by the test tree.

## Acid Precipitation Effects

There are two acid precipitation effects that may be implemented in this version. Cation deficiency can be simulated by reducing soil solution cation concentrations. Root turnover may be increased to simulate increased damage to fine roots due to soil acidification.

## Advanced Parameterization

### Setting Up Multiple Runs

The TREGRO interface allows the user to set up a series of model simulations that can be run unattended. To increase efficiency, input files may be modified as desired, queued in the interface and run overnight. This can be useful due to the time required to do extended runs, especially when using the Farquhar photosynthesis module.

To set up the runs, click "Change Model Parameters" on the Main Menu and enter the day range and other options as you would for a single run. These settings will apply to each of the model runs. After clicking "Continue" and going to the Input Parameter File(s) screen, click the "Multiple, Unattended Runs" radio button. Enter the number of desired runs from 2 to 10, as requested, and note that the requisite number of name fields has been added to the screen. Any existing files that had previously been

listed in a multiple run setup will still be listed. You may choose to keep some or all of these, or to replace them. Clicking in any of the name fields will bring up a dialog asking whether you want to create an input file or use a existing one. The list can be filled in whatever order you like, but the simulations will be run starting with the top of the list and progressing to the bottom. Blank name fields will be ignored.

Often, you will want to do a series of related runs in which the files differ in only one or a few parameter values. This can be done manually or by using Experiment Setup, described below. To do this manually, set up your first input file and use this as a base for subsequent files. After clicking in the second file name field, select "New", name the file with a unique name, and choose your first file as the base file. Note that when you are returned to the Input Parameter File(s) screen, the arrow to the left of this name field is highlighted. This highlighting indicates the file whose parameters will be displayed on going to the Input Parameter Menu. Any file's parameters can be viewed at any time by clicking the corresponding arrow to highlight it.

The parameters of interest can now be adjusted by going to the Input Parameter Menu and saving the changes on returning to the Input Parameter File(s) screen. Repeat for the next file using the the first file as the base, and so on. When all the files have been set up, return to the Main Menu and click "Start a Model Run". The runs will then be done in the order listed. Remember that new output files will replace older files of the same name, so if you have used an input file or file name before and you want to keep previous results, move the old output files from that folder or give the new input file a different name.

A couple of warnings when setting up multiple runs:

1. Be sure to run TREGRO as the foreground application. Turn off any screensavers that you are using. Otherwise, they will become the foreground application when the screen is blanked. While TREGRO can run in the background, it will only complete the current run and will not progress to the

next run in the list. Likewise, after clicking the "Start a Model Run" button, don't click elsewhere on the desktop, since this will bring another application, like the Finder, to the foreground.

2. Be sure that you have enough hard drive space for the number and duration of runs that you specified. The daily output file takes about 0.75 MB per year plus additional space required for any hourly output. Error files are usually, but not always, negligible in size.

### Experiment Setup

The Experiment Setup function enables the user to quickly set up a number of runs in which selected parameters are varied by a set amount. Proceed as you would in setting up a single run, and select an input file that will serve as the base file. Then, click the "Experiment Setup" button on the bottom left of the Input Parameter File(s) screen. You will be asked to select the Multiple Runs option and to enter the number of desired runs. After doing so, click the "Experiment Setup" button, now labelled "Continue", to go to the Experiment Setup screen.

This screen basically consists of two lists. At the top of the screen is an area in which a parameter can be selected from a list and its modifier entered. At the bottom of the screen is the list of parameters that you want to vary among the multiple runs with the set of modified values.

To begin, click on the "Clear List" button at the top of the screen. This removes any parameters from the bottom list. Next, click the "Select Parameters" button. This brings up a dialog box listing parameters that may be selected. If there are currently parameters listed here, you may choose to keep them for use now or in the future, or you can delete them by clicking on them individually to select one and then clicking the "Delete" button. Other parameters can be added to this list by clicking the "Go Find..." button. A dialog box will appear offering several options. Click "Cancel" to skip the selection of parameters and to return to the Experiment Setup screen. Click "OK. Go

Back" to return to the current list of selectable parameters. Click "OK. Let's Go" to add parameters to the list of selectable parameters.

On clicking "OK. Let's Go", you will be taken to the familiar Input Parameter Menu of the interface, but in a selection, rather than a value entry, mode. In this mode, clicking on a parameter field adds it to the parameter selection list. For example, click on "TNC Capacities". Click next on the "Branch TNC capacity" field to select it for the list. A dialog box appears allowing you to give this parameter a name that will be recognizable to you. Leaving this field blank will give the parameter its internal TREGRO name. This is generally not going to be recognizable to you; it is suggested that you give it another name for your use. Next, you are given a choice of continuing to select parameters from the interface or to return to the selectable parameters list. For now, click "No" to return to the list. You will be returned to the dialog box listing your parameter choices. Select "Branch TNC capacity" (or whatever you named it) and click "OK". You will now see this parameter listed in the display area in the upper half of the Experiment Setup screen. You will also see a number following the parameter name; this is a TREGRO parameter ID number and can be ignored. Next, you must select how you want to modify this parameter. Choose either the "*" radio button to apply a multiplicative modifier or the "+" to increment the value by a certain amount. Then enter the amount in the box to the right. For example, selecting "+" and entering "5" for "Branch TNC capacity" will increment this capacity by 5% in each input file. Remember to use common sense and enter a reasonable parameter modifier for a given parameter. For instance, modifying "Branch TNC capacity" by a factor of 5 would generally not be desired, but multiplying by 1.25 might be reasonable.

Next, click the "Add To List" button. You will now see "Branch TNC capacity" listed on the left in the bottom list box and the values that will be entered in the input files on the right. To add more parameters to this list, return to the "Select Parameters"

button and select another parameter, enter its modifier, and click "Add To List". Any number of parameters may be added in this way.

After you have finished adding parameters to the list, click "Create The Input Files". This creates and names copies of the base input file with the values of each set of the listed parameters modified accordingly. For example, if you initially selected four multiple runs, the series of incremented values of "Branch TNC capacity" might read "30, 35, 40, 45". The first value is the initial value in the base file. The second file, named as *yourinputfile*~2, will have a branch TNC capacity of 35%; the third, *yourinputfile*~3, will be set to 40%; and so on. If you chose to modify more than one parameter, the second (or third, or fourth) values in all of the series will be written to the same file.

You should now find yourself back at the Input Parameter File(s) screen with your list of input files. You can now proceed as you would with any multiple run setup, by clicking "Main Menu" and then "Start a Model Run". Note that had you clicked the "Cancel or Done" button rather than "Create The Input Files", you would have been returned to the Input Parameter File(s) screen without generating any new files. However, any files that were already listed from previous runs would again be run if you then clicked "Start a Model Run".

# 5

# MODEL OUTPUT

## Error File

The error file is an important component in the parameterization process. It is strongly suggested that you check the error file, designated as "*yourinputfile*.ERRORS", after each model run. To do so, click on the button labelled "Check Error File For Each Model Run". You will be asked to select an application to use in reading this text file. Under most circumstances, there should be only the date of the model run and the names (with the full paths) of the input parameter and meteorological files used. Other messages may be due to the parameters used or may indicate problems with the model's operation.

One common problem occurs when the user neglects to correctly specify the location of the desired meteorological file prior to starting a run. If the model cannot locate the file, it will use simulated weather data, indicated by the default file name, *zznoMetFile.0*. Only by checking the error file can the user be assured of noticing this error.

Messages indicating that total TNC in one or more compartments is zero, or that net photosynthate is negative at the end of the day are indications that the tree is not correctly parameterized and that parameters must be adjusted.

## Daily Output File

Each simulated day, TREGRO writes ca. 500 output variables to a binary file named using the format "*yourinputfile*.Dout". The daily output variables available from TREGRO are described in Table XX.

The binary format was chosen to minimize the size of the daily output file. This file is only readable by the TREGRO interface. Two methods, QuickGraph and Custom Graphs and Tables, are available for selectively viewing the output variables. These two methods are described below.

### QuickGraph

QuickGraph employs a quick, but limited, graphing utility built into the interface. Clicking "Quick Graphs or Tables" on the Main Menu will take you to the Select Output Values screen for choosing the output variables of interest. It will first ask if you want to graph over time. Answering "Yes" will put the variable "Day" on the *x* axis. Answering "No" will allow you to choose an alternate *x* variable from the lists. Use the pop-up menus to pick this *x* variable and up to four *y* variables. If there are unwanted variables listed in the window initially, click the button "Start A New List" to clear the list. Individual variables can be deleted or rearranged in the list by the standard methods of selecting, cutting, and pasting. When the list is complete, click "Continue". There will be a short wait while the interface looks up the index numbers of these variables.

On the next screen, confirm that the correct output file (including path name) is listed in the topmost box. If it is not, click "Change Model Output File Name" and select the desired file. A graph name in the form "*yourinputfile*.qg#" will be automatically entered in the next box. If you wish to name it differently or to save it to another folder, click the "Change QuickGraph File Name" button and make the desired changes. Then enter the desired day range. Note that QuickGraph can only display 249 days for each *y* variable. If you have selected a range greater than this, the interface will

warn you and indicate the number of days it will skip. If you want to graph a longer period, or just want to limit the amount of detail shown, enter a number of days to skip in the next box. For example, a "4" entered here would display days 1, 6, 11, 16, etc. When you are ready, click the "QuickGraph" button on the lower right. The interface will then ask for a label for the *y* axis; this can be left blank if desired.

Note that a new graph will write over a previous graph made from that output file unless you give it a unique name. A copy of the graph in color is also automatically placed in the Macintosh clipboard. The graph can then be transferred to another document by going to that document and selecting the standard "Paste" command from the Edit menu.

There are several buttons on the bottom of the QuickGraph screen that provide various functions. The current graph can be modified using the buttons on the right. The "YAxis General [or Exponential]" button toggles between two methods of displaying the *y* axis values. For instance, clicking the button when it is labelled "YAxis General" will change the *y* axis numbers from the general format to the exponential, or scientific, format. The legend can be positioned using the arrow buttons. A shortcut for quickly moving the legend to a corner is provided by holding down the <option> key; the legend will be moved to the corner closest to the arrow's direction in a clockwise direction. The "Help" button offers a readily accessible description of this shortcut. The print graph button prints a copy of the current graph to the printer configured in the Macintosh Chooser. Note that the file is sent immediately to the printer; no dialog box is presented offering printing options.

A new graph can quickly be done using the two leftmost buttons. The first button enables you to plot the same variables from a different output file or for a different day range. The second button takes you back to the Select Output Values screen to select different variables. You can then choose a different output file or day range, or use the same settings as the previous graph.

ASCII text files of the output variables can also be generated using the "QuickGraph" button on the Main Menu. The text file option is described fully in the section, Custom Graphs and Tables. As with a graph, a table done through QuickGraph can contain no more than five output variables (an *x* variable and up to four *y* variables) and 249 days. Note that, because "Day" is automatically output to the text file, it will be output twice per day if it has been chosen as the *x* variable. Generally, if tables are desired for importing data into a full-featured graphing or spreadsheet program, use the "Make Custom Graphs or Tables" option described below.

### Custom Graphs and Tables

Custom Graphs and Tables allows you to view an unlimited number of output variables or days. Choose "Make Custom Graphs or Tables" from the Main Menu. Select the desired output variables, source binary output file, text file name and location, and day range, as described above for QuickGraph. Then click either the "Create ASCII Text File" button to make the text file or the "Create ASCII Text File And Open..." button to make the text file *and* automatically bring up a dialog box allowing you to select the application that you want to use to view the file. The data in this file are formatted with one line per day and variable data separated by tabs. The first line contains the names of the variables. Note that this option automatically adds "Day" to the output text file, so it is unnecessary to select it. This variable will not be visible in the list box on the Select Outputs screen, however.

### Output File Information

Basic information about an output file can be obtained by clicking the "Output File Information" button on the Main Menu. This information includes the input parameter file and TREGRO version used, the model run duration, whether the run was successfully completed, and the Comments field from the input file. A sequence of output files may be examined by clicking the "Check Another File" button, with the information about each file being appended to the scrolling list. At any time, this list

can be cleared by clicking the "Clear Field" button. The list is automatically cleared on exiting this screen.

### Comparing Output Files

Two output files can be compared for differences in output values using the "Compare Output Files" button on the Main Menu. Enter the day range to be compared and the tolerance level in percent. Clicking the "Compare" button brings up two consecutive dialog boxes from which the two files can be selected. These will be listed in the two boxes below this button. The comparison is then compiled until completion, or the mouse is clicked to terminate it. The output variables that differed are listed with their code number and the respective values. To see the variable names, click "Convert numbers to names". This list may be saved as a text file by clicking "Write to file". See the "Hints" button for additional options and warnings.

## Hourly Output File

The user may choose to also see photosynthesis- and respiration-related output variables on an hourly basis. This option can be turned on by entering nonzero values for "Start on day" and "End on day" on the "Starting and Ending Days" screen and turned off by clicking the "Turn Off Hourly Output" button. This output file is named using the format "*yourinputfile*.Hout".

Hourly output can be useful when parameterizing such processes as photosynthesis where looking at hourly values of photosynthesis and respiration during hours of maximum light level and duration will indicate the maximum photosynthesis attained and the ratio between photosynthesis and respiration. Table XX describes the outputs displayed with this option. Some of the outputs pertain to only one of the photosynthesis methods, Farquhar or Lohammer/Running. The first two lines of the hourly output file provide a key to distinguishing between these outputs. The third line contains the output names and their units, as well as any notes regarding specificity to one of the photosynthesis methods. Any output variables not

relevant to your chosen photosynthesis method should be ignored. Be sure to read the whole column label; some are quite long. When viewing these file in a spreadsheet program, you may have to expand the width of the columns in order to see all of the information in the header. Note that the three header lines are repeated for each year of the model run.

When turning on hourly output, the start and end days must be relative calendar days (i.e., between 1 and 365). Be sure to enter start and end days that fall within the non-dormant growth periods of the tree. Because each day generates 24 output lines, it is best to limit the number of days of hourly output to the few crucial ones in order to minimize file size.

## Zelig Output File

# .c.6

# TROUBLESHOOTING

**[TO BE ADDED]**

- xx. When monitor is set to greater than 8-bit, stack may lose effects (this noted by who?)

# .c.7

# REFERENCES

**[TO BE UPDATED]**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# APPENDIX A. Functional Flow Diagrams for the TREGRO Program

**[TO BE ADDED]**

# Converting Parameter Files from Previous Versions

**[TO BE ADDED]**