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A Preliminary Submodel of Carbon Translocation

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A PRELIMINARY SUBMODEL OF CARBON TRANSLOCATION

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INTRODUCTION

The aim of this report is to present a simple version of the translocation submodel which may serve as a focal point for discussion on the development of a series of submodels of differing complexities.

In constructing this preliminary submodel, we have set forth four questions to be answered in sequence: (a) What compartments should be included in this submodel? (b) What flows between compartments should be considered? (c) What factors control the rates of these flows? and (d) What are the mathematical forms of the equations relating flow rates to the factors affecting them? Our answers to these questions have been based on a combination of the results of the two previous meetings of the translocation committee, available information from the literature, and informed guesses. We have been guided by a desire to build a submodel in the short time available prior to subsequent meetings, in order to crystallize the problems which we have to confront.

ASSUMPTIONS

The following major simplifying assumptions have been made in order to facilitate the construction of the present preliminary submodel:

1. The compartments (plant organs and carbon fractions) and flows in the submodel are shown in Figure 1 (a and b). The vertical line in Figure 1a separates flows which take place at the beginning of the growing season (right side) from those which occur later (left side). The flows at the beginning of the season are distinguished into three different life forms considered in this submodel. After the beginning of the growing season, it is assumed that the only carbon translocation occurring is that from photosynthetic to other organs, and distinction among life forms is then unnecessary.

2. The carbon fixed during each time step is put directly into the reserve carbon fraction of the photosynthetic organ.

3. All carbon translocations among organs involve the reserve fraction only; such translocations are performed prior to any transfers between different carbon fractions.

4. Growth is defined as an increase in structural carbon. Therefore, the model deals with two related but different processes, viz. growth, and fluctuation of the relative amounts of reserve carbon and protein carbon.

Assumptions concerning the factors affecting the flows, and the mathematical forms of the equations expressing the rates of flows as functions of these factors are explained in the following section.

REMARKS ON THE FORTRAN IMPLEMENTATION OF THE WHOLE-SYSTEM MODEL

Before describing the translocation submodel, the overall structure of the whole-ecosystem model (Fig. 2) and the manner in which information is passed among submodels (Fig. 3) will be briefly reviewed.

The boxes in Figure 2 represent subroutines in the FORTRAN implementation of the whole-ecosystem model. Subroutines above the broken line do not model any biological processes. The main program reads initial values of the state variables, calls some of the subroutines, and handles various bookkeeping chores. The subroutine EXOGEN provides exogenous data such as air temperature, precipitation, irradiation, etc. Tabular and graphical print-out are provided by the subroutines REPORT and GRAF, respectively. Sensitivity analysis is performed by SENSIT, SENOUT and DERIVD. The subroutines VEGET, ANIMAL and SOILS either model the plant, animal and soil subsystems or call other subroutines which model separate processes of these subsystems. The processes considered in the plant subsystem are phenology (PHENOL), photosynthesis (PHOTOS), respiration of non-photosynthetic organs during dark hours (RESPIR), translocation of carbon among organs and changes in the amounts of different classes of carbon compounds (TRANSL), uptake of nitrogen and minerals from the soil and their distribution to each of the organs (MINUPT), and organ abscission and death (VDEATH). The subroutine KOVER calculates the fraction of ground covered by each species. The subroutine VSTVAR handles miscellaneous bookkeeping chores.

The common block /INCOMV/ contains variables and switches generated by the various plant submodels and required by more than one of these submodels. For example, the one-dimensional array "PHENST(I)" which is an output from the phenology submodel, and an input to the translocation submodel, indicates the current phenological state of the *i*'th species age class. Inputs required by the submodel which are read in at the start of simulation are placed in the common block /PARAM/ if they are real numbers, and in the common block /IPARAM/ if they are integers. The common block /SPEC/ contains specifications required by all of the programs such as the number of species, the number of organs, etc. The common block /METEOR/ contains exogenous variables (mostly meteorological). State variables are contained in the common block /STAT/, and increments to the state variables in the common block /CHANGE/. The common block /TOTALS/ contains summations of various combinations of state variables. Selected state variables and output variables not contained in the previously mentioned common blocks are included in the common block /OTHER/.

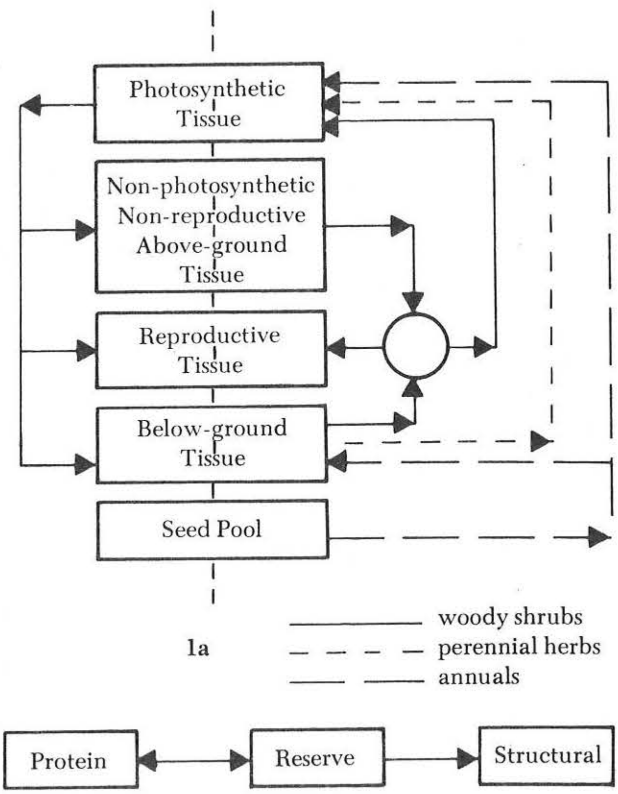

Figure 1. Compartments in translocation model.

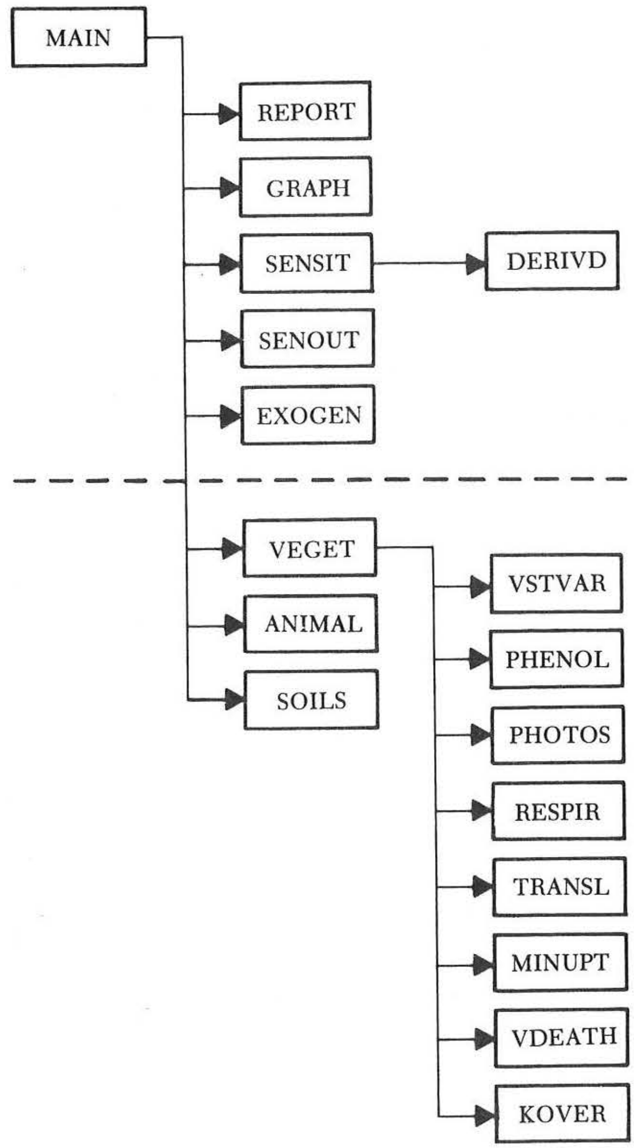

Figure 2. Procedures in FORTRAN implementation of whole-ecosystem model.

/INCOMV/	/SPEC/	/CHANGE/
/PARAM/	/METEOR/	/TOTALS/
/IPARAM/	/STAT/	/OTHER/

Figure 3. Common blocks used by translocation model.

DESCRIPTION OF THE TRANSLOCATION SUBMODEL*

GERMINATION AND LEAFING-OUT

Germination and leafing-out are considered to be affected by soil water potential in bars (SWP), soil temperature (ST), and the ratio of the amounts of reserve to total carbon (RC:TC). The translocation rate is related to SWP by a modified Mitscherlich function (equation 1 and Figure 4), to ST by a fourth-order polynomial (equation 2 and Figure 5), and to RC:TC by an exponential function (equation 3 and Figure 6). In these and subsequent equations, lower case letters represent parameters. RTR1 and RTR2 are relative rates varying from zero to one, and the overall rate equals the product of TR, RTR1 and RTR2. In equation 1, c and SWP are negative numbers.

The reserve carbon translocated during germination is distributed to roots and shoots according to read-in ratios. In perennial grasses and herbs, the translocation during leafing-out occurs from a single donor organ (below-ground) to a single recipient organ (above-ground photosynthetic). In woody shrubs, translocation occurs from two donor organs (stems and roots) to one or both of two recipient organs (leaves and fruits). In the latter case, the amounts translocated from each of the donor organs are summed and the resulting amount is distributed between leaves and fruits according to read-in ratios.

VEGETATIVE AND FRUITING STAGES

The rate of translocation from the photosynthetic organ to other organs is a function of water potential (WP), temperature and RC:TC in leaves. The value used for WP is the SWP of each soil horizon weighted by the root biomass in the respective horizon. For above-ground organs the translocation rate depends on air temperature, and for below-ground organs it depends on the temperature of the respective soil horizon. The relationships between the translocation rate and each of these three variables are as indicated in equations 1, 2 and 3 and Figures 4, 5 and 6 respectively.

If the species is fruiting the fraction of the translocate that goes to fruits is an exponential function of RC:TC (Fig. 7). The fraction of the remaining amount of translocate which is transferred to below-ground organs is also an exponential function of RC:TC; the rest is transferred to stems. This manner of distribution is based on the assumption that as conditions become more favorable, fruits receive a progressively larger proportion of the translocate, and stems a progressively smaller proportion.

CARBON FRACTION DYNAMICS

The ratio of reserve to protein carbon (RC:PC) at which no flow occurs between these two fractons (CR = critical ratio) is a negative exponential function of WP (equation 4 and Fig. 8), and the nitrogen to protein carbon ratio (N:PC; Fig. 9). For above-ground organs the value used for WP is the weighted SWP described in the previous section, and for below-ground organs, it is the unweighted SWP. The dependence on N:PC ensures that if nitrogen uptake is low, protein synthesis will be depressed.

If the actual current RC:PC is greater than the critical ratio, carbon flows from the reserve fraction to the protein and structural fractions. The rates of these two flows are exponential functions of RC:PC and RC:SC (where SC= structural carbon) respectively. On the other hand, if the actual value of RC:PC is below the critical ratio, then there is only one flow; from protein to reserve carbon. The rate of this flow is a negative exponential function of RC:PC.

FINAL REMARKS

In order to fulfill our ultimate objective of building a series of translocation submodels, and to improve the above submodel, which may be considered the simplest of this series, we need to address ourselves to the questions below. It is expected that each submodel of the series will have a different set of answers to these questions:

1. Are there any compartments and flows that should be added to and/or deleted from the present submodel?
2. Are there any data available bearing on the relationship between the flows and the factors influencing them which are assumed in the above submodel, or is there any information indicating that there are better choices of factors?
3. Are there time series data available providing the relative amounts of protein, reserve and structural carbon present in each organ of representative species?
4. Should any of the mathematical equations expressing the rates of flow be modified or replaced by others?

*A flow chart of the submodel is provided in Figure 10.

$$RTR1 = 1 - \exp(-b\,(SWP - c)) \qquad (1)$$

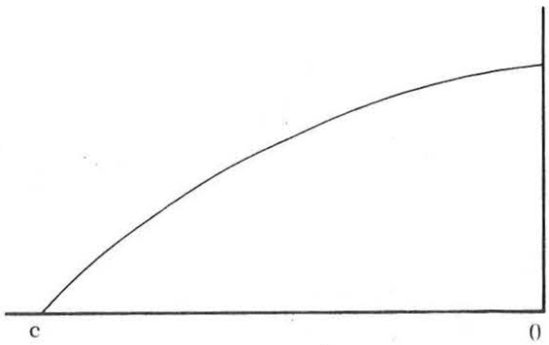

Figure 4

$$RTR2 = b \cdot ST + c \cdot ST^2 + d \cdot ST^3 + f \cdot ST^4 \qquad (2)$$

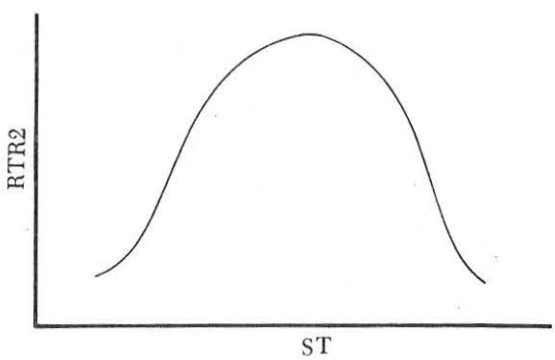

Figure 5

$$TR = a + b \cdot \exp(c \cdot RC{:}TC) \qquad (3)$$

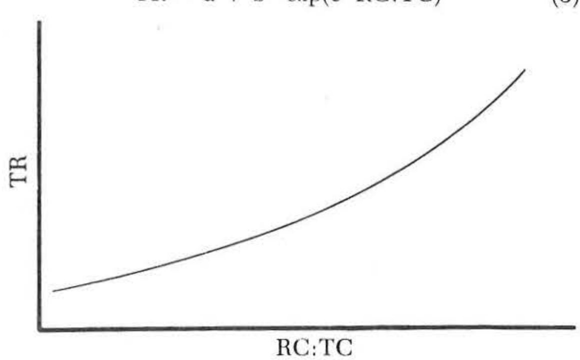

Figure 6

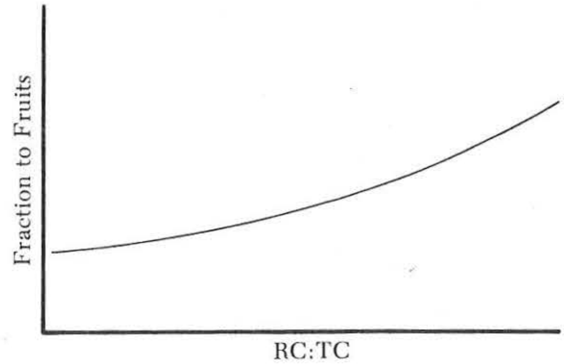

Figure 7

$$CR = a + b \cdot \exp(-c \cdot WP) \qquad (4)$$

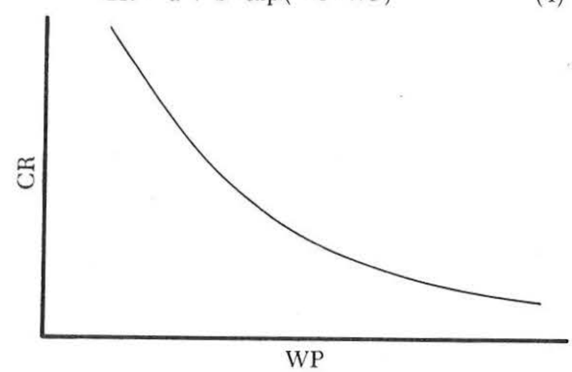

Figure 8

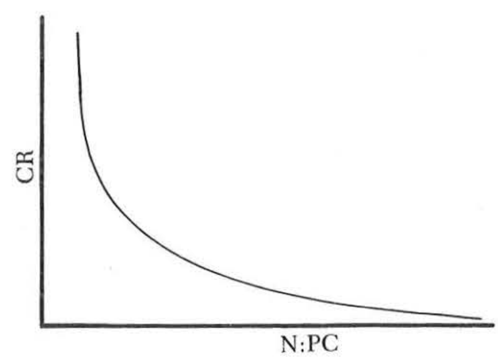

Figure 9

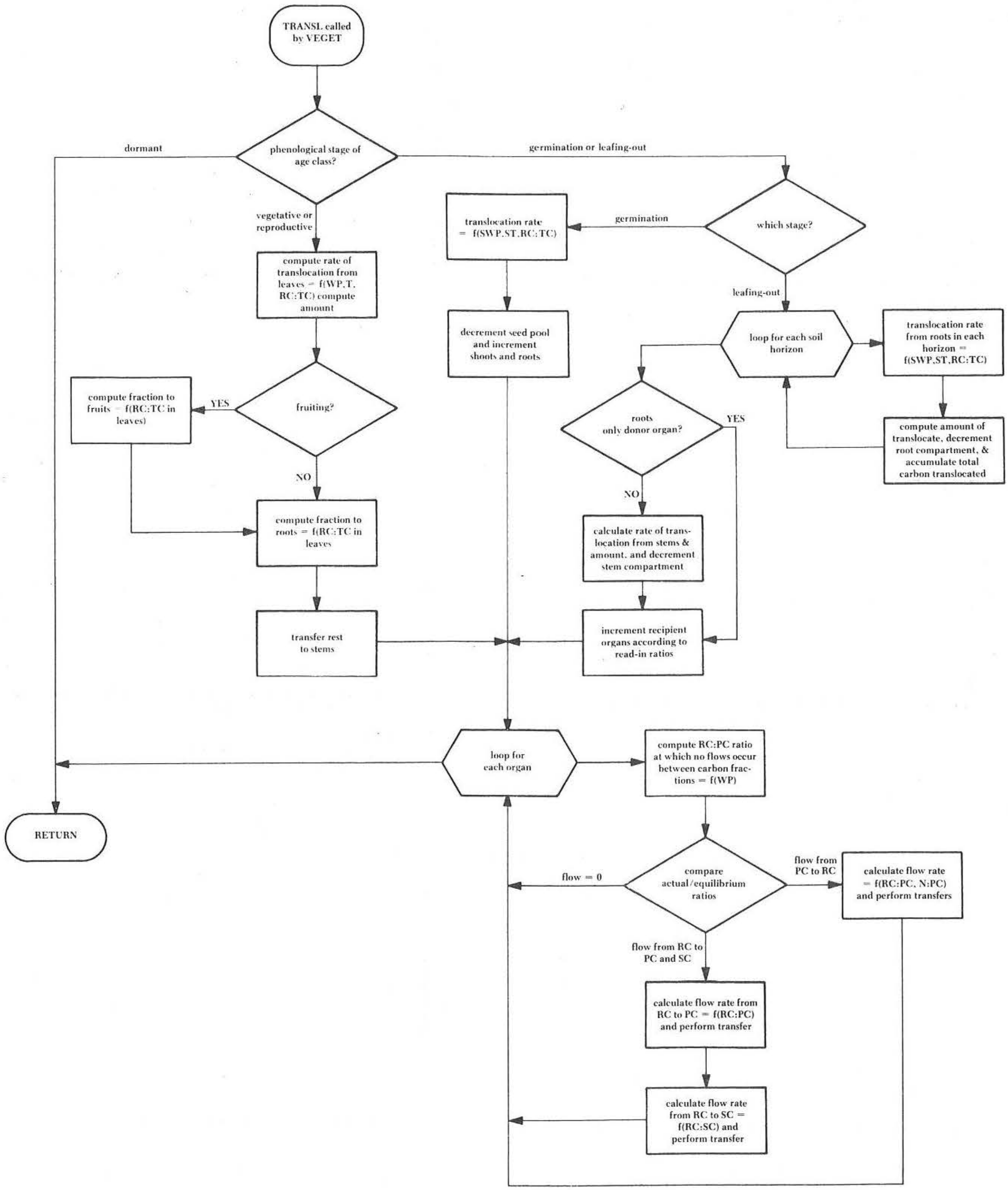

Figure 10. Flow chart of the translocation submodel.