

SIMULATION OF CLIMATIC AND  
MANAGEMENT EFFECTS ON WHEAT PRODUCTION<sup>1, 2</sup>

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Abstract.--The status of an explanatory, process oriented model for the simulation of growth, development, and yield of winter wheat is presented. The objectives of this model are discussed relative to empirical and explanatory modeling strategies. Future modeling and research needs are given.

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## INTRODUCTION

The purpose of this presentation is to discuss the current status of the Winter Wheat growth model. Model objectives and strategies are discussed first, followed by an outline of the Winter Wheat model in which emphasis is directed towards describing new additions or corrections to the model. In the final section of the paper, future directions in modeling strategies and experimentation will be addressed.

The Winter Wheat model was first described, in abstract form, in 1978 (Smika et al. 1978). More recently, a thorough documentation of Winter Wheat was published with flow charting, Fortran code and corresponding explanatory text (Baker et al. 1982). The conceptual development of Winter Wheat is along the lines of Gossym (Baker et al. In press), which simulates cotton growth and yield. Many of the processes have been adopted or changed to accommodate differences in growth and development between cotton and wheat plants. Adjustments were made according to information found in the literature and unpublished data, although in some cases, responses understood qualitatively have had to be quantified. Thus, while the model is currently running and simulating some reasonable output, it is still in its initial stages of development. We envision the modeling effort of Winter Wheat as an ongoing process whereby, through a systematic effort of formulating, testing and if necessary, re-formulating new hypotheses, a more successful model will evolve.

What constitutes success in a modeling effort is clearly dependent upon the objectives for the project. The objectives for Winter Wheat are "to identify and assemble in a plant growth model the factors determining winter wheat growth and yield in a format which will aid 1) system design (breeding and new cultural practices, and combinations thereof), 2) crop management decision making at the farm level, and 3) yield forecasting" (Baker et al. 1982).

It is a fair question to ask whether or not any one model can satisfy such a wide range of objectives. An explanatory, process oriented model would clearly be most appropriate for objective 1, although more empirical approaches may be taken with objective 2 and certainly with objective 3 where only yield information is required. The question is then whether or not an explanatory model would be appropriate for objectives 2 and 3 where only a small proportion of the information generated would be utilized. The answer, to a large extent, depends on the uniformity of the plant material and microclimate.

In simulating fairly simple systems with little change in the plant and climate boundaries, development of a corresponding simple empirical model may be the best approach to take since the data base may be relatively easy to acquire. Statistical or empirical models with adequate data bases generally perform better than more complex models (Norman 1982).

The appropriate model for a more complicated system is perhaps more difficult to determine. In the case of empirical approaches, data bases for constructing model algorithms may become prohibitively large in more complex systems because the potential plant response surface may increase dramatically. There is, thus, an impetus to develop a more explanatory,

process oriented model for complicated systems because the plant response surface may be generated internally by the model instead of having to sample it. The dynamic interaction of various plant and soil processes simulated in the model at lower levels of organization actually define the potential plant response at higher levels. Much of the information for this kind of explanatory model is already in the literature (Norman 1982). There are, however, problems with this approach. The first is that many plant processes are well understood only in terms of one, two or several independent variables, and often the interactions of these variables and of the plant processes themselves are not known, or understood poorly at best. When these processes are simulated and allowed to interact dynamically in a modeling exercise, the modeler is in reality extrapolating well beyond the limits of experimentation. This kind of guesswork can lead to serious errors (Gold 1977). Secondly, as more information is obtained about the physiological responses of plants to their environment, it is becoming increasingly clear that some of the basic physiological responses of plants may vary considerably from one cultivar to another. One such example is the ability to osmoregulate, which is cultivar specific in wheat (Morgan 1977). Thus, process level models may also require rather large data bases depending upon what processes are simulated.

Another potential source of error that both empirical and more explanatory models are subject to are the simplistic assumptions implicit in the various model algorithms. Such assumptions are not necessarily bad, but actually constitute the basis for model building. However, if these assumptions cause the model response to be insensitive to environmental and genetic variability, then obviously, the model will not perform as well in atypical situations although model response may be satisfactory with "normal" conditions. An example is predicting plant growth from algorithms which estimate plant water loss and then converting that estimate to a quantity of dry matter (Hanks 1974; Russo and Seem 1980). This approach assumes a constant water use efficiency of the crop, although much experimental information would indicate that water use efficiency is not a constant (Levitt 1980; Rawson et al. 1977). Although empirical models are probably more prone to this kind of error because of the very nature of their construction, more explanatory models may also be affected because of the difficulty in estimating and understanding some of the more basic physiological plant responses required in such models. The amount of error introduced by simplifying assumptions depends to a large extent on the degree of extrapolation and interpolation from the experimental data sets, where functions or algorithms were developed, to the simulated system.

In summary, there is probably no clear cut answer to the question concerning what complexity level would be most appropriate for developing a model intended for crop management decision making and yield forecasting because the system is still poorly understood. An explanatory, physical/physiological process model of intermediate complexity (Norman 1982) depicting wheat growth and development is being developed to meet the first objective of gaining a better understanding of wheat growth and development for the purpose of altering the system to benefit man. This kind of model may or may not be most appropriate for achieving objectives 2 and 3 concerning management decision making and yield forecasting. At the very

least, an explanatory model will provide direction and indicate the limitations of more empirical models. Because of the process orientation of Winter Wheat, ultimate success will depend not only on yield prediction capabilities under a wide variety of soil and climatic conditions, but also on its ability to simulate dynamic plant and soil processes. Testing and sensitivity analysis of the model is currently underway at Fort Collins.

This presentation summarizes much of the information in the publication just released by Baker et al. (1982). However, some important changes are being incorporated in the model as a result of early testing and evaluation. These changes will be clearly identified and discussed along with reasons for them. Proportionately less emphasis will be directed towards describing portions of the model which are already well documented (Baker et al. 1982; Whisler et al. 1981), although a general discussion will be given to insure continuity.

### THE WINTER WHEAT MODEL

A general outline of the model is given in Figure 1. This figure is a simplified flow chart of the MAIN program of Winter Wheat. Discussion of the model will be along the lines of this outline.

Daily climatic information, consisting of radiant flux density (R), minimum and maximum ambient air temperatures, precipitation, form of precipitation (natural versus irrigation), relative humidity, and calendar day are read by the MAIN program and passed into CLYMAT. Photoperiod is calculated as a function of latitude and calendar day. The average daytime and nighttime air temperatures are calculated as functions of maximum and minimum air temperatures. This information is then used with photoperiod in calculating a daily average ambient temperature. Percentage canopy interception of R ( $R_{int}$ ) is also calculated in CLYMAT as a product of a ground cover term, the maximum effective leaf length divided by row width, and a Beer-Lambert type light attenuation term based on leaf area index (LAI). The extinction coefficient, 0.4, was taken from Monteith (1965). Soil profile temperatures at 5-, 10-, 20- and 41-cm depths are calculated by the subroutine TMPSOL from regression equations of McWhorter and Brooks (1965). These equations express soil temperature as linear functions of the running average air temperature for the preceding 7 days.

The microclimatological data set generated by CLYMAT from input weather data is passed to several subroutines which require the information as driving variables. For instance, air and soil temperatures are used to calculate rates and durations of potential daily organ growth increments in the GROWTH, RUTGRO and MORPH subroutines. Plant respiration is calculated as a function of temperature in PNET.  $R_{int}$  is utilized in PNET for estimating daily canopy photosynthesis. Precipitation is added and distributed in the soil profile in GRAFLO. The relative humidity information is utilized in WATERUP for modeling plant water relations and transpiration.

The subroutine SOIL and its sub-programs were adopted from Rhizos (Whisler et al. 1981), a model detailing soil and root processes in the rhizosphere. The empirical evapotranspiration subroutine (ET) (Baker et al. 1982) is being replaced by EVAP and WATERUP<sup>4</sup>, which will be discussed in some detail. ET was adopted from Ritchie (1972). Because Ritchie's model applied to row crops with unlimited soil water, an empirical transpiration reduction factor, developed from experiments conducted in Mississippi, had been incorporated in the model for use under limiting soil water conditions. It is doubtful that an empirical transpiration factor developed in a humid climate would perform adequately in the Great Plains. The inclusion of WATERUP in Winter Wheat strengthens the water relations portion of the model considerably over the previous version. In WATERUP, transpiration is assessed by an iterative procedure that converges an energy balance and a root resistance model. The physiological process structure of WATERUP would indicate better predictive capabilities under a wide range of environmental conditions compared to the previous version. Testing is currently underway to confirm if this concept is true.

In SOIL, processes are simulated within a 6 X 20 two dimensional matrix (Figure 2). In one dimension, the width of 6 soil columns are adjusted according to the planting row width. In the other dimension, 20 soil layers of 10 cm depth each span the potential root zone depth of 2 meters. A third dimension is fixed at 1 cm thickness and is assumed to be longitudinally representative of the crop row and inter-row areas. On the assumption that soil processes occur in a symmetrical pattern in row crops, simulation occurs only in columns 1-3. Mirror images of the results are then assigned to columns 4-6, thereby saving considerable computer time.

On the first day of simulation, FRTLIZ is call to incorporate N fertilizer and crop residue into the top two soil layers. FRTLIZ may be recalled on any future day in which N fertilizer is again applied. Ammonia and nitrate N are modeled separately. Ammonium ions are assumed to be absorbed on soil colloids and to be stationary. Nitrate ions, on the other hand, are assumed to be in solution and move by mass flow with the water.

GRAFLO, EVAP, UPTAKE, WATERUP and CAPFLO simulate various phases of soil-plant-water relations. In GRAFLO, water and nitrate are distributed vertically in the profile. Evaporation from the soil is executed by EVAP in two stages according to Ritchie (1972). In stage 1, evaporation is limited only by the energy supply to the surface. Hydraulic soil properties determine the slower evaporation of stage 2. The amount of water evaporated in EVAP is then imposed on UPTAKE.

UPTAKE functions to actuate and budget the water movement from the soil cells, through the plant and soil surface to the atmosphere, and to simulate N uptake by the plant. In the last version of Winter Wheat (Baker et al., 1982), N was moved into the plant passively via the transpiration stream. The results of the initial testing of Winter Wheat indicated a problem with modeling N uptake in this fashion. Throughout the simulation, average leaf N

<sup>4</sup>WATERUP was developed by W. J. Parton, Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, Colorado.

content dropped from an initialized value of 3% to less than 2% (Figure 3). Although some decline in plant N content occurs as the plant matures, mostly due to increasing proportions of structural material, the almost continual drop in leaf N from day one of simulation throughout the growing season is not characteristic of observed N dynamics. Furthermore, the importance of active mineral uptake in crop systems is well established (Russell 1977). With the assistance of Dr. Vernon Cole, an active, Michaelis-Menton type N uptake is being superimposed on the mass flow already in place. Estimates of the kinetic constants  $V_{max}$  and  $K_m$  are from Huffaker and Rains (1978). Mineralization and nitrification are simulated in NITRIF.

WATERUP, a modified version of the model suggested by Saugier et al. (1974), estimates plant water loss. A radiation balance model simulates the temperatures of dead and live leaves and transpiration water loss. The driving variables for the radiation balance model include: reference height air temperature and dewpoint, soil surface temperature, and short wave solar radiation absorbed by the dead and live leaves in the plant canopy.

A simplified version of the radiation balance equations for the dead and live leaves is shown by the following equations:

$$R_N^D = \frac{C_p}{r_b} L_D (T_D - T_R) \quad (1)$$

$$R_N^L = \frac{C_p L_G}{(r_b + r_c)} (e_S - e_R) \quad (2)$$

$$+ \frac{C_p L_G}{r_b} (T_L - T_R)$$

Where  $R^D$  and  $R^L$  are net all-wave radiation for the dead and live leaves,  $P$  = density of the air,  $r_b$  = the boundary layer resistance,  $r_c$  is the stomatal resistance,  $\gamma$  is the psychrometric constant,  $L_D$  and  $L_G$  are the leaf area of dead and live leaves,  $T_D$  and  $T_L$  are the dead and live leaf temperatures,  $T_R$  is the reference height temperature,  $C_p$  is the specific heat of air at constant pressure,  $e_S$  is the saturation vapor pressure over the live leaf, and  $e_R$  is actual vapor pressure at the reference height.  $e_R$  is calculated from the reference height dewpoint temperature. Since live leaf temperature is unknown at this point,  $e_S$  is also unknown, yielding two equations with three unknowns ( $T_D$ ,  $T_L$  and  $e_S$ ). This problem is dealt with using Myrup's (1969) equation which describes saturation vapor pressure as a quadratic function of air temperature. This equation permits us to express  $e_S$  in terms of  $T_L$ , reducing the number of unknowns to two.  $R^D$  and  $R^L$  are calculated as a function of the absorbed short wave radiation and the long wave radiation to and from the sky, soil surface, and dead and live leaves.

The model of Saugier et al. (1974) uses the Stefan-Boltzman equation ( $P = \sigma T^4$ ) to predict long wave radiation fluxes. The use of this equation requires that leaf temperatures be found by iterative solution. Over the temperature range of interest to us (0-50°C), the radiation flux predicted by the Stefan-Boltzman equation can be well approximated by a linear equation.

Such an equation was developed by regressing the Stefan-Boltzman estimates against temperature ( $R = 0.44 + .0083T$ ,  $r^2 = .98$ ). Use of this equation permits a direct solution for live and dead leaf temperatures and yields a substantial savings in computation time.

The radiation balance model is connected to a root water uptake model (Belman et al. 1979). The model developed by Belman et al. (1979) calculates water uptake by layer as a direct function of the difference between the plant water potential and the soil water potential and as an inverse function of the soil and root resistance. Soil hydraulic resistance is modeled in CAPFLO, a subroutine of Rhizos (Whisler et al. 1981), and then passed into WATERUP. Root resistance is calculated in WATERUP from root length and age class estimates made in RUTGRO, another subroutine of Rhizos. The stomatal resistance term used in the radiation balance equation is a function of plant water potential. An iterative approach is used to estimate the plant water potential and corresponding stomatal resistance which results in a prediction of root water uptake that is equal to the transpiration water loss calculated by the radiation balance model. If the two initial estimates of water flux are at variance, a new estimate of plant potential is made. A second estimate of water flux is made by the root uptake model using the new plant water potential. A new stomatal resistance, corresponding to the new plant water potential is calculated and this term is used to produce a second estimate of leaf temperatures and water flux using the radiation balance model. The two estimates of water flux are compared and iteration continues if they disagree by more than 5%. When the solutions converge, estimates of transpiration water loss and leaf temperature are obtained which are consistent with each other and with both the soil water and radiant environments. As in EVAP, the potential water losses calculated in WATERUP are passed to UPTAKE.

Redistribution of water within the soil profile occurs in CAPFLO. Again, nitrate nitrogen moves with the soil water. Conductivity of the soil to water movement is also calculated in CAPFLO. These calculations require a fairly detailed description of the physical properties of the soil profile (see Whisler et al. 1981).

The synthesis of organic matter for growth and development is simulated in the subroutine PNET, which describes canopy gross photosynthesis. Daily gross photosynthesis is first estimated as a function of  $R_{int}$  from a data set collected by Baker (1982). Recall that  $R_{int}$  was estimated in CLYMAT. The maximum daily rate is adjusted if plant water or N are limiting. The effect of plant water stress on photosynthesis is realized by multiplying the maximum daily rate by a water stress reduction factor, which is a linear function of leaf water potential, taken from Figure 1 of Lawlor (1976). Similarly, a N reduction factor is used to adjust the maximum rate when average leaf N concentrations fall below 2%. The factor is arbitrarily calculated as the leaf N concentration divided by 2. The threshold value was 1% in the previous version of Winter Wheat. Although a good data base is not available for winter wheat on a canopy basis, there are considerable data in the literature showing strong correlations between leaf photosynthesis and leaf N content, with some of the information involving leaf N contents as high as 5% (Bolton and Brown 1980; Natr 1975; Osman 1977). Although it is difficult to extrapolate this information to the canopy level, a change in the threshold value from 1 to 2% seems justified at the present time. Further field experiments are being planned to more thoroughly investigate the effects of canopy plant N contents on photosynthesis.

Photosynthesis is currently modeled with no temperature effect. Given the information in the literature of photosynthetic response to temperature (Milthorpe and Moorby 1974; de Wit 1978), a temperature function needs to be developed. There are, however, considerable difficulties in extrapolating much of the temperature data to the canopy level. This topic will be discussed more thoroughly below.

After daily photosynthesis has been estimated, daily respiration by the plant is calculated and subtracted from photosynthesis to obtain daily net photosynthate production. Respiration is a function of temperature and biomass (Baker et al. 1982).

In GROWTH, photosynthate accumulated in a 24-hour period is distributed among the plant organs. Algorithms for above ground processes were developed mainly from Sofield et al. (1974) and Friend et al. (1962). The below ground growth is handled in RUTGRO, a subroutine from Rhizos.

A potential growth increment for above ground biomass is calculated for all plant organs. In the case of head parts other than the developing grain, the potential growth increments are constants which change with phenological stages of development. At the heading stage, grain growth becomes a function of daily average temperature. Stem growth potentials are also growth stage dependent constants. Potential growth of leaves is temperature dependent with maximum rates occurring at 20 C average daily temperature and no potential growth occurring below 0 or above 40 C. Leaf growth duration is a function of the average running temperature calculated for each leaf. All of the organ potential growth rates are adjusted by a water stress reduction factor calculated in RUTGRO.

Next, RUTGRO is called to calculate potential change in root weight. Potential root growth is calculated on a cell-by-cell basis, and is a function of age, daylength, layer temperature and water stress.

The potential root growth is summed for the whole soil profile and then added to the total above ground potential to obtain the total carbohydrate demand for plant growth. A plant carbohydrate pool is calculated by adding the daily total plant photosynthate production to any carbohydrate reserves. If the whole plant carbohydrate pool is greater than the whole plant demand, then all organs will receive a potential allocation of carbohydrate equal to their respective demands. Remaining carbohydrate goes into plant reserves. If the pool is less than whole plant demand, then potential allocation is to the heads until their demand is satisfied. The remainder is portioned equally (on a demand basis) among the other plant organs. Whether or not the various organs can utilize their potential carbohydrate allocations for growth depends on plant nitrogen status. Allocation of plant nitrogen to the various organs is processed in NITRO in a similar fashion as carbohydrate, with priority to heads. The reserve pool of N consists of daily root N uptake and plant N reserves which may be mobilized. Actual organ growth is then realized according to whether or not the nitrogen reserves are sufficient to meet the carbohydrate demands and C:N ratios of each organ. If nitrogen reserves are insufficient, then growth is reduced. If reserves are plentiful, then the potential allocation of carbohydrates are utilized for growth, with any excess plant nitrogen being allocated to reserves.



Maximum leaf weight is used to calculate maximum leaf length for estimating  $R_{int}$  (from CLYMAT). Finally, leaf area index is calculated by converting leaf dry weight to area.

MORPH is the last subroutine of major importance to be executed in Winter Wheat. In MORPH, the initiation and duration of various phenological and morphological events are simulated. A daily census is taken which keeps an account of all plant organs and their respective maturity status.

The initiation of tillering, head differentiation, jointing, booting, heading and anthesis for the main stem occur upon the accumulation of a specified number of degree days. The degree day accumulator has a lower limit of 0 C required for accumulation and no upper limit. The data base for these phenological events was obtained by Baker (1982). Differentiation of all the heads occurs once the main stem has accumulated the required degree days. Jointing of all stems is then spread out over a potential range of up to 15 days from the occurrence in the main stem. The spread of these jointing events is determined as an arbitrary function of plant water stress and carbohydrate and N supply demand ratios. From this point on, a range of tiller ages, with respect to morphological development, of up to 15 calendar days is possible. Booting, heading and anthesis are then modeled separately for each stem with the same degree day functions used for the main stem.

In addition to keeping track of all the plant organs, the daily census in MORPH also calculates running average temperatures which have occurred since the youngest organ in each organ class (leaves, tillers, secondary roots) was initiated. This information is then used in simulating the initiation of tillers, secondary roots, and leaves.

Briefly, tillering is modeled as a function of running average temperature, soil water potential, leaf N content, carbohydrate stress, and root/shoot ratio. The tillering period extends from its initiation to jointing. The running average temperature function was arbitrarily chosen (Baker 1982). When the plant has at least 4 primary tillers, decisions are made concerning tiller abortion. New tillers may be aborted if soil water potential is less than -1 bar in the root zone, if leaf N is less than 3 percent, or if carbohydrate demands are greater than supplies for that day. Tillers may also be aborted after spring green up if leaf water potentials are less than -20.0 bars or there are less than an average of four secondary roots per tiller.

Secondary root development is modeled as a function of running average temperature and a threshold soil water potential of -1.0 bar. Below that threshold, secondary root initiation does not occur. The period of secondary root development extends from tillering through booting.

Leaf initiation is modeled on each tiller as a function of running average temperature, with a minimum of 4 days between leaves. The maximum leaf number per tiller is nine.

Variation in grain number is realized partly through changes in potential spikelet number. Spikelet number may be reduced from a maximum of 22 as a result of shortages in carbohydrate or N. Grain number may also be affected by water stress for three days after the beginning of anthesis of each head. During this time period, up to 25% of the florets may be desiccated daily if the average leaf water potential falls below -15 bars. Floret number per head ranges from 10 to 60.

Finally, the time for grain filling is modeled separately for each head as a function of temperature. The maximum time period of grain filling is set at 50 days.

The time step for most processes is one day. The model runs from plant emergence in the fall to maturity the following summer. No simulation occurs during the winter when daily average temperatures fall below 0 C.

#### FUTURE RESEARCH NEEDS

The changes which are currently being incorporated into Winter Wheat are the first of many to come as a result of the testing, hypothesis re-evaluation, and substitution of better process models as they become available. Baker et al. (1982) have outlined a number of improvements which need to be made in Winter Wheat, some of which have already been mentioned. Other proposed changes include incorporating N, P and carbohydrate effects on canopy photosynthesis, temperature and nutrient effects on potential dry matter accretion rates in the various organ classes, temperature effects on morphological events, head differentiation, winter survival, and nutrient remobilization within the plant. Preliminary testing of the model indicates that improvements need to be made in modeling plant senescence, phenology and canopy gas exchange. While some of the information may be extracted from the literature, there are problems with fitting that information into the structure of Winter Wheat. This indicates a need for further research efforts. The nature of these problems is shown below in relation to two plant mechanisms (water stress and temperature effects on canopy gas exchange) which need to be evaluated for eventual inclusion in the model.

Relationships between leaf water potential ( $\psi_1$ ) and leaf apparent photosynthesis (AP) from two different experiments involving wheat are shown in Figure 4. Recall that the data of Lawlor (1976), indicated by the triangles and solid line, are currently used in Winter Wheat to adjust gross photosynthesis for water stress. Results from a previously unpublished experiment by J. A. Morgan were used in fitting the broken lines. Experimental procedures were essentially the same in both studies with one major exception. In Lawlor's study, plants were given only 24 hours to adjust to different root nutrient solution osmotic potentials before AP measurements were taken. The initial solution water potential before adjustment was probably greater than -0.5 bars. In contrast, Morgan gradually lowered the osmotic potential of the nutrient solution for a period of three weeks from -0.5 bars to approximately -18 bars, thereby lowering  $\psi_1$  to -27 bars. As a result, the wheat plants in Morgan's study maintained higher AP, particularly at lower values of  $\psi_1$ . The ability to maintain AP at low  $\psi_1$  was due, in large part, to the ability of the plant to osmoregulate. The more rapid

decline in AP with  $\psi_1$  in Lawlor's study was probably due to insufficient time for osmoregulatory adjustment to occur (Sionit et al. 1980). Consequently, there is a time element to take into account when relating AP to  $\psi_1$ . There is also evidence indicating that preliminary stress cycles may condition a plant to tolerate further stress cycles, although that conditioning may be lost if enough time has elapsed between drying cycles (Turner 1978). Because the mechanism and regulation of osmoregulatory conditioning are currently not well understood, a rather large data set may be required to properly map the response surface describing the effect of different rates of change in  $\psi_1$  on the response of AP to  $\psi_1$  and its components.

Another problem of modeling canopy water relations is the extrapolation of information and concepts from the organ level (the leaf in this case) to the canopy level of organization. The present assumption in the model is that the relationship between  $\psi_1$  and photosynthesis is essentially the same for leaves and canopies. The effects of water stress are observed visually first in the older leaves, progressing from the leaf tips to the collars in each leaf (Ludlow 1975). Whether or not the progression of these events can accurately be described by a canopy model constructed from information at the organ level remains to be seen. Clearly, further experimentation in which plant water relations are examined at the two organizational levels is needed.

Another limitation of the current model is the absence of a temperature function of canopy photosynthesis. Both canopy and single leaf AP in wheat and other plants are temperature sensitive (Black 1973; Brown and Trlica 1977; Leach 1979; de Wit 1978). In the case of wheat and other C<sub>3</sub> plants, the optimum temperature for AP is in the range of 15 to 25 C (Black 1973; Leach 1979). This wide range is partly due to a conditioning effect of growth temperature on the optimum temperature for AP (Bjorkman 1975; Milthorpe and Moorby 1974). As in the previous example of water stress and its history of development, there is a need to collect a data base sufficient to describe temperature effects, including temperature history, on wheat photosynthesis. A complication in generating such a data set is that there is presently no adequate technique for separating CO<sub>2</sub> assimilation and respiration known to occur simultaneously in the light (Chollet and Ogren 1975). If temperature affects these two processes differently, as it apparently does (Chollet and Ogren 1975), then methods must be developed to measure or estimate the two fluxes to better understand their respective responses.

There are processes other than photosynthesis which will need further development in Winter Wheat, some of which were mentioned earlier. While much improvement will come from a continuing literature search, it is clear that further experimentation will be required to describe the system adequately within the framework of Winter Wheat. This is a necessary aspect of modeling a complex system. We believe that the advantages of understanding the system and the capability of predicting winter wheat yields justify the effort.

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# WINTER WHEAT

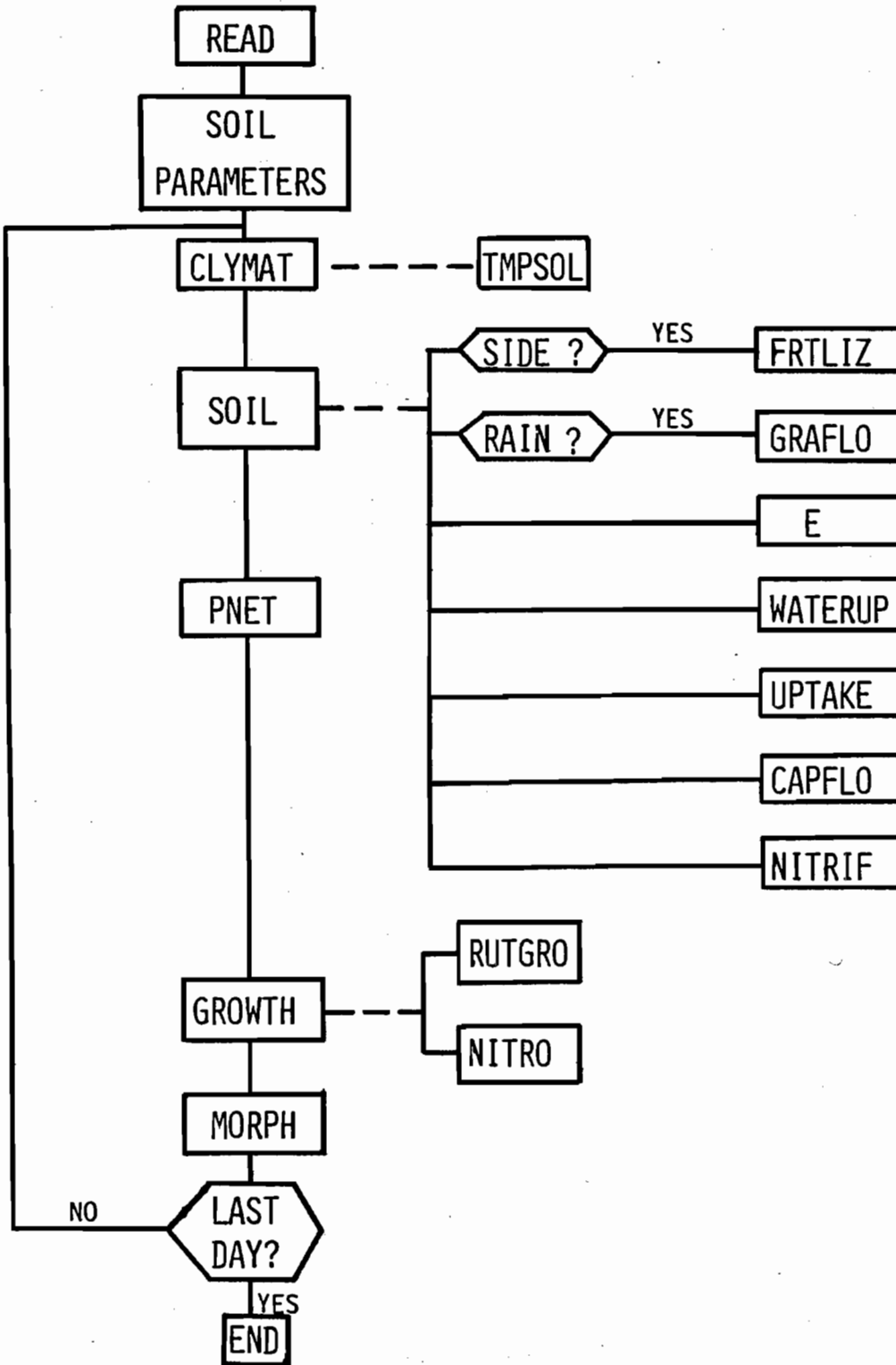


Figure 1. General outline of MAIN program of Winter Wheat.

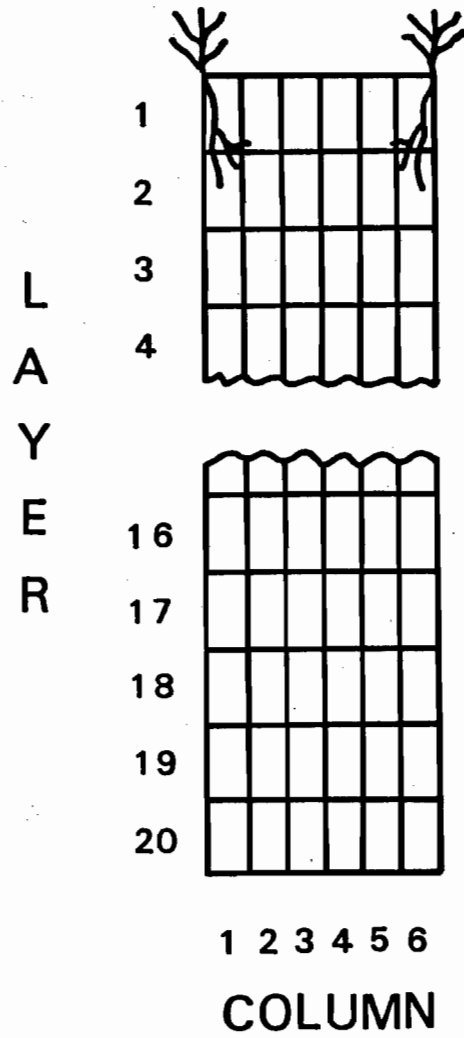


Figure 2. Two-dimensional matrix of SOIL subroutine of Winter Wheat.

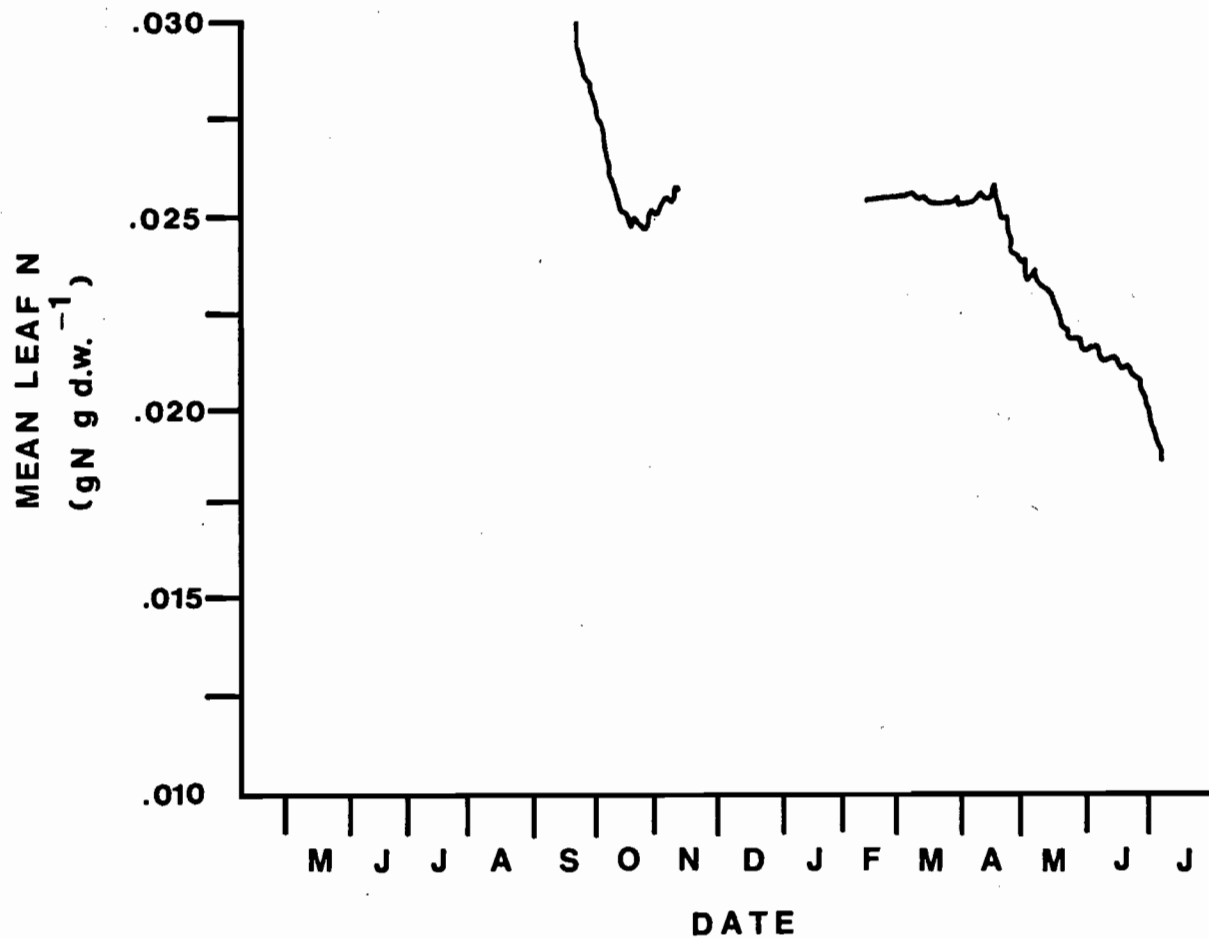


Figure 3. Simulated mean leaf N content of canopy leaves throughout growing season. No simulation occurs during winter months in which average daily temperatures are below 0°C.



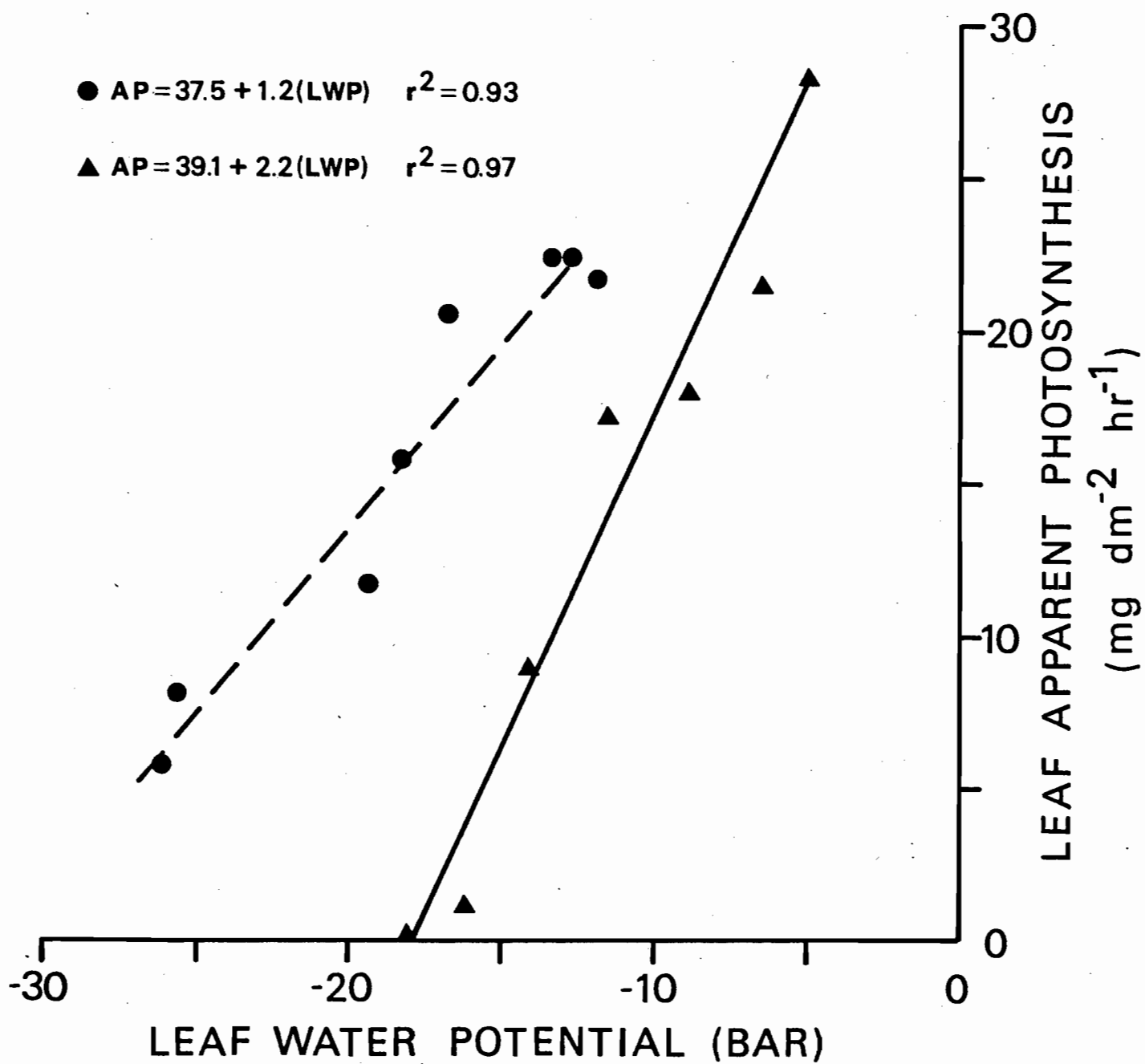


Figure 4. Leaf apparent photosynthesis of wheat as affected by leaf water potential. Linear regression was used to fit the data of Lawlor (1976, ▲—▲) and J. A. Morgan (unpublished data, ●—●).