Simulation of water use, nitrogen nutrition and growth of a spring wheat crop

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'I saw in a dream seven ears of corn, full and ripe growing on one stalk. Growing up after them were seven other ears, shrivelled, thin and blighted by the east wind'
'The seven good ears of corn are seven years, ... and the empty ears of corn blighted by the east wind will be seven years of famine'

Genesis 41: 22,23; 26,27

'Well to begin with and just among ourselves: in these fourteen years things were neither quite so definitely good nor so definitely bad as the prophecy would have them. It was fulfilled, no doubt about that. But fulfilled as life fulfils, imprecisely. For life and reality always assert a certain independence, sometimes on such a scale as to blur the prophecy out of all recognition. Of course, life is bound to the prophecy; but within these limits, it moves so freely that one almost has one's choice as to whether the prophecy has been fulfilled or not'
'In the long run it is quite impossible to narrate life as it flows, what would it lead to. Into the infinite. It would be beyond human powers. Whoever got such an idea fixed in his head would not only never finish, he would be suffocated at the outset. Entangled in a web of delusory exactitude, a madness of detail'

Thomas Mann, 'Joseph the Provider'
Chapter IV

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Preface

This book has its roots in a cooperative Dutch-Israeli research project entitled 'Actual and potential production of semi-arid grasslands' that was partly funded by the Dutch Directorate General for International Cooperation (DGIS). Cooperation between scientists from Israel and the Netherlands extended over a period of about fifteen years during which time many participated directly or indirectly in different aspects of the project. Some who played a more prominent role deserve special mention.

Prof.dr.ir. C.T. de Wit and the late prof.dr. N.H. Tadmor ('Kofish') initiated the project in the early seventies and the many discussions with them have influenced the approach adopted in this book. Much of the field work that was necessary to obtain the data needed for calibration and validation of the model was carried out with competence and infectious enthusiasm by R.W. Benjamin, BSc., who was assisted by Mr. M.Yanuka, MSc, and Mr. R.Yonathan. Mr. Z. Hochman, MSc, was actively involved in the development of the model during its early stages and Dr. E.D. Unger put order into a mass of meteorological and other data. Mrs. Hagit Baram willingly rendered invaluable assistance in computer services for storing, processing and retrieval of data. Mrs. R. Helder typed the earlier versions of the manuscript with never a complaint and Mrs. M.F. Wulff, without whom the book would not have been completed, finished what seemed to be an endless task. The figures were drafted by Mr. G.C.Beekhof and Mr. J.Engelsman.

To all, and to those of our colleagues whom we have not mentioned specifically, we extend our gratitude and sincere thanks.

H. van Keulen
N.G. Seligman

1 Introduction

Wheat *(Triticum aestivum L.)* is the world's major food crop, cultivated in all regions of the world, with the exception of the lowland humid tropics. Its origin is traced back to western Asia, where a large number of wild and partially cultivated species can still be found (Zohary et al., 1969; Harlan & Zohary, 1966; Zeven & de Wet, 1982, p. 93). The success of wheat as a worldwide staple food under a wide range of environmental conditions may be partially due to *Aegilops squarrosa* being among its progenitors, a species that was originally distributed over a wide range of environmental conditions.

The importance of wheat as a food crop has stimulated much research on the crop and practically from the beginning of organized agricultural research (Roberts, 1847), papers on yield potential and management of the crop have appeared. Despite all these efforts, world-wide average wheat grain yields are only 2 t ha^{-1}, although in the temperate zone particularly, spectacular increases in average yields have been achieved especially in the last decades (Stanhill, 1976; de Wit & van Heemst, 1976). The generally low yields in the tropical and subtropical regions are partially due to unfavourable environmental conditions, and partially to the rather low level of inputs, especially of fertilizers, crop protection measures and improved cultivars. Over the last century, field experimentation has been used widely to determine the constraining factors in different situations and to estimate the scope for improvement in various regions. In recent years, the development of explanatory simulation models, promised to increase the opportunities for analysing production potentials and the appropriate technology to achieve them over a wide range of conditions (de Wit, 1970). However, after more than fifteen years of worldwide efforts in simulation of crop growth, it is still difficult to point to solid advances in crop physiology, genetics, crop management or development planning that can be traced back to the development or application of a dynamic simulation model.

This has led to considerable disenchantment with simulation modelling (Passioura, 1973), even to a call for a moratorium until more knowledge is available (Monteith, 1981a). Such a course of action would effectively end the attempts to 'put things together again' because, as a rule, research in plant physiology, agro-meteorology, soil physics, soil chemistry and soil microbiology is not primarily concerned with the interdisciplinary integration of the knowledge generated into a comprehensive dynamic framework. This is still the domain of the carefully thought out simulation model, which despite disappointments, is still a promising means for testing the current concepts about the physiology and growth processes of a crop. It provides a whole conceptual system with the many feedbacks that can and often does reproduce and explain many cryptic interactions between factors that occur so often in experimental research (de Wit et al., 1978). If the model fails because of faulty understanding of the processes involved at the chosen level of study, it provides at least a quantitative and structured evaluation of our ignorance.

For wheat, fairly recent reviews of its physiology highlight the fragmentary nature of most of the information (Fischer, 1982; Evans & Wardlaw, 1976; Austin & Jones, 1975; Evans et al., 1975). Often very thorough studies have been made of individual responses, like tiller number and nutrient level, grain yield and temperature etc. However so much ultimately depends on the context in which the process takes place that it is difficult to judge the significance of the information in explaining the behaviour of the plant or the crop as a whole over its entire development period and under fluctuating and variable environmental conditions. The relevant context includes both the precursor conditions and their effect on the crop, as well as the subsequent developments that eventually influence the final result.

The present model was constructed to provide a framework in which to evaluate some of the available information. An attempt was made to describe the component processes and morphogenesis of the wheat plant realistically, but as simply as possible so as to account for the carbon, nitrogen and water relations from seedling emergence to the ripening of the wheat grain. Such a mission leaves much room for judgment and arbitrary decisions as to what approach to adopt and what details to ignore (Thornley, 1976). The result represents a viewpoint as to how the wheat plant grows, but a consistent one integrated over a whole growth cycle. Fortunately, the implications of the integrated viewpoint can be tested against actual data, and the adequacy of the viewpoint to explain the performance of the crop can be determined quantitatively.

If the model can describe the growth of the wheat crop to an acceptable accuracy, then it can be used to test the sensitivity of the component parameters. This sort of output could be used to identify promising concepts for plant breeding, plant physiology and crop management research. Even though little evidence for the validity of such an assumption can be found, it is, even after more than ten years, still too early to judge. We believe that the present model provides some support for this assumption.

2 Wheat models – a comparative review

2.1 Crop simulation models in general

Crop simulation models are an insidious challenge to those who feel the need to integrate knowledge of plant and environmental functioning into a coherent whole. They appear to offer an approach to the scientific description of forbiddingly complex systems which, in the 'real world', provide a livelihood to both sophisticated farmers and illiterate peasants, even when buffeted about by the vagaries of agricultural fortune. For the farmer, the plant essentially takes care of itself after he has provided certain minimum time-tested measures that combat the hostility of the environment and enhance the natural ability of the plant to mature and provide an abundant yield. He is not particularly concerned about the detailed functions of the plant in its changing environment. That is the domain of the biologist, soil scientist and micrometeorologist. The domain of the agronomist is the set of control variables that influence growth and yield of the crop. The crop growth simulator hopes to build a bridge between these divisions by using the fragmentary scientific knowledge of crop function to derive crop response to both environmental and control variables. Under constant or predictable environmental conditions, the challenge is fairly tractable, but can easily become trivial because under such conditions, there is little a simulation model can add to the knowledge on which it is based. However, most crops are grown under variable and relatively unpredictable environmental conditions and any one of a large number of factors can influence one or a series of plant functions that determine the final harvested yield. Often a characteristic control factor predominates in a given environment: aridity, soil fertility, frost incidence, disease incidence, flooding and so on. Even these factors generally operate erratically and in unusual combinations. It is precisely in this type of situation that the versatility of a complex simulation model should prove its worth. Yet it would be presumptuous to claim that crop models have achieved creditable versatility beyond the conditions for which they have been tested. For such conditions, models have been shown to perform 'reasonably well' or 'satisfactorily', in the sense that they approximate crop performance often with commendable and even surprising, if not suspicious, accuracy. Sensitivity analysis can point to areas that deserve attention. But the gap between successful simulation and new, useful information on crop behaviour or crop management, is seldom bridged.

2.2 An approach to crop simulation modelling

At present, the crop simulation modeller could well limit any presumption to build a generally applicable crop model by defining a set of problems that appear to be valid and of some importance, as well as a set of control or management variables that can be manipulated so as to affect the set of problems. The objective of the simulation modeller would then be not only to simulate the system satisfactorily, but to show how the control variables can be manipulated to solve the set of problems better than current knowledge or practice would allow.

A secondary aspect, but probably no less important to successful crop simulation modelling in the long run, is the need to reduce unnecessary complexity, or built-in redundancy, in a model. It would seem self-evident that increased complexity can be justified only if the result is better overall performance in the problem solving sense suggested above. However, complex simulation models are seldom tested against simpler models to determine how much 'better' they are (Versteeg & van Keulen, 1985), possibly because they are sometimes significantly 'worse'! (Seligman, 1975). As a rule, complexity is added according to available information, inclination and intuition of the modeller. The justification is that reality is complex and that scientific explanation of biological function should be based as far as possible on the chemistry and physics of the plant and its environment. Whereas this approach is the essence of process models, especially where the process can be clearly defined in chemical and physical terms, it leads to a false realism in whole system crop simulation models because of the inevitably arbitrary mixture of sweeping empirical functions and detailed descriptions of selected processes that have been more generally studied. The wide boundaries of a crop model cannot easily be restricted as they are dictated by the fact that the whole life cycle of a population of organisms is the subject of study.

In order to avoid the Scylla of labyrinthine complexity as well as the Charybdis of sterile descriptive functions, it is necessary to define constraining or controlling processes that normally determine plant growth and yield. This involves conceptualization of underlying processes into empirical functions that are valid for a wide range of conditions. Sometimes it is possible to derive such empirical functions from detailed process models. This is the idea behind 'hierarchical modelling' (Van Keulen, 1976b), as well as behind the division of biological science into levels of organisation. But even such concentration of information can lead to very complex models if all processes are to be taken into account. In general, that would not be necessary if the model is designed to study the effects of selected control variables, as is usually the case. The danger is that under certain circumstances, possibly even in those under which the model is meant to function, the source of deviation between reality and the model predictions may be one or more of these functions that have been ignored or represented in insufficient detail. As that is a real danger, model results can be no more than an hypothesis to be tested in the laboratory or in the field. That is a modest but worthy objective because the hypothesis will at least have been tested theoretically before investment of considerable field and laboratory resources. A closer look at some wheat models can provide an idea of what has been achieved till now.

2.3 Wheat models

Wheat crop models range from rather sophisticated statistical yield predictors to fairly complex simulation models. The examples reviewed in this section do not include all existing wheat models, but they are representative of the range of approaches and the degree to which objectives were achieved.

2.3.1 Soil moisture estimates for predicting wheat yields (Baier and Robertson, 1968)

Crop yield predictions based on empirical correlations with various climatic variables have met with 'varying degrees of success' (Baier and Robertson, 1968). Relating yield to a soil moisture budget via a multiple regression model improves the yield estimate considerably. The soil moisture capacity in the maximum rooted depth is divided into six zones; the plant growth cycle is divided into five phenological development stages. The soil moisture budget (the 'versatile budget, VB' in the authors' terms) is based on daily precipitation and potential evaporation, adjusted for soil dryness and for the effect of varying atmospheric demand rates (as reflected in the PE values compared to the normal) on the transpiration ratio AE/PE. Soil moisture characteristics and consumptive water use by plants during the season are taken into account. The mean daily moisture budget is calculated for each zone and development stage separately, resulting in 24 soil moisture variables.

Data from several years and from eight stations in Canada, where Marquis (spring) wheat was grown, are used to compare the prediction efficiency of rainfall and temperature as compared to the VB model in a multiple regression model. Using the four most significant soil moisture variables, r^2 was 0.71, compared to 0.17 for the rainfall model and 0.48 and 0.58 for the maximum and minimum temperature models, respectively. Increasing the number of soil moisture variables that enter into the multiple regression from four to 16 gave $r^2 = 0.90$, but the additional variable coefficients were not significant. As with many multiple regression models, the variables chosen often hint at other variables that were not considered but appear to be important operative factors. In this study, the partial correlation coefficients for the soil moisture model are strongly positive up the heading and negative in the later development stage of the plant. Is high soil moisture per se reducing yield later in the growing season, or is it related to another factor like lower radiation or temperature that accompanies rainy weather during the reproductive stage? The authors mention further development in investigating soil moisture and minimum temperature interactions.

The VB model was used to predict yield components as a basis for predicting yields. For the same number of independent soil moisture variables, the prediction was poorer, $r^2 = 0.69$ for the yield component model versus 0.83 for the direct yield prediction model (Baier and Robertson, 1967). This is one example where greater detail, meant to improve realism, produced poorer results.

2.3.2 A study to determine the optimal rainfed land-use systems in a semi-arid region of Israel (Zaban, 1981)

This study describes a wheat model which is based on an approach similar to that used by Baier and Robertson (1968), but instead of using regression equations with the water balance as independent variables, it uses calculated monthly crop transpiration. The model uses a similar approach to the soil moisture budget. The soil is subdivided into layers (or 'zones') and the crop is represented by: 1) a root system which grows in dependence of soil moisture; and 2) a canopy cover which increases to 100%, also in dependence of soil moisture, in a manner similar to that of the root. Transpiration is a function of pan evaporation, canopy cover and the relative water content in the rooted soil depth. The relative water content is the soil moisture as a fraction of the water holding capacity in the root zone. Infiltration, runoff and deep drainage are calculated on a daily basis.

The multiple regression coefficients relating yield to monthly or total seasonal transpiration were calculated from measured wheat yields and monthly and total seasonal transpiration data calculated with the model for 42 fields in the northern Negev and southern coastal plain in Israel. The fit was fairly good for total seasonal transpiration ($r^2 = 0.62$) and very good for monthly transpiration from December through to May, ($r^2 = 0.92$). The model was then validated on data collected in the subsequent year from 120 fields in the same regions. The regression coefficients calculated in the previous years were not changed. The overall predictive accuracy was an impressive $r^2 = 0.89$. It was a little lower for continuous wheat ($r^2 = 0.87$), even lower for wheat following a fallow ($r^2 = 0.84$) and better for wheat following a summer crop ($r^2 = 0.91$).

The set of 120 fields was then used to recalculate the regression coefficients and to determine the predictive value of early season rainfall data. The new $r^2 = 0.92$ was the same as that based on the previous years coefficients, even though the coefficients themselves were quite different for the constant term and all the months from December through to May. Reducing the number of months that were included in the regression, reduced goodness of fit but retained considerable predictive value: based on months December to February, $r^2 = 0.79$ and on December only, $r^2 = 0.55$, December including November in all cases. These values can be compared with a best fit of $r^2 = 0.66$ between grain yield and monthly rainfall.

The lesson that can be learned from these relatively sophisticated simulation/regression models, is that they can be used rather effectively to predict yields when calibrated for a given region with given agrotechnical practices.

The regressions based on transpiration appear to be particularly effective even though there is little meaning that can be attached to the regression coefficients, as very different coefficients can give similarly good fits. This paradox is not unusual for multiple regression models with correlated independent variables, as is often the case with serial climatic factors. As explanatory, process or quasi-process models are often comparatively poor yield predictors, even though they depend on a considerably wider data base, they seem to illustrate another paradox: the greater the information input to simulation models the poorer their predictive value; or, the more you know the less you understand! It would seem that their strength is also the source of their weakness: a large number of explanatory functions, each with its own complement of noise, often adds up to a large deviation from reality. It would seem that large simulation models should have clearly conceptualized control variables that do not erode as more explanatory detail is added. The lack of a clear method to identify and define such variables, may well be a basic reason for the luke-warm results of many crop simulation models. Some of these are discussed in the following sections.

2.3.3 TAMW: A wheat growth and development simulation model (Maas and Arkin, 1980a; 1980b).

This model which deals mainly with winter wheat has no explicitly stated utilitarian aim, although it is implicit that yield prediction on a regional scale is an important objective. It is maintained that the 'main obstacle to success (in previous attempts at simulating the wheat crop) has been the lack of quantitative descriptions of vernalization and tillering' (Section 1.1, ibid.). This emphasis is particularly relevant to winter wheat and also prompted the choice of an individual plant as the unit to be modelled. Field yield is estimated by assuming a field of 'identical wheat plants, in a regularly configured stand' (Section 1.2, ibid.).

TAMW is made up of four sub-models, that cover:

- phenology
- tiller production and survival
- grain formation and filling
- soil-water balance.

Phenology is based on individual shoots and the total growth cycle is divided into four stages: emergence of main shoot or tiller; vegetative growth to floral initiation; reproductive growth from floral initiation to anthesis; grain filling phase from anthesis to maturity (soft-dough). Duration of emergence is determined by soil moisture status and temperature; that of the vegetative phase is dependent on photoperiod and vernalization. Vernalization, in turn is a function of average daily temperature. The duration of the reproductive phase is a function of photoperiod and average daily temperature; and that of the grain filling phase, of temperature only.

Tiller production and survival determine the number of heads that mature. Tillering is dependent on the rate of leaf production which is a function of temperature, competition and soil moisture conditions. The number of ears (per unit area) at heading is an empirical, cultivar-dependent function of number of shoots at jointing. The number of ears determines how many of the tillers formed will head and how many will senesce. Leaf area is a function of total number of leaves per shoot and determines the level of competition. Leaf area is influenced by snow cover and frost damage.

Grain formation and filling depends on the number of florets that have been formed during the reproductive phase, as a function of photoperiod and temperature. The fraction that fills is a constant (about 0.25) and can be slightly higher when heavy fertilizer applications are given. Extreme temperatures during grain development can significantly reduce grain set. Grain weight is dependent on duration and rate of grain filling, both temperature dependent.

Soil water balance is based on theoretical considerations developed by Ritchie (1972). It is a compartmentalized soil model (de Wit and van Keulen, 1972) with a root penetration function dependent on soil moisture status.

Data requirements include weather (daily maximum and minimum temperatures, rainfall, total daily solar radiation and snow depth). Cultivar-specific parameters are required for the phenology, leaf and tiller submodels. Soil moisture is initialized per compartment. The model explicitly avoids simulating photosynthesis, because it is maintained that light saturation for winter wheat occurs at relatively low radiation levels. As a consequence, growth is more closely related to temperature. In addition, partitioning of photosynthate presents considerable difficulties in crop models, and is therefore considered an obstacle to be avoided (p. 1.6-1.7, ibid.)

Model validation was conducted in ten fields situated in four states in the central USA. It is concluded that 'the model appears to simulate phenology and components of yield with a reasonable degree of accuracy' (Maas and Arkin, 1980b). The phenological performance of the model as the mean of ten fields was as follows:

Days from emergence to	Observed	Simulated
Floral initiation	191	207
Anthesis	241	240
Soft dough	263	269

The average absolute deviations were 13 days for floral initiation and 4 to

5 days for the other phases. Over the season there was some compensation between phases as the over-estimate for floral initiation was followed by an under-estimate for the period to anthesis.

Yield component estimates were variable. The relative differences, (calculated as the mean absolute difference between observed and simulated values as a fraction of the mean observed values), were 26% for ears/plant, 9% for fertile spikelets/ear, 18% for grains/ear and 16% for weight of grain. Whereas the simulated mean grain weight/plant was 91.7% of that of the observed grain weight, the relative difference was 30%, excluding one highly deviant plot that was fertilized differently. Excluding another highly deviant plot, reduces the mean relative difference to 19.5%. The respective standard deviations of the difference between observed and simulated as a fraction of the mean observed grain weight/plant were 24% and 13.4%.

2.3.4 *Wheat in a semi-arid environment: a field and simulation study of effects of water stress on yield (Hochman, 1982; 1978)*

This model is part of a study on potential primary production in a semi-arid mediterranean environment (van Keulen et al., 1983). It is based on a simulation model which calculates herbage growth in a situation where plant nutrients do not limit growth, by using the relative transpiration deficit (E/E_0) to scale down potential growth (van Keulen et al., 1981; van Keulen, 1975). Potential daily gross CO_2 assimilation is calculated as a function of leaf area, total daily radiation and latitude. The calculation is based on tables derived from a physiological process model (de Wit et al., 1978). In a later version these tables were replaced by an algorithm based on the same data and developed by Goudriaan and Van Laar (1978a).

Gross assimilation is converted into wheat dry matter after reduction for respiration, by allocation of assimilate to the root and shoot. The assimilate allocated to the shoot is partitioned between a reserve pool, leaf, stem and other non-leaf blade structures, and grain. Conversion of assimilate into tissue dry matter is dependent on the chemical composition of the various tissues (Penning de Vries, 1974). The allocation functions are dependent on the development stage of the plant which is scaled from 0 to 1 as the plant proceeds from emergence to maturity. Its derivative, the development rate is temperature dependent only and the main phenological stages that affect model function are: emergence, spike initiation (actually terminal spikelet initiation), anthesis and maturity. The scaled values are 0.08, 0.24, 0.55 and 1.00, respectively.

Initiation and development of organs are, as a rule, dependent mainly on assimilate flow per organ and on current development rate. Tillering rate, spikelet formation rate and grain set are, in addition, dependent on nitrogen concentration of the tissue.

Nitrogen uptake and redistribution in the plant as well as soil nitrogen transformations are modelled, but were not tested critically as the model was developed under conditions were nitrogen supply (as fertilizer) was ample. As the title indicates, the focus was on effects of moisture stress.

Hochman (1978) states that the model tests the hypothesis 'that water stress affects only those processes which are concurrent with stress and that effects of stress on yield can be quantitatively accounted for by the transpiration ratio' (p. 116, ibid.). After testing the model against field results, it is concluded that this hypothesis holds when stress is applied late in the growth cycle during grain filling, but not when it is applied during earlier stages. Recovery from stress during tillering resulted in a surge of new tiller growth causing a 'shift in carbohydrate allocation favouring vegetative growth over seed production' (p. 117, ibid.) Recovery from stress during flowering did not remove residual effects on mid-day leaf water potential nor on stomatal resistance which remained higher even after water supply became adequate again.

The study concludes that:
1) residual moisture stress effects cannot be ignored in a wheat model for conditions where such stress is encountered; and 2) that cultivars that do not tiller profusely after early stress, are likely to produce heavier grain yields under semi-arid conditions.

This study used a simulation model to analyse a field experiment. Deviations between the model and the observed results were used as indicators for inadequacies in the concepts, used to improve the model and, where the model performance was better than observed, as indications as to how different plant characteristics may lead to higher yields. From which it can be concluded that models do not necessarily have to simulate reality exactly in order to be useful. However, the usefulness of model 'falsification' will depend on the overall conceptual soundness of the model, a characteristic that may be impossible to measure but which can generally be recognized.

2.3.5 A simulation model of the wheat crop (Goutzamanis and Connor, 1977)

The aims of this model appear to be essentially the production of a model to be compared with results observed in the field, in order to improve the model. This modest objective is probably quite realistic in view of the presumption involved in defining more utilitarian objectives. The available publication however, provides no information on performance of the model and so it can be assessed only on structure and intention.

The model consists of five submodels that deal with the carbon, water, nitrogen, and phosphorus cycles and with the phenology. The carbon model uses approximations of gross (potential) photosynthesis based on irradiance, leaf area and leaf angle. Temperature, water, nitrogen and phosphorus stress all affect photosynthesis. Respiration is treated in some detail as is photosynthate allocation.

The nitrogen submodel includes detailed treatment of soil nitrogen transformations, uptake of nitrogen by the plant and nitrogen allocation in the plant. Phosphorus is treated in similar detail. The water submodel treats interception of rainfall, infiltration of throughfall, redistribution of soil water, plant water uptake, intra-plant allocation and evapotranspiration.

This model is comprehensive in the sense that it tries to cover many relevant aspects of the wheat crop. The representation of the processes is relatively rigorous scientifically and concentrates a large amount of information. Development of a model of this scope to the stage where its performance can be evaluated will involve a heavy investment in research resources.

2.3.6 Other models

Not all published wheat models have been treated in this section. A more thorough comparative study would have to include those by O'Leary et al. (1985), Stapper (1984), Morgan (1976) and Connor (1975).

2.4 The present model

2.4.1 Objectives

The immediate objectives of the present model are to provide a means for analysing the effects of soil moisture and nitrogen nutrition on the growth and grain yield of spring wheat. The interaction between these two central variables is particularly complex in semi-arid environments where interseasonal variation in precipitation amounts and distribution cause dramatic fluctuations in dry matter and grain yields (van Keulen, 1975; Benjamin et al., 1982). Nitrogen nutrition is problematic under these conditions because luxuriant vegetative growth may cause high moisture losses that eventually reduce grain yields (Amir et al., 1981; Syme, 1972). A validated wheat model in combination with suitable climatic and soil data could provide long term series of dry matter and grain yields for a given region as a function of different nitrogen and other agrotechnical regimes. In addition, it could be used to simulate the effect of different phenological and morphological plant characteristics on the performance of the crop and so provide a structured and quantified evaluation of cultivar performance. In droughty regions it could also be used to analyze long term climatic data to determine the probabilities of crop failure and the value of the canopy as pasture. These problems were encountered during a study on potential primary and secondary production in arid regions (van Keulen et al., 1982) and are common in many parts of the world where spring wheat is grown.

The present model is designed to account for effects of moisture and nitrogen availability on the growth and organ formation of wheat, growing on deep non-saline, more or less neutral soil that has no severe mineral deficiencies except for available mineral nitrogen. The study is restricted to spring wheat especially where it is grown during the winter and spring in regions with temperate winters. Vernalization problems are not considered; nor are problems of weeds, pests and diseases.

2.4.2 Approach, conceptualization and structure

This model, which is a development of the model discussed in Subsection 2.3.4 above, is based on the state variable approach. Its integration time step and consequently, its resolution is one day. Processes that can be defined only with finer resolution, must therefore be represented by approximate empirical functions. As a result, the model cannot handle specific plant responses that are governed by processes with relaxation times much smaller than one day. Thus, for instance, analysis of stomatal response to midday stress resulting from high evaporative demand is beyond the scope of this model.
The present model treats the following aspects of crop growth:

- soil moisture balance
- soil nitrogen balance
- dry matter accumulation
- phenological development
- assimilate allocation
- organ formation

The climatic data requirements of the model include daily rainfall, maximum and minimum air temperatures, total daily radiation, air humidity (dew-point temperatures at 08.00 h and 14.00 h) and wind run. Most functions are formulated to account for moisture and nitrogen stress at any point in the growth cycle. Data on wheat yields in the northern Negev, Israel, were used for calibration. Other data sets from Israel, Australia and Syria were used for validation.

Soil moisture balance

The soil is treated as a compartmentalized system of soil layers (de Wit & van Keulen, 1972) where for each compartment i:

$$W_i = f_{i-1} - f_i - t_i - e_i$$

where

W_i is daily change in soil moisture content
f_i is flow through the lower compartment boundary
t_i is contribution of compartment to canopy transpiration
e_i is contribution of compartment to soil surface evaporation

Precipitation is cascaded through the soil layers. Potential evaporation is calculated according to Penman (1956). Transpiration is dependent on live canopy cover, rooted depth and soil moisture status.

Soil nitrogen balance

A simplified model of soil nitrogen transformations was developed, based on the following state variables:
- stable organic nitrogen
- labile organic nitrogen
- mineral nitrogen
- nitrogen in the microbial biomass.

The detailed models of Beek and Frissel (1973) and especially van Veen (1977) served as important sources of information and data.

The labile organic nitrogen fraction represents the nitrogen in the fresh organic material added to the soil each year by decomposing roots and plant litter. Whereas the stable organic nitrogen in the humic fractions turns over at a potential rate of ca. 0.015 yr^{-1}, the labile fraction can decompose rapidly, depending on its chemical composition. The labile fraction includes the NH_4-N whereas the mineral fraction represents NO_3-N. This construction is made so as to simplify the flow functions and is based on the assumption that transformation of NH_4-N to NO_3-N is rapid in comparison to decomposition rates. This assumption limits the generality of the model as there are situations where the activity of the nitrifying bacteria is constrained by current environmental conditions (Krul et al., 1982).

The aeration of the soil is not modelled, on the assumption that under rainfed semi-arid conditions, aeration is a problem limited to specific sites. Consequently, denitrification is neglected. This is probably an oversimplification (Seligman et al., 1985; Feigenbaum et al., 1984). However, loss of ammonia by volatilization from the upper soil layer is accounted for because of the relatively high pH of most dryland soils in semi-arid regions.

The size of the microbial biomass is related to the availability of carbon and nitrogen which are necessary for maintenance and growth of the microorganisms. Maintenance respiration is an important factor in determining the growth and death rate of the microbial population, but as the reported values are highly variable (Clark, 1967), rough approximations are used.

The soil nitrogen section poses a difficult dilemma. Increasing its generality is highly desirable but involves a much larger number of parameters most of which are unavailable or very difficult to measure. Progress in this area is, among other factors, dependent on advances in quantitative soil microbiology, particularly with regard to the dynamics of the microbial biomass.

Dry matter accumulation

The growth of the crop canopy and its root system is based on the model developed by van Keulen (1975). It calculates potential gross CO_2 assimilation as a function of daily radiation, latitude and total green plant area from a given photosynthesis-light response curve of individual leaves, characterized by its initial light use efficiency and the diffusion limited maximum assimilation rate at high light intensities (Goudriaan & van Laar, 1978a). The effect of temperature on gross assimilation is taken into account by applying a reduction factor on the light saturated assimilation rate when daytime air temperatures are below 10 °C. In addition, soil moisture and the nitrogen status of the plant influence gross assimilation in a number of different ways. Nitrogen status affects the potential assimilation rate of individual leaves under saturating light conditions. Plant water status is not calculated explicitly, but the influence of soil moisture on daily gross photosynthesis is accounted for by assuming a proportional relation between the reduction in transpiration and in gross CO_2 assimilation.

Respiration is subdivided into two components: maintenance respiration is calculated as a fraction of plant dry weight, taking into account the effect of temperature and nitrogen content; growth respiration is expressed as the conversion efficiency from primary photosynthates into structural plant material again taking into account the composition of the material formed.

Phenological development

The process of development from germination to final maturity and senescence is described as temperature-dependent only. A small effect of nitrogen status on development rate is taken into account, operative till the end of floral initiation. Photoperiodic effects are ignored as most temperate semi-arid regions where spring wheat is grown are in the lower latitudes where unequivocal photoperiodic effects have not been recorded (Angus et al., 1981). The life cycle of the plant is divided into two major development phases, – till anthesis and after anthesis. Germination is treated simply as a function of time and soil moisture. The main phenological stages that mark changes in allocation of assimilates and in organ development are: emergence, floral initiation, terminal spikelet formation, stem elongation, anthesis, grain set, grain dehydration and dead ripeness.

Cultivar differences in earliness would be expressed as a function of the number of day degrees needed to reach anthesis. The number of day degrees from anthesis to maturity appears to be relatively constant between cultivars (Vos, 1981) but can also be varied in the model.

Assimilate allocation

Current assimilates are allocated to a reserve pool, shoots and roots. Reserve and shoot assimilate is allocated to leaf, non-leaf material and grain. Allocations change with development stage and are controlled by empirical functions derived from literature. Allocation is affected by moisture stress (transpiration deficit in the present model) and by the nitrogen status of the plant expressed by leaf nitrogen content.

The empirical functions that control allocation represent changing sink strengths, modified by moisture and nitrogen stresses. They can be regarded as a genetically controlled, consecutive series of active metabolic sites. Cultivar differences (e.g. long straw vs. short straw) could be defined as different values for the allocation functions.

Organ formation

The number of grains depends on the number of antecedent organs, florets, spikelets, spikes and tillers. The number of organs formed at one stage, generally sets a limit to the number of organs that can be formed at a subsequent stage. In the present model the rate of organ initiation at any stage depends on the rate of carbohydrate flow to the meristematic sites and the minimum requirement of carbohydrate flow needed to produce a viable organ. The minimum carbohydrate requirement for organ initiation is derived from experimental data but is difficult to determine unequivocably. Temperature influences the number of organs formed indirectly by determining the duration of the phenological phase and directly by its influence on the formation rate. Nitrogen availability affects organ number indirectly by its effect on development rate as well as on leaf area expansion and photosynthesis which determine the rate of carbohydrate flow. The effect of moisture stress on organ formation is indirect also through its effect on gross assimilation.

In the following chapters the concepts introduced here will be developed in greater detail. It will be necessary to add a number of subsidiary functions, some of which are based on well-established experimental data, while others are still controversial. In this sense the present model is incomplete and can not be applied to all situations where spring wheat is grown. Nevertheless, it reflects much of what is known about the wheat crop today and can provide a base for further refinement and more detail in the future.

3 Plant growth processes

3.1 Germination

As this study is predominantly concerned with dryland conditions, moisture availability is regarded as the major factor determining the onset of germination. Germination is assumed to start if the soil moisture content in one of the top three compartments (upper 10 cm of the soil) is higher than 1.2 times wilting point. As long as this condition is satisfied, germination proceeds unhampered through its various phases (Bewley & Black, 1978), until at the end of seven days germination is assumed to be completed and emergence occurs. If the soil dries out to less than 1.2 times wilting point within 4 days after the onset of germination, the process is halted and will resume after rewetting from the point where it stopped. If drying out occurs four or more days after the onset of germination, deterioration of the germinating seeds takes place. If the dry conditions persist for more than six days, the seeds are assumed to die and there will be no crop unless it is resown.

This procedure works reasonably well but it may be preferable to replace the number of days involved in the various phases with temperature sums as has been done in the description of phenological development after emergence (Reinink et al., 1986).

3.2 Phenological development

The phenological development of a growing plant is characterized by the order and rate of appearance of vegetative and reproductive plant organs. The order of appearance of the organs varies between species but is virtually invariable within species. The timing and rate of organ appearance is dependent on environmental conditions and is consequently highly variable (van Dobben, 1962a). Prediction of phenology is of prime importance in a crop growth model of the type developed here, since the partitioning of assimilates between various organs of the plant is related to, and often governed by the phenological phase of the plant (van de Sande Bakhuysen, 1937). Detailed scales to describe the succession of phenological stages in cereals have been developed (cf. Nerson et al., 1980; Zadoks et al., 1974; Large, 1954; Feekes, 1941) but these have limited application in physiologically based crop growth models where detailed morphological aspects are ignored.

The major environmental factors influencing phenological development are temperature and day length (cf. Halloran & Pennell, 1982; Kontturi, 1975; Deputat, 1974; Riddell et al., 1958), whereas the level of irradiance is only of minor importance. Nuttonson (1955; 1953) has reviewed the literature on the relationship between temperature and phenology. His main source of information for the pioneering work done in the 18th and 19th century was a comprehensive review by Abbe (1905). Réaumur, in 1735, first used a temperature sum to characterize a phenological period. Since then, various approaches have been tried, including temperature sums above a base temperature (Mangon, 1897; Gasparin 1843-48; Adanson, 1750) and exponential functions of temperature (Price, 1909-10). Some have found a relationship between the logarithm of the length of a phenological phase and temperature (Mutsaers, 1976). The most commonly used approach is based on the temperature sum above a base temperature (usually between 0 and 4°C for C_3 plants) for the duration of a phenological phase (Robertson, 1984). The result is fairly reliable for a given variety and deviations from observed values have coefficients of variation around 4-9% (Nuttonson, 1955; 1953).

The development rate can be defined as the inverse of the duration of a development phase and has the dimension time^{-1}. As the duration is a function of temperature, the rate can then also be expressed as a function of temperature. For modelling purposes this concept has the advantage that the rate can then be directly integrated to yield a development stage related to ontogenetic phases in the life cycle of plants. This approach has been used successfully to describe the processes of germination (Wagenvoort & Bierhuizen, 1977; Bierhuizen & Wagenvoort, 1974; Feddes, 1971); leaf initiation and expansion (Gallagher, 1979), vegetative development (van Dobben, 1962a) and grain filling (Vos, 1981).

In the present model the pre-anthesis and the post-anthesis development phases are considered separately because there is evidence that the ratio between the temperature sums for both periods varies between cultivars. On the whole, differences in growth duration between cultivars are mainly due to differences in the length of the period from emergence to anthesis (Nuttonson, 1955; 1953). The post-anthesis period ends with grain maturity ('dead-ripe'). The intermediate stages are scaled between 0 and 1 for each phase separately. An overall development stage, s_o, can be defined as the mean of the pre-anthesis, s_v, and the post-anthesis, s_r, development phases,

$$s_o = (s_v + s_r)/2 \qquad (1)$$

so that s_o is also scaled between 0 and 1.

3.2.1 *Pre-anthesis development*

Relationship between development rate and temperature

In Figure 1 the results of various experiments carried out both in the field and under controlled conditions are summarized. In each case the inverse of duration in days between emergence and anthesis is plotted against the average growth temperature during that period. For experiments carried out under

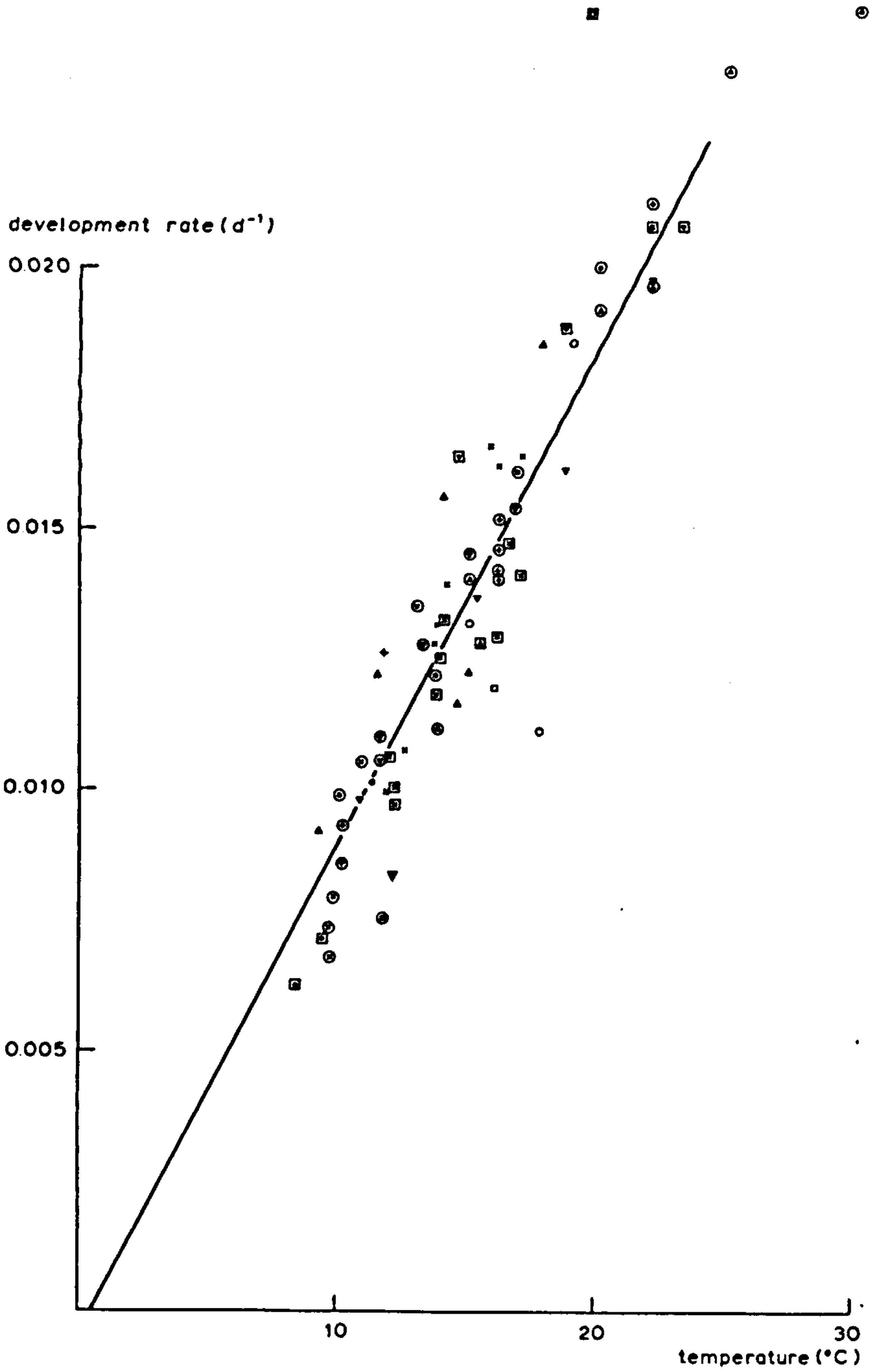

Figure 1. Relation between temperature and development rate of spring wheat in the pre-anthesis phase.
⊙ van Dobben, 1960; 1962b; ⓐ Friend et al., 1963; ▣ Aitken, 1966; ⊗ Fischer & Kohn, 1966a; o Thorne et al., 1968; ⧈ Rawson & Hofstra, 1969; ▲ Cackett & Wall, 1971; ⓥ Spiertz et al., 1971; ▽ Gale & Marshall, 1973; ⍓ Fischer, 1975; ⍔ Krenzer & Moss, 1975; ⊡ Connor, 1975; ▽ Spiertz, 1977; ⊠ Bagga & Rawson, 1977; ● Hochman, 1978; ▵ Bremner & Davidson, 1978; × Doyle & Fischer, 1979; ⧈ Campbell & Davidson, 1979a; + Winzeler, 1980; Ⓐ Whingwiri & Kemp, 1980; ▼ Campbell et al., 1983, ▫ Vos, pers. commun. (For details see Table 1).

controlled conditions where temperatures were maintained at a constant level, this procedure is straightforward. For field experiments, average temperatures were calculated for the relevant growth period in as much detail as was provided in the reports. Details on the various experiments used to construct Figure 1 are provided in Table 1. The data suggest that for the cultivars included, a linear relation exists ($r^2 = 0.84$), between the inverse of the growth duration ('development rate') and temperature. The regression line, which has a slope of 0.00094 T crosses the x-axis at a temperature of 0.49 °C indicating a base temperature of about 0 °C for pre-anthesis phenological development in spring wheat. Base temperatures commonly used for wheat range between 0 and 4 °C. (Angus et al., 1981; Nuttonson, 1953). Whether the residual variability is determined by cultivar characteristics or is only the result of experimental error cannot be concluded from the data. Small cultivar differences show up in some experiments, where the phenological development of different cultivars is compared under controlled conditions (cf. Halse & Weir, 1974 (is not included in Table 1); Spiertz et al., 1971; Rawson, 1970; Aitken, 1966). An example that clearly falls out of the range given in Figure 1 is presented by Rawson and Hofstra (1969), where cv. Sunset grown at a day/night temperature regime of 21/16 °C, which is an average of 17.7 °C (cf. Rawson, 1970) took 40 days to anthesis, equivalent to a temperature sum of 708 d°C, compared to a mean of 1090 d°C.

Phenological stages in the pre-anthesis phase

a. Tiller formation

Tillering begins soon after emergence and generally stops at the onset of stem elongation (Fischer, 1982; Evans et al., 1975). Although other control mechanisms may be involved, it appears that tiller initiation stops because of lack of assimilates due to the development of other, more powerful sinks. When at a later stage alternative sinks cannot cope with assimilate supply, tiller development can be resumed (Hochman, 1978). This situation is not covered by the present model.

b. Floral initiation

The heat sum required for floral initiation, T_{fi}, defined here as the first appearance of the double ridges, is the integrated effective temperature from seedling emergence till floral initiation. Some data are summarized in Table 2, showing a fairly wide variation in development stage for floral initiation. There is a tendency for development stage for floral initiation, s_{fi}, to be later as temperature, T, increases ($s_{fi} = .0065\ T + 0.113$, $r^2 = 0.48$). The calculated regression on the available data gives s_{fi} values between 0.18 and 0.24 for temperatures between 10 and 20 °C. In view, however, of the low r^2 and the small value of the slope, a constant value of 0.21 is used in the model.

Table 1. Development rate during the pre-anthesis phase for various spring wheat cultivars

Source	F/C$^{1)}$	Variety	Experiment$^{2)}$	T	1/D$^{3)}$	Details
Doyle and Fischer, 1979	F	Timgalen	1973-T1	12.5	0.01075	emergence estimated at two weeks after sowing
			1973-T2	14.1	0.01389	
			1973-T3	17.0	0.01640	
			1974-T1	11.8	0.00990	
			1974-T2	13.9	0.01316	
			1974-T3	16.1	0.01639	
			1975-T1	13.7	0.01282	
			1975-T2	15.8	0.01667	
Hochman, 1978	F	Lahish	–	11.3	0.01010	
Cackett & Wall, 1971	F	Tokwe	1969	14.6	0.01158	Salisbury
			1970	15.0	0.01226	
Winzeler, 1980	F	Famos/Kolibri	–	11.7	0.01258	
Spiertz, 1977	C	Orca	–	10.7	0.00971	phytotron temperatures weighted for day/night
Vos, 1981	C	Bastion/Adonis	–	16.0	0.01195	data averaged for Expts. II, III & IV
Thorne et al., 1968	C	Jufy I	HL/HL	18.75	0.01852	emergence estimated at 5 days after sowing
			CL/CL	15.0	0.01333	
			HS/HS	17.9	0.01225	
Winzeler, 1980	C	Famos	WKV I	16.1	0.01420	emergence estimated at thinning
		Kolibri		16.1	0.01458	
		Famos	WKV II	10.1	0.00847	
		Kolibri			0.00926	
		Famos		16.1	0.01408	
		Kolibri			0.01515	
		Famos		22.1	0.01961	
		Kolibri			0.02128	

Table 1. (continued)

Source	F/C$^{1)}$	Variety	Experiment$^{2)}$	T	1/D$^{3)}$	Details
Fisher & Kohn, 1966a	F	Heron	T62 1	9.8	0.00676	emergence estimated
			2	9.6	0.00735	at 10 days after sowing
			3	9.7	0.00787	
			5	10.4	0.01053	
Spiertz et al., 1971	F	Opal	D1	11.6	0.01099	+ personal communica-
			D2	13.0	0.01351	tion ten Hag
			D3	16.9	0.01338	
		Orca	D1	11.6	0.01053	
			D2	13.2	0.01282	
			D3	17.0	0.01449	
van Dobben, 1960	C	Peko	–	20.0	0.02000	
van Dobben, 1963	C		–	13.7	0.01320	
Whingwiri & Kemp, 1980	F	Gamenya	–	13.6	0.01176	emergence estimated at 10 days after sowing
Aitken, 1966	F	Insignia	S1	16.7	0.01603	emergence estimated
			S3	11.7	0.00757	at 10 days after sowing
Friend et al., 1963	C	Marquis		10.0	0.00990	averaged over three
				15.0	0.01408	light intensities
				20.0	0.01923	
				25.0	0.02381	
				30.0	0.02500	
Bremner & Davidson, 1978	F	WW15/Timgalen	S1	9.2	0.00926	emergence estimated
				11.4	0.01220	at 10 days after sowing
				14.0	0.01563	
				17.8	0.01852	
Connor, 1975	F	Sherpa	1971	8.4	0.00625	
			1972	9.4	0.00714	

Table 1. (continued)

Source	F/C1)	Variety	Experiment2)	T	1/D3)	Details
Bagga & Rawson, 1977	C	Kalyansona		12.1	0.01000	
				13.9	0.01250	
				17.0	0.01408	
		Condor		12.2	0.00971	
				13.9	0.01176	
				16.1	0.01282	
		Janak		11.9	0.01064	
				14.0	0.01333	
				16.5	0.01470	
Campbell et al., 1983	C	Manitou		22.0	0.01960	emergence estimated at 5 days after sowing
				18.7	0.01613	
				15.3	0.01370	
Campbell & Davidson, 1979a;1979b		Manitou		22.0	0.02083	
				18.7	0.01887	
Gale & Marshall, 1973		Chinese spring		12.1	0.00833	

1) F is field experiment; C is controlled conditions
2) Designation of experiment
3) D is duration of the period from emergence to anthesis (d)

Table 2. The ratio of temperature sum between emergence and floral initiation to that between emergence and anthesis (T_f/T_{an})

Source	F/C	Variety	Experiment	T	T_f/T_{an}	Comments
Thorne et al., 1968	C	Jufy I	HL/HL	18.75	0.22	
			CL/CL	15.0	0.19	
Cackett & Wall, 1971	F	Tokwe	1969	15.1	0.15	
			1970	16.8	0.18	
Friend et al., 1963	C	Marquis		10	0.25	
				15	0.215	
				20	0.26	
				25	0.31	
				30	0.31	
Whingwiri & Kemp, 1980	F	Gamenya		14.2	0.22	
Aitken, 1966	F	Insignia	S1	16.7	0.25	
			S3	11.7	0.44	
Bagga & Rawson, 1977	C	Kalyansona		17.0	0.20	
		Condor		17.0	0.24	
		Janak		17.0	0.20	
Rawson & Bagga, 1979	C	Kalyansona		11.7	0.21	
				17.7	0.21	
				23.7	0.26	
		Condor		11.7	0.20	
				17.7	0.20	
				23.7	0.24	
		Janak		11.7	0.22	
				17.7	0.20	
				23.7	0.26	
Oosterhuis & Cartwright, 1983	C	Devuli		19.3	0.285	Long-day treatment only. Total duration till anthesis obtained from relation in Figure 2.

c. *Spikelet differentiation*

Almost concurrently with the development of the first double ridges, spikelet differentiation takes place (Friend et al., 1963; Bonnett, 1966). Since double ridges have to be present first, the development stage for the beginning of spikelet initiation, s_{si}, is assumed to be 0.24. Even though the period available for spikelet formation appears to be a major determinant of final yield in wheat (Thorne et al., 1968; Pinthus, 1967), very little work seems to have been done on the relation between environmental conditions and the timing of terminal spikelet formation. The few data that are available are presented in Table 3. Here, too, there is a tendency for the development stage for terminal spikelet formation, s_{ts}, to be later at higher temperatures. ($s_{ts} = 0.0084\ T + 0.342$, $r^2 = 0.60$). Within the range of 10-20 °C it occurs at development stage 0.43-0.51. Again, because of the small data base, a constant value of 0.47 is used in the model.

d. Stem elongation

The onset of stem elongation marks an important stage in the life cycle of the plant, since the developing stem constitutes a major sink for assimilates and so induces a substantial change in the growth pattern. Stem elongation starts shortly after floral initiation (Friend, 1966; Bunting & Drennan, 1965; Jensen, 1918). Stem weight data determined by Rawson & Hofstra (1969), as reported by Wardlaw (1975), show stem elongation to start around development stage 0.20, whereas extrapolation of the data by Puckridge and Donald

Table 3. The ratio of temperature sum between emergence and formation of terminal spikelet to that between emergence and anthesis (T_{ts}/T_{an})

Source	F/C	Variety	Experiment	T	T_{ts}/T_{an}	Details
Friend et al., 1963	C	Marquis	–	10	0.41	days to score 25, expressed as a fraction of days to anthesis
				15	0.48	
				20	0.48	
				25	0.64	
				30	0.54	
Whingwiri & Kemp, 1980	F	Gamenya	–	14.2	0.52	
Bagga & Rawson, 1977	C	Kalyansona	–	17.0	0.43	
		Condor		17.0	0.43	
		Janak		17.0	0.46	
Rawson & Bagga, 1977	C	Kalyansona		17.7	0.47	days to emergence estimated at 3, 5 and 7 days after sowing, respectively, for the three temperature regimes
				23.7	0.50	
		Janak		17.7	0.41	
				23.7	0.50	
		Condor		17.7	0.48	
				23.7	0.46	

(1967) indicate stem extension to start at about development stage 0.16. A value of 0.175 was chosen in order to be closer to the latter value which is more clearly based on dry matter distribution and accordingly more appropriate for the terms of the present model.

3.2.2 Post-anthesis development

Relationship between development rate and temperature

The duration of the post-anthesis phase is described in the same way as the pre-anthesis development phase (Subsection 3.2.1). The results of various experiments carried out both in the field and under controlled conditions are summarized in Figure 2. The relevant period is that between anthesis and maturity. The grain is regarded as mature ('dead ripe') when its moisture con-

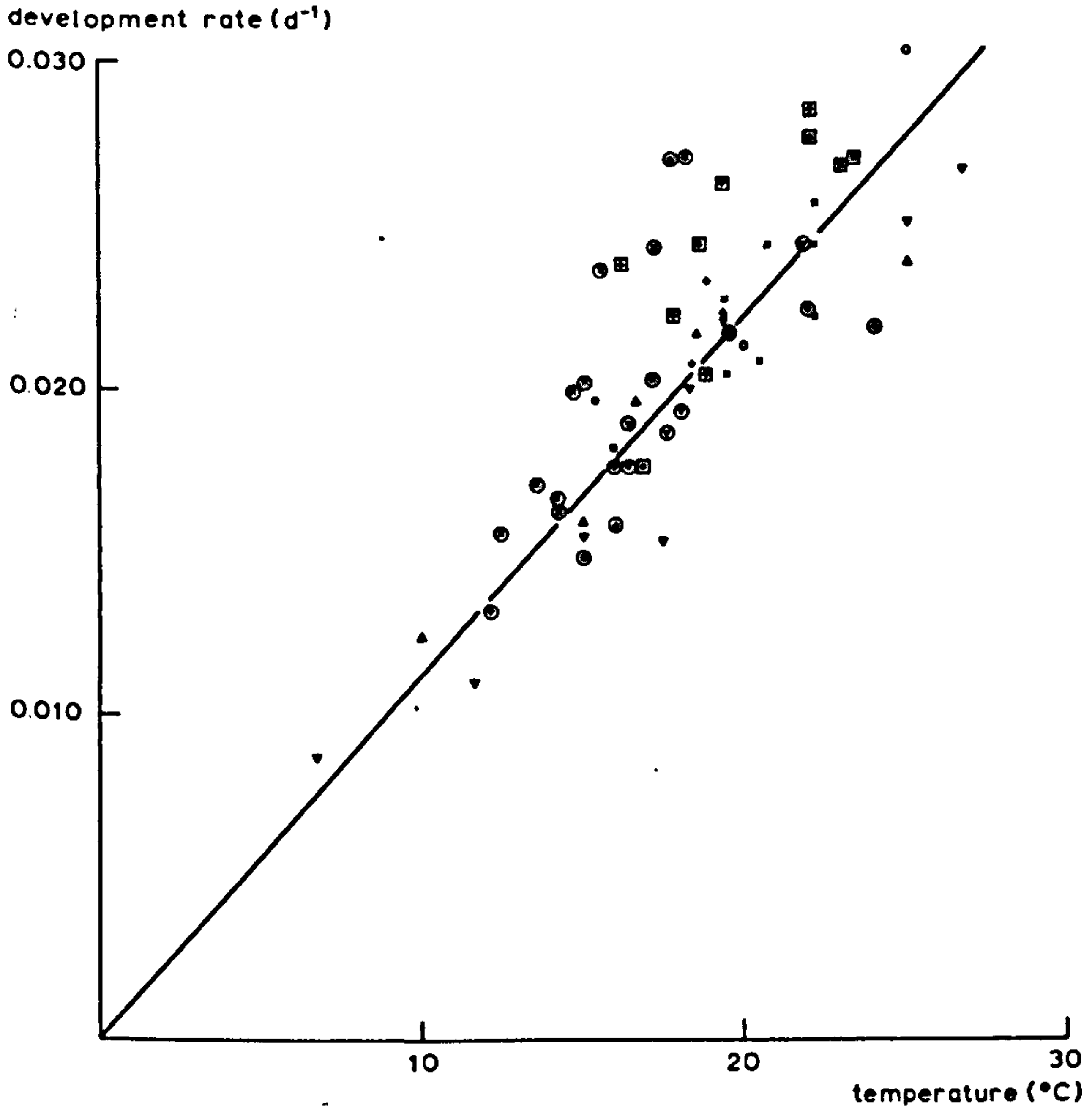

Figure 2. Relation between temperature and development rate of spring wheat in the post-anthesis phase.
⊙ Geslin & Jonard, 1948; ◉ Aitken, 1966; ▲ Cackett & Wall, 1971; ⊗ Marcellos & Single, 1972; ▿ Spiertz, 1974; ▵ Spiertz, 1977; ■ Sofield et al., 1977a (Spica); ▿ Sofield et al., 1977b (average 3 varieties); ⊞ Bremner & Davidson, 1978; · Hochman, 1978; ⊡ Radley, 1978; ▣ Campbell & Davidson, 1979a; × Doyle & Fischer, 1979; ⊕ Winzeler, 1980; ▲ Barlow et al., 1980; ⊞ Waters et al., 1980; + Winzeler, 1980; ▵ Vos, 1981 (Expt. II); ⊙ Vos, 1981 (Expt. III); ⊠ Sayed & Gadallah, 1983. (For details see Table 4).

Table 4. Development rate during the post-anthesis phase of various spring wheat cultivars

Source	F/C1)	Variety	Experiment2)	T	1/D3)	Details
Doyle & Fisher, 1979	F	Timgalen	1973-T1	19.5	0.02041	to reported 'maturity'
			1973-T2	20.5	0.02083	
			1973-T3	22.1	0.02439	
			1974-T1	19.6	0.02174	
			1974-T2	20.7	0.02439	
			1974-T3	22.1	0.02222	
			1975-T1	19.4	0.02273	
			1975-T2	22.2	0.02564	
Hochman, 1978	F	Lahish	–	15.4	0.01974	
Cacket & Wall, 1971	F	Tokwe	1969	16.6	0.01973	Salisbury
			1970	18.4	0.02075	
Winzeler, 1980	F	Famos/Kolibri	FV76	18.8	0.02326	
	C	Famos/Kolibri	WKV I	12.1	0.01156	maturity estimated
				16.1	0.01379	from last measured
				24.1	0.02198	point
Sofield et al., 1977a	C	Spica		16.0	0.01902	
	C	Triple Dirk/		6.7	0.00867	taken from Chowdury &
		WW15/		11.7	0.01089	Wardlaw, 1978
		Timgalen		17.7	0.01536	
				26.7	0.02669	
Vos, 1981	C	Bastion		15.0	0.01458	cessation of ear
				20.0	0.02124	respiration or
				25.0	0.03030	latest measurement
	C	Adonis		16.0	0.01568	used
				22.0	0.02236	

Table 4. (continued)

Source	F/C$^{1)}$	Variety	Experiment$^{2)}$	T	1/D$^{3)}$	Details
Spiertz, 1974	C	Orca		15.0	0.01537	graphs in Figure 2 extended to intersection with 90% dry matter point
				18.3	0.02008	
				21.7	0.02268	
				25.0	0.02500	
Spiertz, 1977	C	Orca		10.0	0.01235	
				15.0	0.01588	
				25.0	0.02381	
Marcellos & Single, 1972	F	Gabo		12.5	0.01552	data points in Figure 3
				13.6	0.01704	
				14.1	0.01659	
				14.7	0.01989	
				17.1	0.02571	
		Festiguay		14.2	0.01714	
				15.0	0.02022	
				15.5	0.02353	
Geslin & Jonard, 1948	F	Vilmorin-27*		18.0	0.01923	Figure 4
		Vilmorin-23*		16.3	0.01754	Figure 3.1
				16.4	0.01887	Figure 3.2
				17.6	0.01852	Figure 3.3
				16.0	0.01818	Figure 3.4
Radley, 1978	C	Kleiber		16.7	0.01754	Figure 2b
Bremner & Davidson, 1978	F	WW15/Timgalen	S1	17.8	0.02222	
			S2	16.2	0.02381	
			S3	18.9	0.02041	
			S4	19.3	0.02632	
Aitken, 1966	F	Insignia	sowing 1	16.8	0.02439	
			sowing 3	17.7	0.02703	

Table 4. (continued)

Source	F/C1)	Variety	Experiment2)	T	1/D3)	Details
		Holdfast	sowing 1	17.1	0.02083	
			sowing 2	17.1	0.02083	
			sowing 3	18.2	0.02703	
Sayed & Gadallah, 1983	F	Average 11 cultivars	1978/79	23.3	0.02695	
			1979/80	23.0	0.02667	
				18.7	0.2439	
Campbell & Davidson, 1979a	C	Manitou.		22.0	0.01778	
Barlow et al., 1980	C	SUN 9E		19.3	0.02222	

1) F is field experiment, C is controlled conditions

2) Designation of the experiment

3) D is duration from anthesis to 'dead ripe'

* winter wheat

tent is below 0.15 kg kg^{-1}. When this point is reached, the vegetative structures may be still green and apparently functioning, or they may be completely senesced. This is the source of some confusion in the determination of maturity, so that some interpretation was required when collating the data in Table 4. Details of the procedure are given in the table. The regression line through the data points in Figure 2 shows, that the duration of the post-anthesis phase in spring wheat is governed by temperature over a wide range of temperatures. Some data on winter wheat are included and those suggest that virtually the same relation holds for these cultivars too. The base temperature is close to 0 °C, just as in the pre-anthesis phase. The residual variation in development rate is a little smaller ($r^2 = 0.86$) than for the pre-anthesis phase ($r^2 = 0.84$) suggesting that the heat sum for grain filling among cultivars may be somewhat less variable than the heat sum required for the pre-anthesis phase. This tendency was observed by Pinthus & Sar-Shalom (1978) in experiments with cultivars of different growth duration in Israel. The same phenomenon was also observed in rice (van Keulen, 1976a).

Phenological stages in the post-anthesis phase

The genetically determined pattern of grain growth is modified by environmental conditions that determine the supply of assimilates and nutrients to the developing grain. As a rule, an initial exponential phase (the lag phase) is followed by a period of linear growth, that ceases rather abruptly (viz. Vos, 1981; Warrington et al., 1977; Sofield et al., 1977a; Geslin & Jonard, 1948). During the lag phase, grain set is determined. The length of that phase is related to the total duration of grain filling as shown in the reports cited. In Table 5, data on the duration of the lag phase are summarized, expressed in accumulated day degrees as a fraction of the total accumulated day degrees during the post-anthesis phase. Very often the data were difficult to interpret, since they had to be derived from rather small graphs. The correlation between the calculated fraction and temperature is very low ($r^2 = 0.063$) even when outrider values are removed ($r^2 = 0.176$). From this, it can be deduced that the lag phase is a fairly constant fraction (0.11) of the post-anthesis phase. In the model the small increase in grain dry weight during the lag phase is neglected and grain fill is calculated from the end of the lag phase, that is the beginning of the linear growth phase. The sudden cessation of dry matter accumulation in the grain is apparently a result of lipid deposition in the phloem strands that supply the grain (Sofield et al., 1977b; Zee & O'Brien, 1970a; 1970b). It is not clear what triggers this change but it generally occurs when grain dry matter content is approximately 0.65 kg kg^{-1} (Seligman et al., 1983; Spiertz, 1974; Geslin & Jonard, 1948; 1946). The abrupt end of linear growth in individual grains is not so apparent on a field basis, because differences among individual grains result in a more gradual approach to final grain yield. The end of the linear growth phase was estimated as the point of intersection between the extrapolation of the linear growth curve and final grain weight (Table 5). The accumu-

Table 5. The ratio of temperature sum between anthesis and the end of the lag phase to that between anthesis and maturity (T_l/T_m)

Source	Variety	T	T_l/T_m	Details
Sofield et al., 1977a	Timgalen	11.7	0.07	graphs of linear growth extended till intersection with ordinate (Figure 2)
		17.7	0.08	
		26.7	0.08	
	WW15	11.7	0.09	
		17.7	0.08	
		26.7	0.11	
	Spica	16.0	0.07	(Figure 8)
Sofield et al., 1977b	Triple Dirk	17.7	0.09	(Figure 4)
Ellen & Spiertz, 1980	Donata*	16.5	0.06	(Figure 2)
Vos, 1981	Adonis	16	0.10	A16, (Figure 2)
		22	0.15	B22, (Figure 2)
		16	0.17	III, N2, (Figure 1)
Dalling et al., 1976	Argentine IX Insignia	±25	0.085	(Figure 1)
Walpole & Morgan, 1970	Maris Widgeon*	–	0.14	(Figure 1) no temperatures given thus inferred from number of days
Barlow et al., 1980	SUN 9E	–	0.09	(Figure 2)
Warrington et al., 1977	Gamenya	15	0.10	(Figure 1, averaged) combined with Table 3.
		20	0.12	
		25	0.13	
Evans & Rawson, 1970	Sonora	21	0.13	(Figure 4)
Geslin & Jonard, 1948	Vilmorin-27*	18.0	0.17	(Figure 4)
Radley, 1978	Kleiber	16.7	0.06	(Figure 2b)

* winter wheat

lated day degrees between anthesis and the end of linear growth are expressed as a fraction of the total accumulated day degrees for the post-anthesis phase. The results are given in Table 6. In this table there are two extreme values (0.57 and 0.84), which appear to be due to special circumstances. There is almost no correlation between the calculated fraction and temperature ($r^2 = 0.104$ for all data; $r^2 = 0.14$ without the outriders). The development stage for the end of the linear growth period is thus taken as a constant. The mean value for 20 °C is 0.717, and the mean SD for the data (excluding the outriders) is ± 0.026. The end of linear growth appears to be more closely related to de-

Table 6. The ratio of temperature sum between anthesis and the end of the linear grain growth phase to that between anthesis and maturity (T_{el}/T_m)

Source	Variety	T	T_{el}/T_m	Details
Sofield et al., 1977a	Timgalen	11.7	0.71	Figure 1
		17.7	0.68	
		26.7	0.57	
	WW15	11.7	0.68	id. estimated from point, where linear growth ceased.
		17.7	0.69	
		26.7	0.70	
Sofield et al., 1977b	Triple Dirk	17.7	0.69	Figure 4
Spiertz & Ellen, 1978	Donata*	16.5	0.74	field experiment, temperatures monthly means, cessation assumed at 2/8; Figure 2
Vos, 1981	Adonis	16	0.75	A16 cessation estimated from intersect of linear growth rate with final grain weight
		22	0.77	
		16	0.73	III, N2, 16
Dalling et al., 1976	Argentine IX Insignia	±25	0.73	Figure 1
Walpole & Morgan, 1970	Maris Widgeon*	–	0.62	no temperatures recorded, inferred from number of days
Warrington et al., 1977	Gamenya	15	0.84	grain filling may not have ceased completely here
		20	0.73	
		25	0.71	
Evans & Rawson, 1970	Sonora	21	0.73	estimated from Figure 4
Geslin & Jonard, 1948	Vilmorin-27*	18.0	0.71	Figure 4
Radley, 1978	Kleiber	16.7	0.64	Figure 2b, maturity estimated by extending water content line till 15%
Barlow et al., 1980	SUN 9E	19.3	0.82	Figure 2

* winter wheat

velopment stage than to an independently determined grain size. Accordingly, the post-anthesis development stage for cessation of linear growth has been set at 0.72.

3.2.3 Effect of water and nitrogen deficiency on phenological development

Water deficiency in the plant results in stomatal closure and consequently a lower transpiration rate. With less evaporative cooling, the temperature of the canopy rises. Differences in canopy temperatures of up to 8 °C have been measured in the field between well-watered and water stressed plants (Blum et al., 1983). Similarly, nitrogen stress may cause stomatal closure at higher plant water potentials (Radin & Ackerson, 1981), or a reduction in water supply by increased root resistance (Radin & Boyer, 1982). As a result, transpiration is reduced (Shimshi & Kafkafi, 1978; Shimshi, 1970a; 1970b). In the field, differences of up to 4°C in canopy temperatures have been measured between fields optimally supplied with N and fields under nitrogen stress (Seligman et al., 1983). As phenological development is dependent on canopy temperature, an indirect effect of water and nitrogen shortage on phenological development can be expected. Such effects have been reported where a field grown crop of wheat, growing under N deficient conditions, reached maturity up to 5 days earlier than crops growing with adequate nitrogen (Seligman et al., 1983). This delay would have needed somewhat less than 1 °C temperature difference during the main growth period between booting and early grain fill. It has been observed, that drought-stricken crops also tend to speed up their phenological development (Turner, 1966). Severe stress can, of course, delay or stop development, although it is not clear at what point this can happen (Angus & Moncur, 1977).

In the present model, canopy temperatures are not simulated in detail. However, a function that relates the difference between canopy temperature and ambient temperature to the transpiration deficit has been included to allow for sensitivity tests of crop response to increased canopy temperatures following moisture stress. The effect of nitrogen status on the actual transpiration, t, is discussed in Subsection 3.3.2.

3.2.4 Conclusions

From the evidence presented in this section, it is apparent that a major part of the variability in phenological development of spring wheat can be explained in terms of heat sums. It seems advisable to separate the pre-anthesis and post-anthesis phases into independent units, because phenological differences among cultivars appear to be expressed differently in the pre-anthesis and in the post-anthesis phases. Whereas photoperiodic effects on spring wheat phenology have been reported (Angus et al., 1981; Wall & Cartwright, 1974; van Dobben 1962a), no clear effects were noted in the data analysed here, possibly because the photoperiod was limited to 8-16 hours in practically all experiments. Accordingly photoperiodic effects have been ignored in the present model.

In Table 7 the relevant phenological stages that have been distinguished in

Table 7. Phenological events and their associated development stages as used in the model

description	development stage in pre-anthesis phase (DVSV)	development stage in post-anthesis phase (DVSR)
seedling emergence	0.	0.
start of tillering	0.	0.
ear initiation	0.22	0.
spikelet differentiation	0.24	0.
start of stem extension	0.35	0.
end of tillering	0.50	0.
formation of terminal spikelet	0.52	0.
anthesis	1.00	0.
start of grain set	1.00	0.07
start of grain filling	1.00	0.11
end of effective grain fill	1.00	0.70
maturity	1.00	1.00

the model are summarized. A single value is given for each stage. Variations among individual plants and especially among different tillers cause variations within a plant population, but these are not simulated by the model.

3.3 Crop water relations

3.3.1 Potential transpiration

When stomata are open to allow entry of CO_2 into the plant, water diffuses out from the substomatal cavity, where water vapour pressure is saturated, into the generally drier air. Transpiration, or the rate of water loss from the plants depends on the energy available for vapourization, on the difference in vapour pressure between the plant (mainly leaf) and the surrounding air and on the resistance to water vapour diffusion from the stomatal cavity to the atmosphere. Potential transpiration is the water loss from a field crop that covers the soil completely and has an optimum supply of water from the soil. It can be calculated from environmental conditions and the reflectance of the canopy (Penman, 1956; 1948). Actual transpiration must also take into account the water supply from the soil and the leaf area of the canopy. When the leaf area of the crop does not cover the soil completely there is also water loss due to direct evaporation from the soil surface. These two terms of field water loss are treated separately in this model, evaporation being discussed in Section 4.1.

In this model, the procedure used to calculate transpiration is the same as that used in a model developed for natural vegetation (van Keulen, 1975). The energy flux for transpiration from the vegetation is obtained by the combination method (Goudriaan, 1977):

$$\lambda E = (sR + \delta_p)/(s + \gamma^*) \qquad (2)$$

where

E is potential transpiration rate of the vegetation (kg m^{-2} s^{-1})
λ is latent heat of vaporization (J kg^{-1})
s is slope of the saturated vapour pressure curve at leaf temperature (mbar °C^{-1})
R is absorbed radiant flux (J m^{-2} s^{-1})
δ_p is drying power of the atmosphere (J m^{-2} s^{-1} mbar °C^{-1})
γ^* is apparent psychrometric constant (mbar °C^{-1})

This formulation may be used at any moment both for an individual leaf or for a leaf layer in a canopy with appropriate values for the parameters. The drying power of the atmosphere is obtained from:

$$\delta_p = (e_s - e_a)\, \rho c_p / r_{bh} \qquad (3)$$

where

e_s is saturated vapour pressure at air temperature (mbar)
e_a is actual vapour pressure of the air (mbar)
ρc_p is volumetric heat capacity of the air (J m^{-3} °C^{-1})
r_{bh} is boundary layer resistance for heat exchange (s m^{-1})

The apparent psychrometric constant is:

$$\gamma^* = \gamma\, (r_{bv} + r_{lv})/r_{bh} \qquad (4)$$

where

γ is psychrometric constant (mbar °C^{-1})
r_{bv} is boundary layer resistance for water vapour exchange (s m^{-1})
r_{lv} is stomatal resistance for water vapour exchange (s m^{-1})

Daily potential transpiration is calculated from daily values of the above expressions, integrated both over time and over the entire transpiring leaf area. Daily absorbed radiation, R, is calculated from the measured total global radiation:

$$R = (\rho R_g - R_l)\,(1 - e^{-kq_a}) \qquad (5)$$

where

ρ is reflection coefficient of the vegetation for total radiation (dimensionless)
R_g is measured total global radiation (J m^{-2} d^{-1})

R_l is net outgoing long wave radiation (J m^{-2} d^{-1})
k is extinction coefficient for total radiation (dimensionless)
q_a is leaf area index of the vegetation (dimensionless)

Net outgoing long wave radiation is estimated from a formula similar to that proposed by Brunt (1932), although it is used here for shorter periods of time than intended by the author:

$$R_l = \sigma\,(T_{ae} + 273)^4 \bullet (0.58 - 0.092e_a) \bullet (1 - 0.9f_o) \tag{6}$$

$$T_{ae} = T_{mx} - 0.25\,(T_{mx} - T_{mn}) \tag{7}$$

where

σ is Stefan-Boltzmann constant (J m^{-2} d^{-1} K^{-4})
T_{ae} is weighted average daytime temperature of the air (°C)
f_o is fraction of the day that the sky is overcast (dimensionless)
T_{mx} is daily maximum air temperature (°C)
T_{mn} is daily minimum air temperature (°C)

Some of the coefficients in Equation 6 are location-specific (Brutsaert, 1975) and may be replaced when known, but they are not expected to vary significantly from those given above.

The value for the slope of the saturated vapour pressure curve, s, is calculated at the weighted air temperature with an analytical expression, approximating the saturated vapour pressure curve:

$$s = (\delta e_{st}/\delta T)_{T_{ae}} \tag{8}$$

$$e_{st} = 6.11\ e^{(17.4\ T_{ae}/(T_{ae} + 239))} \tag{9}$$

where

e_{st} is 'effective' saturated vapour pressure during daytime (mbar)

The integrated drying power of the atmosphere, δ_{pt}, is calculated as:

$$\delta_{pt} = \alpha\ q_a\ \delta_p \tag{10}$$

where

α is proportionality factor accounting for partial stomatal closure in the deeper layers of the canopy (dimensionless)
δ_p is average daytime drying power of the atmosphere obtained by substituting e_{st} and e_{at} in Equation 3

The value of α is a function of both the leaf area index of the canopy and the level of irradiance above the canopy. At higher values of q_a a proportionally greater part of the leaves is situated in positions where the level of irradiance is too low for stomatal opening (van Keulen et al., 1987); and at higher levels of irradiance above the canopy, the level at a given position inside the canopy will also be higher. Values of α for various combinations of the two independent variables have been calculated with a detailed model for canopy assimilation and transpiration (de Wit et al., 1978). The results are presented in Figure 3. The values given here are somewhat higher than those presented previously (van Keulen, 1975), since another relation between the level of irradiance and stomatal aperture was used that gives better agreement between measured and simulated rates of transpiration (van Keulen et al., 1987).

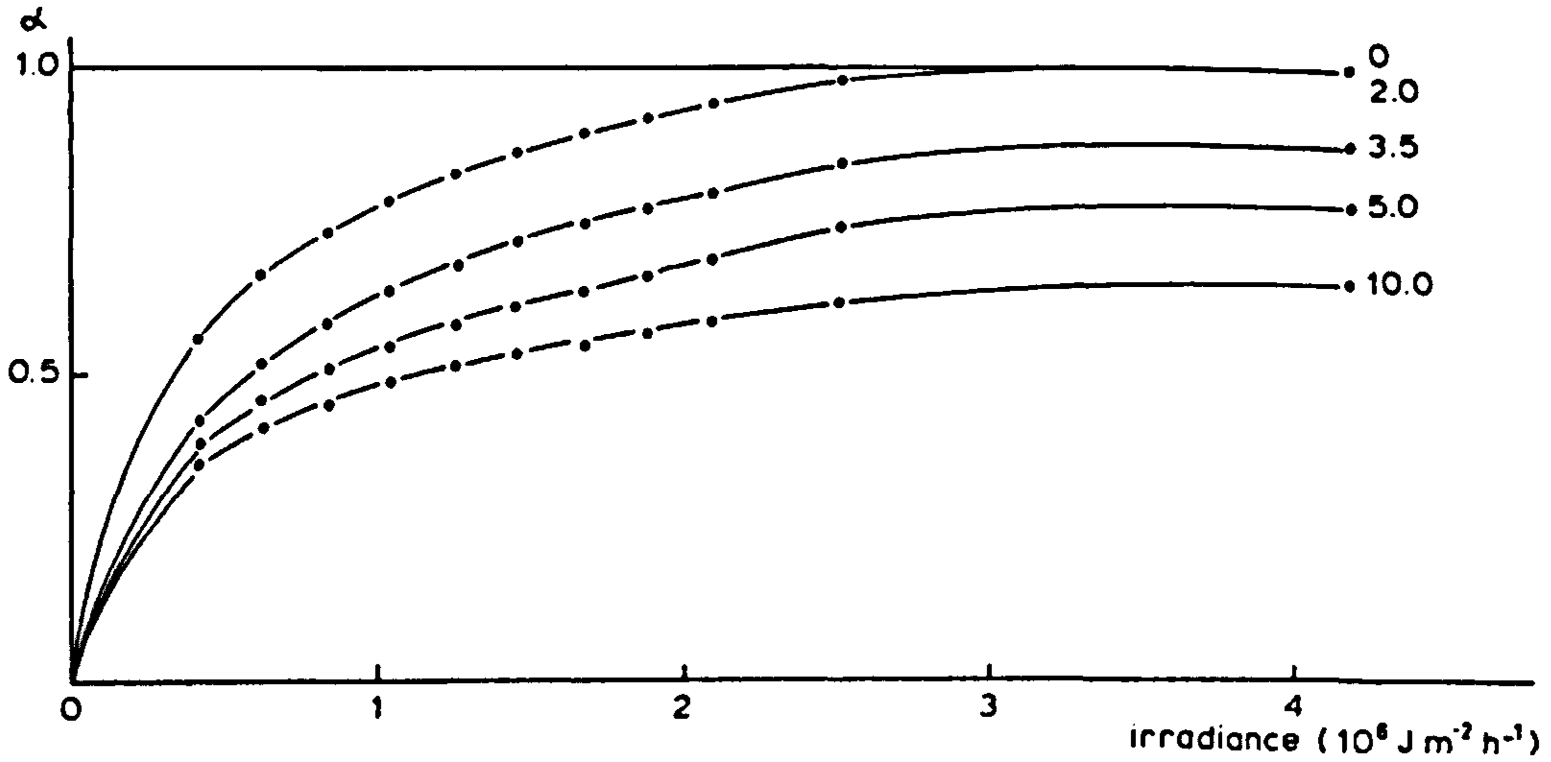

Figure 3. Relation between average irradiance and reduction factor for transpiration, α, for various values of the leaf area index.

The actual daytime vapour pressure, e_{at}, is calculated by the expression given in Equation 9, by substituting T_{de}, the daytime dew point temperature, for T_{ae}.

The resistance for heat exchange, r_{bh}, consists of the resistance of the boundary layer surrounding the leaf, r_{lh}, in series with r_{th}, the turbulent resistance inside and above the canopy for transport of vapour from the leaf towards the atmosphere. Both terms are dependent on wind speed and on the geometry of the canopy. The boundary layer resistance for heat exchange may be calculated from semi-empirical formulae, which include the Nusselt number, related to wind speed, the diffusivity for heat of the air and a characteristic leaf dimension (Goudriaan, 1977). For an average leaf width of 1 cm:

$$r_{lh} = c \cdot u^{-0.5} \tag{11}$$

where

c is an empirical constant $(s\ m^{-1})^{0.5}$
u is average wind speed ($m\ s^{-1}$), read from daily wind run. It is assumed that the wind speed during daytime is twice that at night

For the calculation of the turbulent resistance inside and above the canopy, aerodynamic theory is applied. It includes determination of zero plane displacement and surface roughness as functions of crop height and the mixing length as a function of crop height and mean width of the leaves (Goudriaan, 1977). The turbulent resistance, r_{th}, then follows from:

$$r_{th} = 0.74\ h_i^2 / (k_k^2 \bullet u) \qquad (12)$$

where

$$h_i = \ln((h_r - d_o)/z_o) \qquad (13)$$

and

h_r is reference height (m)
d_o is zero plane displacement (m)
z_o is roughness length (m)
k_k is von Karman's constant (dimensionless)
ln takes the natural logarithm of the argument

For the entire canopy, the resistance for the exchange of heat then follows from:

$$r_{bh} = r_{lh} + q_a \bullet r_{th} \qquad (14)$$

and

$$r_{bv} = 0.93\ r_{bh} \text{ (Goudriaan, 1977)} \qquad (15)$$

To calculate potential transpiration it is assumed that for stomatal resistance, r_{lv}, (see Equation 4), the minimum value, 120 s m^{-1}, may be applied throughout (van Keulen et al., 1987).

All the elements for the calculation of potential crop transpiration throughout the life cycle of the plant are now available.

3.3.2 Actual transpiration

The actual rate of transpiration depends on the potential rate, (Subsection 3.3.1) and on the availability of water in the soil profile. The rooting density of a graminaceous crop growing in a normally dense stand is not considered a limiting factor for moisture uptake (van Keulen et al., 1975). Data on root densities measured in the field (Gregory et al., 1978; Hurd, 1974; Lupton et al., 1974; Baldy, 1973), indicate that these are generally higher than what is needed for diffusion of the water in the rooted soil volume to the root surface within a day. Water uptake is thus limited by the water potential in the rooted soil volume rather than by root density. The procedure applied to account for the influence of soil moisture status on transpiration is described in Section 4.2.

The nitrogen status of the vegetation can influence its transpiration rate (Radin and Ackerson, 1981). Many studies have indicated that water use efficiency, i.e. the amount of dry matter produced per unit of water consumed, increases with increasing nitrogen availability (van Keulen, 1975; Black, 1966;

Viets, 1962). Interpretation of these results is in most cases difficult, since no distinction is made between transpiration by plants and evaporation from the soil surface. When plants grow under nitrogen stress, they are generally much smaller, as is their leaf area, so that complete soil cover is reached much later than for plants growing under optimum conditions, if at all. That leads to a much larger proportion of non-productive water loss from the soil surface and hence to a lower water use efficiency. In the early experiments on water use, where direct evaporation from the soil surface was prevented, no influence of moderate nitrogen stress on water use efficiency was found (Tanner & Sinclair, 1982; de Wit, 1958). Recent experiments where assimilation and transpiration of plant species were determined at different levels of nitrogen in the plant, have in general confirmed the latter hypothesis for maize (Goudriaan & van Keulen, 1979; Wong et al., 1979) and *Panicum maximum* (Bolton & Brown, 1980) but far less so for tall fescue and *Panicum milioides* (Bolton & Brown, 1980). In the latter species the ratio of apparent photosynthesis to transpiration increased almost twofold over a range of N-concentrations in the leaf tissue from 0.01 to 0.05 kg kg^{-1}.

A comprehensive study on the interactions between nitrogen and water stress, mainly in cotton, has been conducted by Radin and associates (Radin, 1983; Radin & Boyer, 1982; Radin, 1981; Radin & Ackerson, 1981; Radin & Parker, 1979a; 1979b). They found that in nitrogen deficient plants, stomatal response to water stress becomes increasingly sensitive possibly because of higher ABA levels in the leaf (Radin & Ackerson, 1981). In such plants, stomatal closure occurs at much higher plant water potentials, ψ, than in plants adequately supplied with nitrogen, $\psi = -1$ MPa vs $\psi = -1.8$ MPa (Radin & Ackerson, 1981). Diurnal fluctuations in ψ, especially on bright days could easily lead to values as low as -1 MPa in well-watered wheat plants and remain below that level for most of the day, – from 9.00 to 16.00 hours (Hochman, 1982; Martin & Dougherty, 1975). Shimshi (1970a; 1970b) has shown that transpiration in nitrogen-deficient plants is reduced, particularly at high levels of soil moisture, but that near wilting point the situation is reversed, possibly because of a much higher proportion of cell wall constituents in the N-deficient plants that reduces stomatal sensitivity. Consequently, stomatal opening is not only restricted under high moisture conditions, but full stomatal closure is prevented near wilting point. Evidence for greater stomatal opening with better N nutrition has also been found in rice (Ishihara et al., 1978; Yoshida & Coronel, 1976) and in wheat (Shimshi & Kafkafi, 1978).

Radin & Boyer (1982) showed that root conductivity is lower in N-deficient sunflower plants, so that lower turgor, higher ψ and stomatal closure could follow. Lower transpiration rates due to nitrogen deficiency could therefore be effectuated by stomatal closure at higher ψ or by lower root conductivity. In the former case moisture stress would be secondary and possibly minor compared to nitrogen stress; in the latter case moisture stress induced by N-deficiency would be the more dominant.

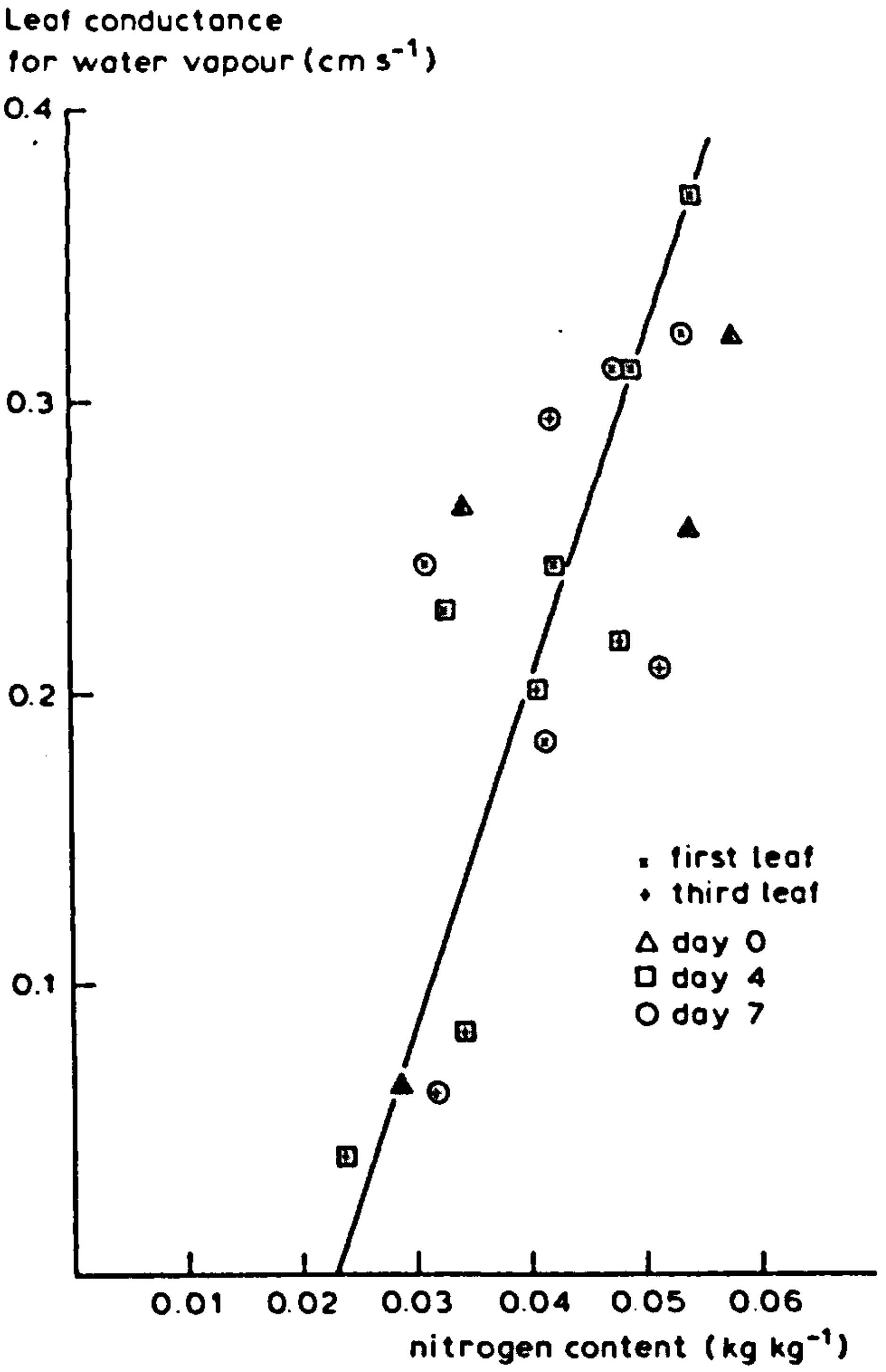

Figure 4. Relation between total nitrogen content in the leaf and leaf conductance for water vapour exchange for rice. Days refer to length of the period after switching nutrient solutions. (Source: Yoshida & Coronel, 1976.)

Data on the relationship between leaf resistance and leaf N concentration have been published by Yoshida & Coronel (1976). Figure 4 is derived from their data and relates leaf conductance to N concentration in the leaf. At high leaf-N concentrations, stomata are open and stomatal conductance is generally around 0.625 cm s^{-1} (Denmead & Millar, 1976a; 1976b). In Figure 4, leaf conductance includes boundary layer conductance, so that stomatal conductance would necessarily be to the left of the eye-fitted regression line. The approximate effect of leaf N concentration on stomatal behaviour can therefore be expressed as:

$$r_{lv} = 1 / C_{lv} \qquad (16)$$

$$C_{lv} = C_{lx} (n_{al} - n_{mn}) / (n_{xl} - n_{mn}) \qquad (17)$$

where

r_{lv} is actual stomatal resistance (s m^{-1})

C_{lv} is actual stomatal conductance (m s^{-1})
C_{lx} is maximum stomatal conductance at high nitrogen concentration (m s^{-1})
n_{al} is current nitrogen concentration in the leaf blades
n_{mn} is minimum nitrogen concentration in the leaf blades, function of development stage
n_{xl} is maximum nitrogen concentration in the leaf blades, function of development stage

3.3.3 Effects of water shortage

Since the pioneering work by Briggs & Shantz (1913) and other American agronomists on the relation between dry matter production and water use by plants, excellent reviews of experimental data and theoretical treatments of the subject have appeared (cf. Tanner & Sinclair, 1982; Hanks, 1974; Arkley, 1963; de Wit, 1958). By and large there is agreement that a strong correlation exists between CO_2 assimilation and transpiration because both are governed by the same physical principles and to a large extent by stomatal opening. However, measured water use efficiencies vary between locations, plant species, years and so on, because the two processes are influenced differently by other factors. The response to irradiance is not identical for the two processes over its full range; neither is the response to air humidity. In addition, differences in chemical composition of the structural plant material being formed, lead to variable respiratory losses. Nevertheless, these effects are secondary to the dominant correlation between the two processes. Therefore, in this model the principal effects of water stress on assimilation are related to t_r, the ratio of actual transpiration to potential transpiration:

$$t_r = t / t_o \qquad (18)$$

where

t is actual rate of moisture uptake by the roots (mm d^{-1}) (Section 4.1)
t_o is potential rate of canopy transpiration (mm d^{-1}) (Subsection 3.3.1)

To account for effects of prolonged stress, which may damage the biochemical machinery of the plants (Hochman, 1978), a relative transpiration deficit is defined as:

$$d_{rt} = (t_o - t) / t \qquad (19)$$

This value is integrated to yield the cumulative relative transpiration deficit, S_{tr}. Under the assumption that mild water stress will not have any lasting effect on the vegetation the values of d_{rt} are integrated only when they exceed an arbitrary limit of 0.4.

3.4 Carbon balance

3.4.1 Gross CO_2 assimilation

Individual leaves

The basis for the calculation of canopy gross CO_2 assimilation is the photosynthesis-light response curve of individual leaves of the crop. This curve is characterized by the initial light use efficiency at low levels of irradiance and the light saturated value, determined by the rate of CO_2 diffusion towards the active sites. Attempts have been made to derive these parameters from photosynthetic biochemistry and leaf structure (Sinclair et al., 1977) but the results were inconclusive. Experimentally determined photosynthesis functions are available in the literature for a large number of wheat cultivars, grown and measured under a wide range of experimental conditions (cf. Fischer et al., 1981; Winzeler, 1980; Dantuma, 1973; van Laar & Penning de Vries, 1972; Khan & Tsunoda, 1970c; Evans & Rawson, 1970; Stoy, 1965). Some of these are presented in Figure 5. There is considerable variability, which can be traced to differences in environmental conditions under which the plants were grown, differences in age and nitrogen status of the leaves, inherent differences among cultivars as suggested by Dantuma (1973) or differences in measuring conditions.

Despite this variability, under optimum conditions the initial light use efficiency, is fairly close to 7.2×10^{-7} kg CO_2 J^{-1} (equivalent to 0.5 kg CO_2

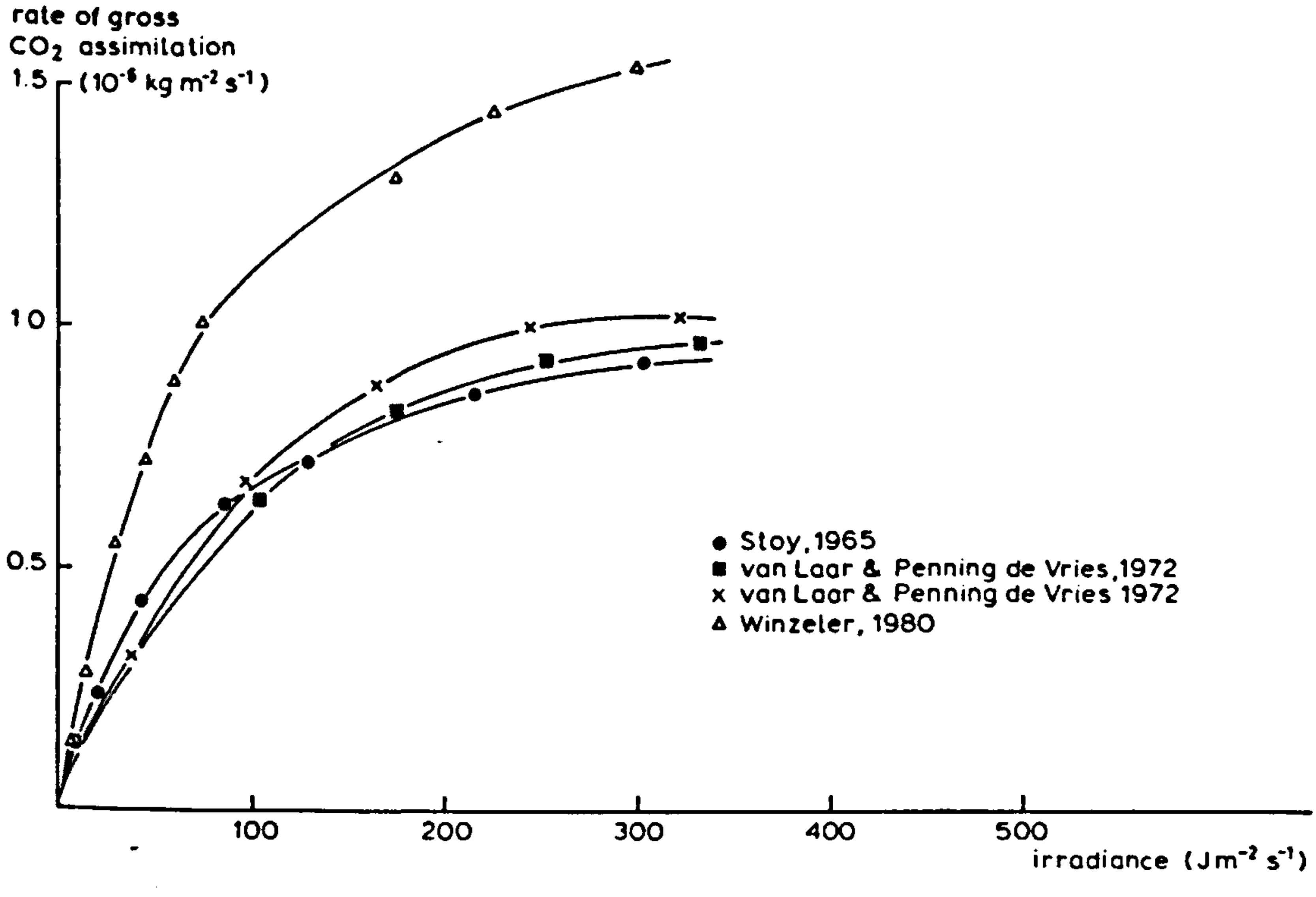

Figure 5. Relation between irradiance and rate of gross CO_2 assimilation for individual leaves of wheat.

$ha^{-1}h^{-1}$ per J $m^{-2}s^{-1}$) and a maximum saturated value, of 1.1×10^{-6} kg CO_2 m^{-2} s^{-1} (equivalent to 40 kg CO_2 ha^{-1} (leaf) h^{-1}) have been found to give good results in simulation studies of canopy photosynthesis (de Wit et al., 1978; van Keulen et al., 1986).

The former value has been adopted in the present model, while the saturated value is treated later in this section.

Canopy gross assimilation

The daily rate of gross CO_2 assimilation of the canopy is calculated by an algorithm developed by Goudriaan & van Laar (1978a), based on earlier work by de Wit (1965). Inputs required are: the initial light use efficiency and the light saturated maximum photosynthetic rate of the light response curve for an individual leaf, the green area index of the canopy, g_a, the fraction of the day that the sky is overcast, f_o, the day number according to the julian calender, j, and the latitude of the site, λ_a.

The essential equations of this algorithm are as follows: Daily gross assimilation expressed in CH_2O in kg ha^{-1} d^{-1}, P_g, is the sum of the assimilation calculated separately for clear, P_{gc}, and overcast, P_{go}, sky conditions, weighted for the proportion of the day during which these conditions apply:

$$P_g = ((1 - f_o) \cdot P_{gc} + f_o \cdot P_{go}) \cdot m_w \quad (20)$$

The factor m_w equals 0.6818 and converts from CO_2 to reduced sugars, CH_2O. The values calculated by the Goudriaan & van Laar algorithm, P_{eo} and P_{ec}, differ slightly from values calculated with a well-validated canopy assimilation model (de Wit et al., 1978), but can be adjusted by means of the following linear regression:

$$P_{go} = 0.9935\ P_{eo} + 1.1 \quad (21)$$

$$P_{gc} = 0.95\ P_{ec} + 20.5 \quad (22)$$

Under overcast conditions irradiance is uniformly distributed over the foliage and so,

$$P_{eo} = q_a \cdot F_m \cdot d_e \cdot f \quad (23)$$

in which d_e is the effective day length (in hours), estimated as the time during which solar height exceeds 8 degrees and f represents the fraction of maximum CO_2 assimilation that can be attained at a given level of irradiance. Thus,

$$d_e = 12(\pi + 2 \arcsin((\sin \lambda_a \sin \delta - \sin 8)/\cos\delta\cos\lambda_a)/\pi \quad (24)$$

$$\delta = -23.4 \cos((j + 10.173)/182.621) \quad (25)$$

$$f = p/(p + 1) \quad (26)$$

$$p = R_o \cdot \epsilon/(F_m \cdot g_a) \quad (27)$$

$$R_o = 0.5 \bullet R_{go}/d_e \qquad (28)$$

where

δ is declination of the sun (degrees)
R_o is average level of irradiance during the daylight hours under an overcast sky (J m^{-2} s^{-1})
R_{go} is daily total global radiation under overcast sky; obtained from standard tables (J m^{-2} d^{-1})
ϵ is initial light use efficiency of the CO_2 assimilation light response curve (kg ha^{-1} h^{-1}/(J m^{-2} s^{-1}))
F_m is light saturated CO_2 assimilation rate (kg ha^{-1} h^{-1})

For clear sky conditions, irradiance is distributed unevenly over the foliage, hence total green area is subdivided into sunlit, g_{sl}, and shaded, g_{sh}, green area. Daily gross CO_2 assimilation under these conditions is calculated separately for the two classes, so that:

$$P_{ec} = P_{esl} + P_{esh} \qquad (29)$$

For sunlit leaves:

$$P_{esl} = g_{sl} \bullet d_e \bullet F_m \bullet f' \qquad (30)$$

$$g_{sl} = \sin (90 + \delta - \lambda_a) \qquad (31)$$

$$f' = p'/(p' + 1) \qquad (32)$$

$$p' = 0.45\ R_c \bullet/(F_m \bullet g_{sl}) \qquad (33)$$

where

R_c is average level of irradiance during daylight hours under a clear sky obtained from standard tables (J m^{-2} d^{-1})

For shaded leaves:

$$P_{esh} = (g_a - g_{sl}) \bullet d_e \bullet F_m \bullet f'' \qquad (34)$$

$$f'' = p''/(p'' + 1) \qquad (35)$$

$$p'' = 0.55\ R_c \bullet \epsilon/(F_m \bullet (g_a - g_{sl})) \qquad (36)$$

For situations where g_a is low and the canopy does not form a closed surface, gross CO_2 assimilation, P_g, is reduced due to incomplete light interception by a factor f_i:

$$f_i = 1 - e^{-0.8g_a} \qquad (37)$$

Influence of water shortage

Because assimilation and transpiration are closely related (de Wit, 1958), a reduction in transpiration due to water shortage will cause an approximately proportional reduction in assimilation. Thus:

$$P_{gw} = P_g \cdot t_r \qquad (38)$$

where

P_{gw} is water limited rate of gross CO_2 assimilation (kg ha^{-1} d^{-1})
t_r is ratio of actual to potential canopy transpiration (Equation 18)

Influence of nitrogen status

The influence of nitrogen deficiency in the vegetation on dry matter accumulation and yield is well documented but the effects on the basic processes of assimilation and respiration are far less clear. The level of CO_2 assimilation at different nitrogen levels in the leaves has been determined for many plant species, such as maize (Ycas, 1984; Goudriaan & van Keulen, 1979; Ryle & Hesketh, 1969), sunflower (Goudriaan & van Keulen, 1979), cotton (Wong, 1979; Ryle & Hesketh, 1969), sugar beet (Nevins & Loomis, 1970), rice (Cook & Evans, 1983a; 1983b; Yoshida & Coronel, 1976; Khan & Tsunoda, 1970b; Takeda, 1961), grasses, both those with C_3 and C_4 photosynthetic pathways (Woledge & Pearce, 1986; Brown & Wilson, 1983; Bolton & Brown, 1980; Lof, 1976; Wilson, 1975a; 1975b), wheat (Migus & Hunt, 1980; Marshall, 1978; Osman et al., 1977; Dantuma, 1973; Osman & Milthorpe 1971; Khan & Tsunoda, 1970a; 1970c), soya-bean (Boon-Long et al., 1982; Lugg & Sinclair, 1981; Boote et al., 1978), Eucalyptus spp. (Mooney et al., 1978), tung (Loustalot et al., 1950) and many wild plant species (Chapin, 1980). In all situations where nitrogen concentration of the leaves was determined, a strong correlation exists between the nitrogen concentration in the leaves and their photosynthetic performance.

The leaf nitrogen concentration can be expressed either on an area basis or on a dry weight basis, the specific leaf weight being the conversion factor between the two. The literature cited above uses both methods. Where the specific leaf weight is reported, the data can be expressed on a common basis. In Figure 6 some data for C_3 species are summarized from situations where it could reasonably be assumed that the applied light intensity during the measurements was high enough to ensure light saturation. Nitrogen concentration in this graph is expressed on a dry weight basis. The data suggest a linear relation between nitrogen concentration and net CO_2 assimilation rate, at least up to a nitrogen level of 0.06 kg kg^{-1}. The calculated regression line between nitrogen concentration and net assimilation rate at light saturation ($r^2 = 0.77$) has a slope of 22.0×10^{-6} kg CO_2 m^{-2} s^{-1} for each unit increase in nitrogen concentration. Some of the residual variation could be due to different ages or development stages of the experimental material (Friedrich & Huffaker, 1980).

Expressing nitrogen concentration on an area basis, gives $r^2 = 0.80$. The

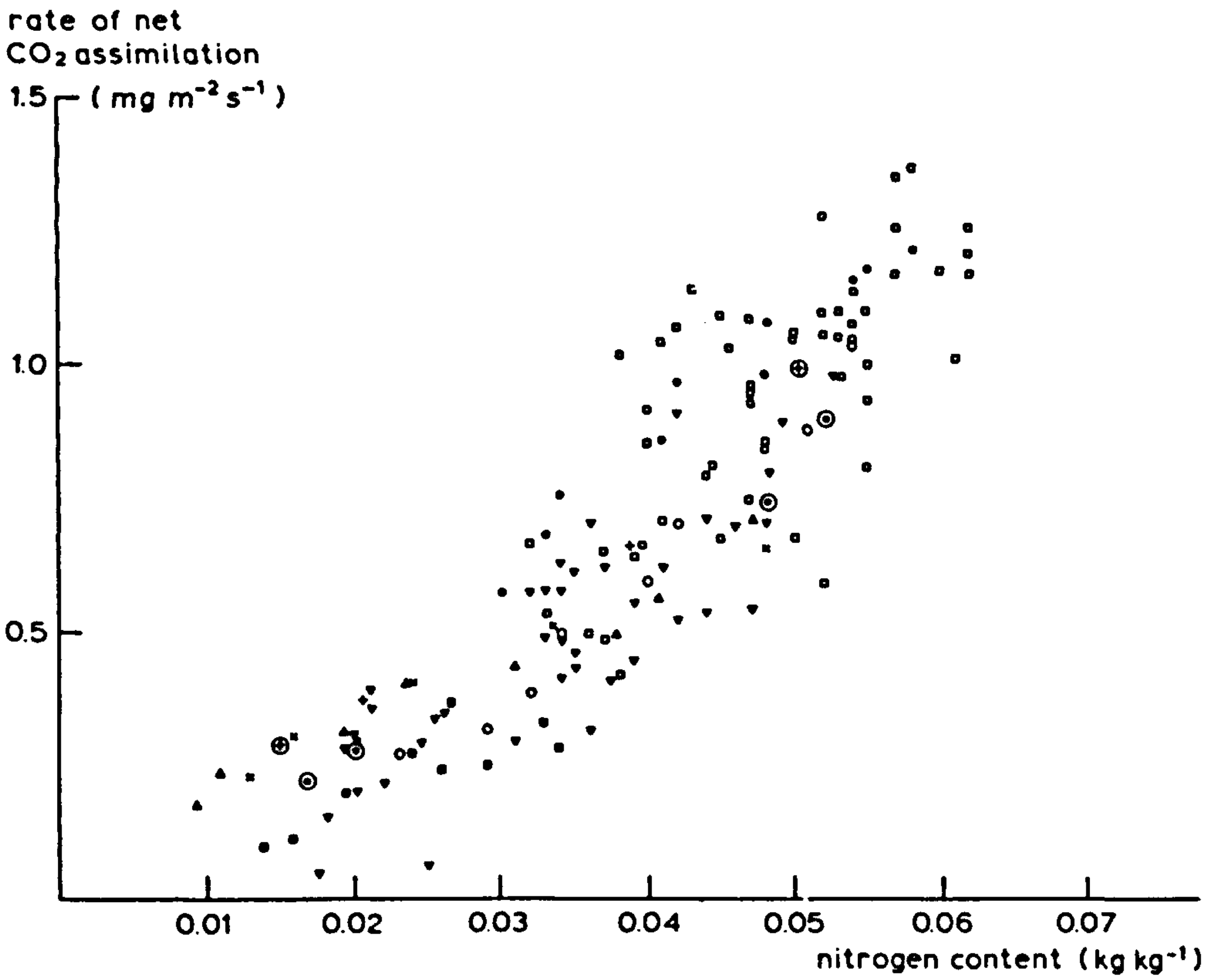

Figure 6. Relation between nitrogen content in the leaf, on a dry weight basis, and its rate of net CO_2 assimilation.
□ tung (Loustalot et al., 1950); ▼ *Triticum aestivum* (Dantuma, 1973); × Lolium perenne (Wilson, 1975a); · *Oryza sativa* (first leaf), ○ *Oryza sativa* (third leaf), (Yoshida & Coronel, 1976); + *Hordeum murinum*, ⊕ *Phalaris minor* (Lof, 1976); ▽ *Triticum aestivum* (Marshall, 1978); ▲ *Festuca arundinacea* (Bolton & Brown, 1980); □ *Oryza* spp. (Cook & Evans, 1983a, 1983b); ⊙ *Panicum* spp. (Brown & Wilson, 1983).

regression line (Figure 7) has a slope of 0.64×10^{-7} kg CO_2 m^{-2} s^{-1} for each unit increase (mg dm^{-2}) in nitrogen concentration. The two slopes would be identical at a value of the specific leaf area of 28.6 m^2 kg^{-1}, a rather high value that would suggest that most experiments were conducted on young, thin leaves (Subsection 3.6.2). A more serious limitation to the calculated regression line, however, is that it crosses the assimilation axis at zero nitrogen concentration. This effect seems mainly to be caused by the sugar-beet data (Nevins & Loomis, 1963). Although there is no obvious reason to doubt the validity of these points (Loomis, personal communication), the regression line was recalculated omitting them. This results in a slightly lower r^2 (= 0.76), a slope of 0.71×10^{-7} kg m^{-2} s^{-1} and zero assimilation at a nitrogen concentration of 0.2 mg dm^{-2}.

Extensive data on assimilation rates of flag leaves of wheat grown at different nitrogen levels in the field are presented by Marshall (1978). These data which cover the period after anthesis are separately reproduced in Figure 8. They also show a linear relation between N concentration and gross pho-

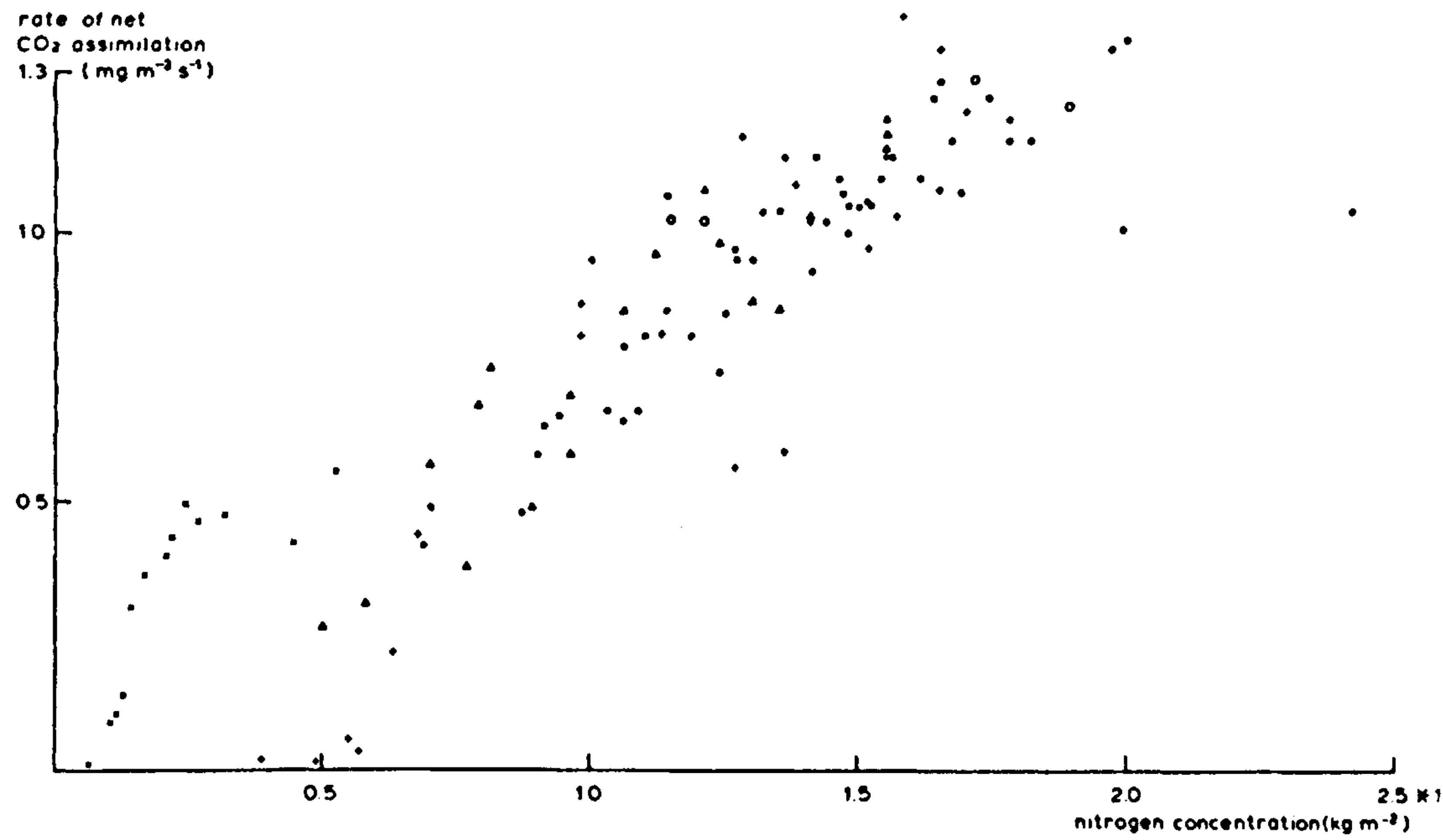

Figure 7. Relation between nitrogen concentration of the leaf, on an area basis, and its rate of net CO_2 assimilation.
× *Beta vulgaris* (Nevins & Loomis, 1970); △ *Oryza sativa* (Yoshida & Coronel, 1976); + *Glycine max* (Boon-Long et al., 1982); ● *Oryza* spp. (Cook & Evans, 1983a, 1983b); ○ *Triticum aestivum* (Evans, 1983).

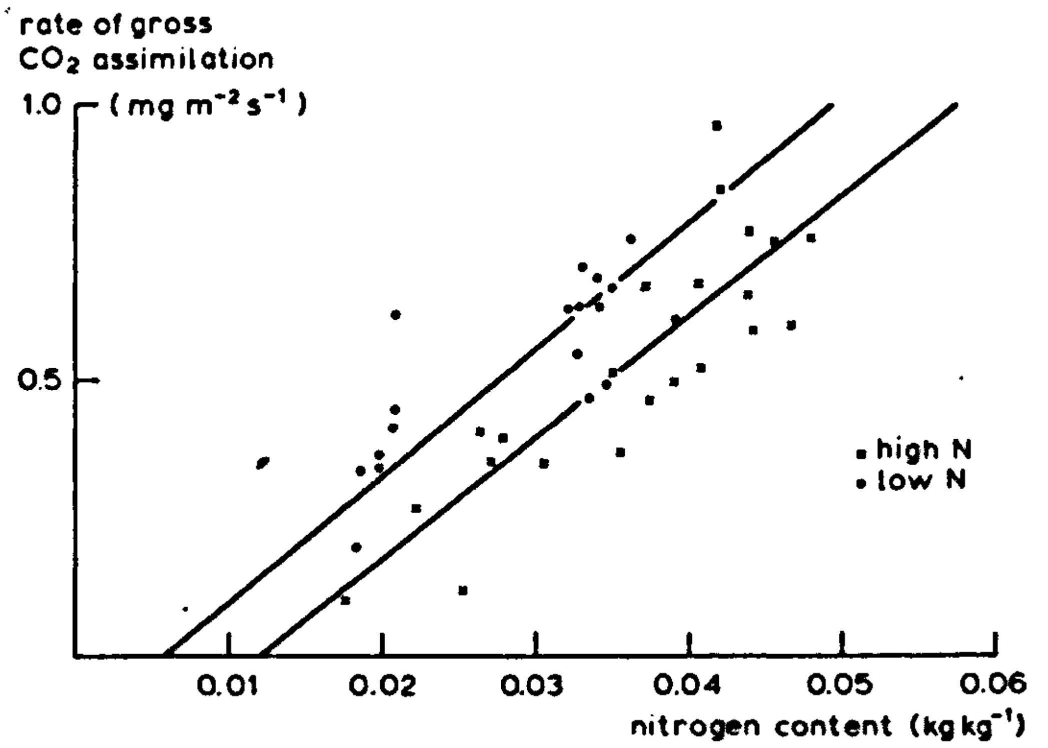

Figure 8. Relation between nitrogen content in the leaf, on a dry weight basis, and its gross rate of CO_2 assimilation for field-grown wheat with high or low N supply (Source: Marshall, 1978).

tosynthesis. The data of the two treatments, however, are clearly separated, leaves from the low N plots having a higher rate of CO_2 assimilation at a given N concentration than those from the high N plots. The slope of both lines is similar to that calculated from Figure 6 (21.9 and 17.0 × 10^{-6} kg CO_2 m^{-2}

s^{-1} for the high and low N, respectively, compared to 22.0×10^{-6}). A possible explanation for the difference in the two treatments could be that in the plants that have been well supplied with N throughout their life cycle, a larger proportion of the nitrogen is in the form of non-active storage proteins. Another possibility is that the leaves reached equivalent N concentrations at an earlier stage of development in the low N plot than in the high N plot.

The effect of leaf nitrogen concentration on the initial light use efficiency, i.e. the slope of the CO_2 assimilation curve at low irradiance, is difficult to determine because of the small values involved and the variance in the data. No significant difference could be detected (Cook & Evans, 1983a; 1983b; Wilson, 1975a; 1975b), but it could well be that small differences in the slope are responsible for some of the measured differences in assimilation rate between canopies with different leaf nitrogen concentrations. In the model, the influence of nitrogen concentration on gross CO_2 assimilation is accounted for by changing the value of the light saturated CO_2 assimilation rate, F_m (Equation 23), in dependence of the nitrogen concentration in the leaf blades:

$$F_{mn} = 725\, n_{al} - 2.75,\ F_{mn} \geq 0. \tag{39}$$

where

n_{al} is nitrogen concentration in the leaf blades.

Influence of temperature

Assimilation is an enzymatic process and such processes are generally temperature dependent (Downes, 1970). In contrast, however, to other processes like maintenance respiration or grain growth rate, there seems to be considerable adaptation of the assimilation process to fluctuating and varying temperatures (de Wit et al., 1978). It would thus be unrealistic to introduce directly the relation between temperature and maximum assimilation rate as measured on plants grown under constant controlled conditions and subjected to different temperatures during measurements. In reality, there appears to exist a wide temperature range for optimum photosynthetic performance under field conditions (Wardlaw, 1974). In the model the temperature effect is accounted for by introducing a reduction factor, $f_{ga,}$ for maximum gross assimilation rate as a function of average temperature during daytime:

$$F_m = F_{mn} \cdot f_{ga} \tag{40}$$

$$f_{ga} = f(T_{ae}) \tag{41}$$

The relation of Eqn. 41 is represented in Figure 9, based on data presented by Van Heemst (1986), Van Laar & Penning de Vries (1972) and others.

Influence of reserve level

There is conflicting evidence in the literature (Neales & Incoll, 1968) on the influence of the level of soluble carbohydrates in the leaves on their photosyn-

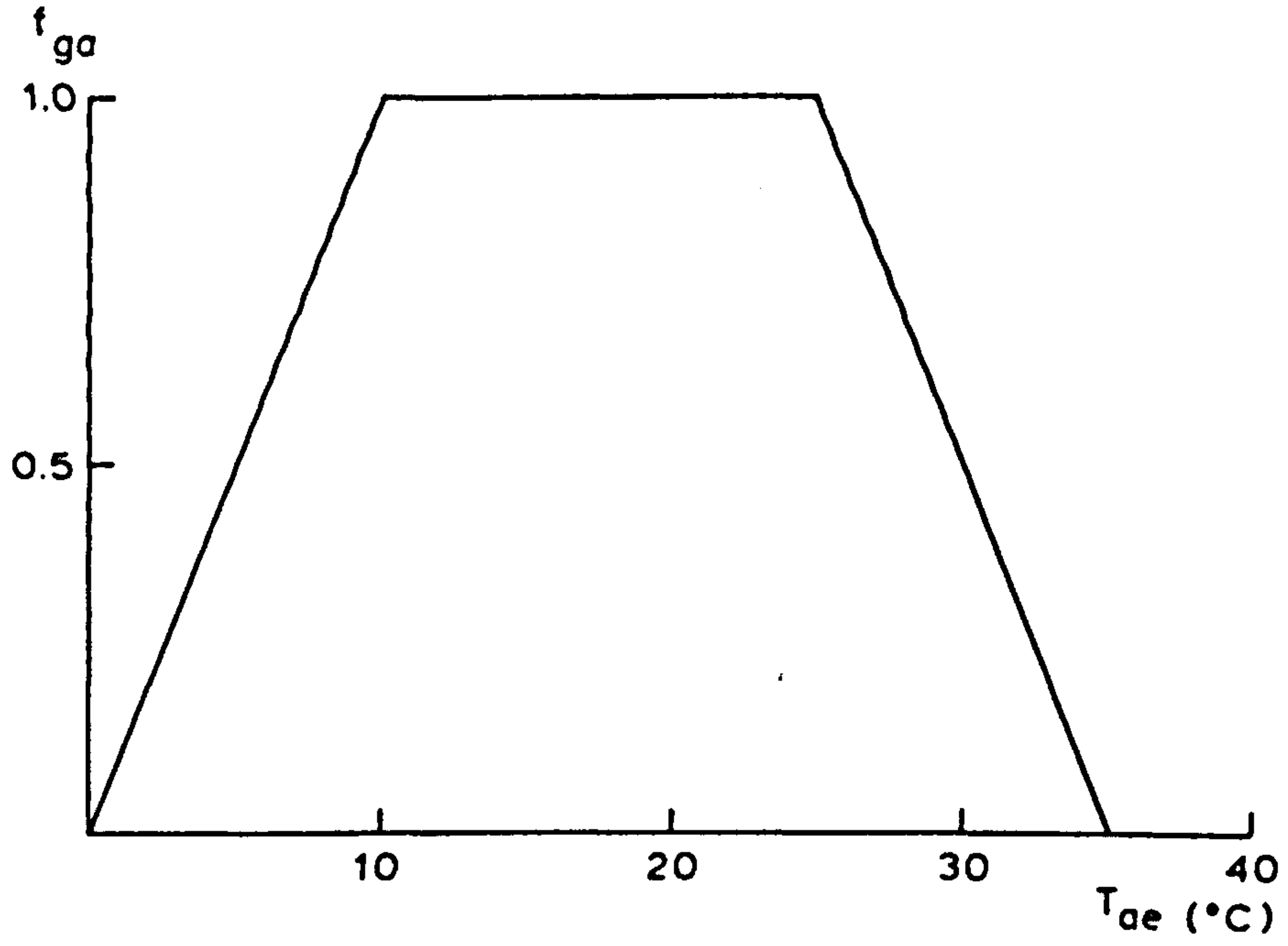

Figure 9. Relation between average daytime temperature, T_{ae}, and the reduction factor for maximum gross assimilation rate of an individual leaf, f_{ga}.

thetic performance. On the one hand where sink strength is reduced (e.g. by removing ears), CO_2 assimilation has been observed to fall, presumably mediated through an accumulation of primary assimilation products in the leaves (King et al., 1967), whereas in other experiments no such correlation could be found (Rawson et al., 1976; Austin & Edrich, 1975). In experiments with maize, where different levels of soluble carbohydrates were created by applying different light and/or dark periods, no difference was found in the level of CO_2 assimilation (Goudriaan & van Keulen, 1979). It seems that over a wide range, the concentration of reserves has no effect on CO_2 assimilation, but under conditions of stress, especially shortage of water or nitrogen, the conversion of primary assimilates to structural tissue is more severely restricted than assimilation itself and consequently primary assimilation products will accumulate in the plant (Alberda, 1960). Similar effects have been noted where fairly high radiation levels and mild day time temperatures are accompanied by low night temperatures (Versteeg, 1985). In the latter reference, it is reported that after a prolonged period under these conditions, total above ground dry matter accumulation, including non-structural carbohydrates, ceases completely. This phenomenon indicates that there must be a point at which a feedback that reduces CO_2 assimilation begins to operate. This is accounted for in the model by:

$$P_{gwr} = (1 - f_r) \cdot P_{gw} \tag{42}$$

$$f_r = (c_a - c_{al})/0.05, \; 0 \leq f_r \leq 1 \tag{43}$$

where

c_a is the concentration of non-structural carbohydrates in the vegetation. According to this formulation CO_2 assimilation will decrease to zero as c_a increases from c_{al} to $c_{al} + 0.05$.
c_{al} is the lowest concentration of non-structural carbohydrates in the vegetation at which assimilation is affected.

It is difficult to quantify the value of c_{al}, the threshold concentration in the total vegetation, including the roots. For assimilation, the concentration in the leaf blades is presumably the determinant factor. In stem tissue values over 0.4 kg kg^{-1} have been reported (Spiertz, 1977), concurrent with 0.15 to 0.2 kg kg^{-1} in the leaf blades. In the model a value of 0.3 for c_{al} has been adopted.

3.4.2 Partitioning of assimilates

The assimilates fixed by the photosynthetic process are partitioned among the various sinks in the plants, including maintenance respiration. Sink strength, which is probably related to the number of growing cells in a particular organ, is an important determinant for assimilate distribution at any time (Gifford & Evans, 1981). The present model does not simulate processes at the cellular level and so partitioning is governed by functions related to the phenological development of the crop. As different organs are formed, they constitute sinks of varying strength.

Maintenance of the various living plant parts has first priority. Maintenance respiration is dependent on the weight of an organ, its chemical composition and the ambient temperature (Penning de Vries, 1975). For each of the organs, i.e. roots, leaves, 'stems' (which in the present formulation also include leaf sheaths and ear structures) and grains, the carbohydrate requirement for maintenance respiration, r_{mx} in kg ha^{-1} d^{-1}, is calculated by:

$$r_{mx} = (\alpha_{mx} \cdot W_x \cdot f_{mn} \cdot f_{mt}) - r_{dpx} \qquad (44)$$

where

α_{mx} is the carbohydrate requirement for maintenance respiration per unit dry weight of an organ at a temperature of 20 °C and a minimum nitrogen concentration, (kg kg^{-1} (dry matter) d^{-1})
W_x is the weight of a plant organ (kg ha^{-1})
f_{mn} is a factor accounting for the influence of nitrogen concentration of the tissue
f_{mt} is a factor accounting for the influence of temperature
r_{dpx} is energy contribution from degrading proteins after anthesis (kg CH_2O $ha^{-1}d^{-1}$)

For each of the organs a specific value for the maintenance requirement per unit dry weight is defined (van Keulen et al., 1982). This differential treatment is primarily related to the contribution of the organ in the total gross assimilation and reflects the cost of transport of photosynthetic products from source to sink. The influence of nitrogen concentration, reflecting the rebuilding of continuously degrading proteins, is obtained by:

$$f_{mn} = (n_{ax} - n_{am})/\Delta n + 1 \tag{45}$$

where

n_{ax} is current nitrogen concentration in the organ.
n_{am} is nitrogen concentration in the tissue where maintenance requirement is equal to the 'standard value'.
Δn is the range in nitrogen concentrations between the absolute minimum and the absolute maximum level.

The value of f_{mn} thus ranges between 1 and 2, which is about the range found in maintenance requirements between low-protein and protein-rich materials (Penning de Vries, 1975). At very low nitrogen concentrations, protein turnover is low and has a small maintenance requirement compared to that needed for maintenance of the ionic balance within the cells. Towards the end of the growth cycle, when current assimilate supply and remobilized reserves together are insufficient to meet the maintenance requirements of the living tissue, it is assumed that accelerated senescence of the tissue takes place. On the other hand, after anthesis when structural carbohydrates increasingly dominate in stem and root tissues, it is assumed that their maintenance requirement decreases and ceases after grain filling ends. Quantification of maintenance respiration for different organs at different stages of development clearly needs further study.

The effect of temperature on maintenance respiration is well established (Penning de Vries, 1975), and can be accounted for with a Q_{10} value of 2. Thus:

$$f_{mt} = 2^{(T_c - 20)} \tag{46}$$

where

T_c is average daily crop temperature and 20 is the reference temperature (°C)

After anthesis part of the nitrogen from degrading proteins in the vegetative tissue is translocated to the growing grain. The carbon from these components is used as an energy source for maintenance requirements (Penning de Vries, 1982). This contribution, r_{dpx}, is defined as:

$$r_{dpx} = 0.5 \cdot v_{pr} \cdot W_x / (W_l + W_s + W_r) \tag{47}$$

where

v_{pr} is rate of protein translocation from the vegetative tissue to the grains (Subsection 3.5.3)

The assimilates remaining after the maintenance requirements of the live organs of the crop have been satisfied, are available for the production of structural plant material:

$$P_n = P_{gwr} - \sum_{1}^{x} r_{mx} \qquad (48)$$

where

x is number of live plant compartments

In the model, the currently produced assimilates are partitioned and allocated to 4 compartments: leaf blades, 'stems' (including leaf sheaths and ear structures), roots, and a reserve-pool of primary photosynthetic products. Under optimum growth conditions, the proportion of P_n allocated to each of the compartments is a function of the phenological state of the vegetation only, representing the variable sink strength of the various organs. Under suboptimum growth conditions the partitioning changes. Whether this is an active process, or the result of a differential influence of stress on the growth of different organs is difficult to judge. Brouwer (1965; 1963) suggests that insufficient moisture supply, resulting in loss of turgidity, affects the conversion of primary photosynthates into structural plant material ('growth') more strongly than CO_2 assimilation. As a result, the level of reserve carbohydrates in the plant increases, which makes more of them available for growth of the root system. Hence, water shortage changes the partitioning of assimilates between shoot and root. Brouwer has called this phenomenon the 'functional balance'. A quantitative assessment of the influence of moisture stress on current partitioning is difficult to obtain, especially for crops under field conditions.

Nitrogen shortage in the vegetation favours growth of roots at the expense of above ground material, generally leading to lower shoot/root ratios at suboptimum nitrogen supply (Cook & Evans, 1983a; Campbell et al., 1977b; Wilson & Haydock, 1971; Colman & Lazenby, 1970; Troughton, 1967; Brouwer, 1965; Brouwer et al., 1962; McLean, 1957). This may be another aspect of the same functional balance. The partitioning between leaf blades and other above ground organs also changes under suboptimum nitrogen conditions and results in a lower proportion of leaves (Campbell et al., 1983; van Os, 1967; McNeal et al., 1966; Boatwright & Haas, 1961).

In the present model these influences are described by assuming a growth check on the shoot (leaf blades and stem) when nitrogen or water shortage occurs. The resulting 'surplus' carbohydrate is partitioned between roots and the reserve pool in a fixed pattern. When stress is alleviated and reserve carbohydrates have accumulated, some can become available for subsequent leaf growth.

Assimilate availability for growth of the leaf blades, P_{nl}, equals:

$$P_{nl} = p_l \cdot r_{nw} \cdot P_n + P_{tr} \qquad (49)$$

where

p_l is partitioning factor for leaf blades, function of development stage (dimensionless)

r_{nw} is reduction factor for leaf growth due to water or nitrogen stress, taken as the minimum of the two values (Section 3.5)

$$P_{tr} = \begin{cases} (c_a - c_{lt}) \cdot (W_l + W_s + W_r)/\tau_{tr}, & p_l \geq 0.25,\ n_{rw} = 1 \\ 0 & \text{, otherwise} \end{cases} \qquad (50)$$

P_{tr} is assimilate transferred from reserves, when reserve level exceeds a threshold value, leaf growth is active and there is no nitrogen or water deficiency.

τ_{tr} is time constant for reserve translocation.

c_{lt} is residual non-remobilizable concentration of non-structural carbohydrates.

Carbohydrate allocated to stem tissue, P_{ns}, is defined as:

$$P_{ns} = p_s \cdot r_{rw} \cdot P_n \qquad (51)$$

The 'surplus' assimilate, P_e, is consequently:

$$P_e = (p_l + p_s) \cdot (1 - r_{nw}) \cdot P_n \qquad (52)$$

The available carbohydrate for growth of the roots, P_{nr}, is:

$$P_{nr} = p_r \cdot P_n + p_{rr} \cdot P_e \qquad (53)$$

where

p_r is partitioning factor for current assimilate to the roots, function of development stage of the vegetation

p_{rr} is fraction of the 'surplus' assimilate allocated to the roots

Non-structural reserve carbohydrates, P_{ne}, may accumulate in the vegetation, presumably because the 'growth potential' of the different organs is insufficient to utilize all available assimilates:

$$P_{ne} = p_e \cdot P_n + (1 - p_{rr}) \cdot P_e - P_{tr} - P_{ng} - P_m \qquad (54)$$

where

p_e is partitioning factor for current assimilate to non-structural carbohydrates, function of development stage of the vegetation.

P_{tr} is rate of assimilate transfer from reserves to growth of vegetative plant tissue (Eqn. 49) (kg CH_2O ha^{-1} d^{-1})

P_{ng} is rate of assimilate supply from reserves to grain growth (kg CH_2O ha^{-1} d^{-1})

P_m is rate of reserve utilization for maintenance respiration, if current assimilate supply is insufficient (kg CH_2O ha^{-1} d^{-1})

In the model translocation of reserves to the grain and to vegetative structures has priority above their use for maintenance respiration, i.e.:

$$P_m = \begin{matrix} -P_n, & P_n < 0;\ W_{rs}/\Delta - (P_{tr} + P_{ng}) > 0 \\ 0 & \text{, otherwise} \end{matrix} \qquad (55)$$

The values of the partitioning coefficients have been derived from various experimental sources. The fraction allocated to the 'reserves', p_e, is difficult to determine from experimental results. In the early growth stages, generally most of the assimilates are converted into structural plant material and the level of non-structural carbohydrates in the plant is low (Barnell, 1938; 1936). After heading, when most of the plant organs have reached their final size, and before the onset of grain fill, there is apparently a surplus of assimilates which accumulates mainly in the stem (Spiertz, 1977; Stoy, 1965; Barnell, 1938; 1936). The allocation function p_e, as a function of the phenological stage of the canopy is given in Figure 10. As grain growth enters the linear phase the increasing sink demand leads to a more or less gradual depletion of the accumulated reserves (Vos, 1981; Spiertz & van de Haar, 1978; Spiertz, 1977; Stoy, 1965). The linear grain growth rate is, in fact, virtually independent of the current assimilation rate because of the existence of the large reserve pool.

For the determination of p_r, data for winter wheat and spring wheat were combined after adjustment to the appropriate development stages (Welbank et al., 1974). Data of plants grown in nutrient solution were also used (Rawson & Hofstra, 1969; van Dobben, 1962b), showing that the partitioning is very similar to that found for soil-grown plants (Figure 11). Details on the proce-

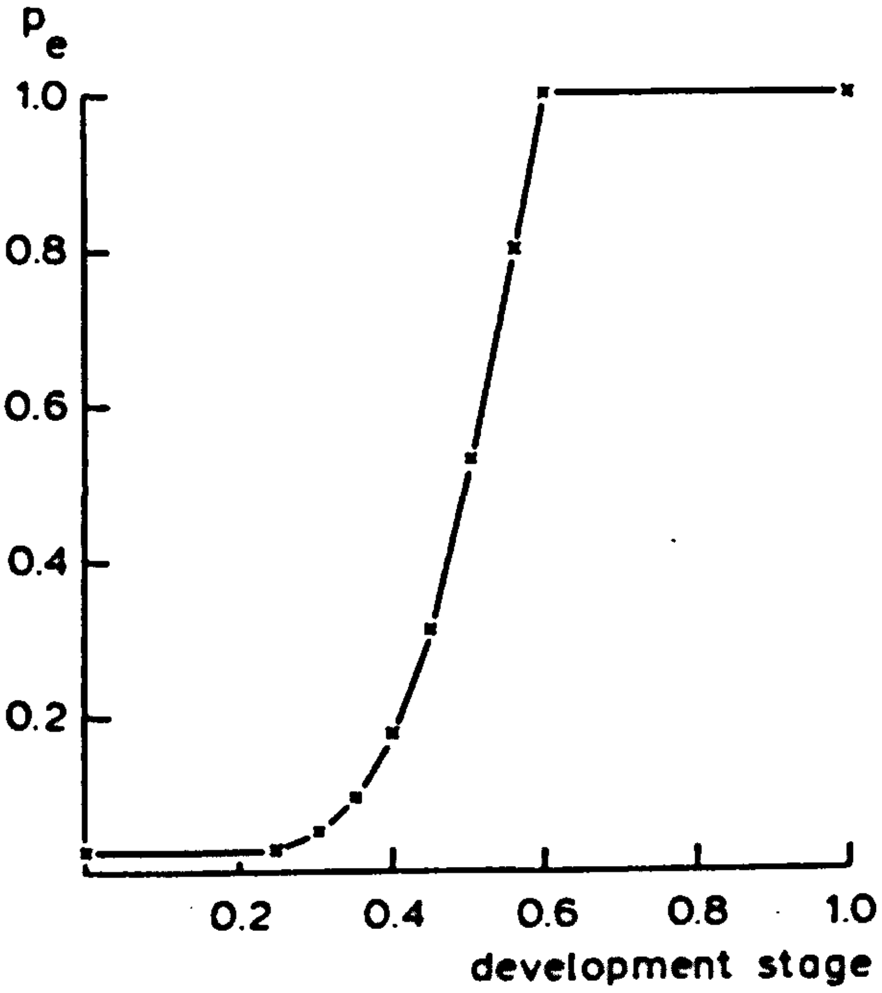

Figure 10. Fraction of current assimilate partitioned to the reserve pool, p_e, as a function of development stage of the crop.

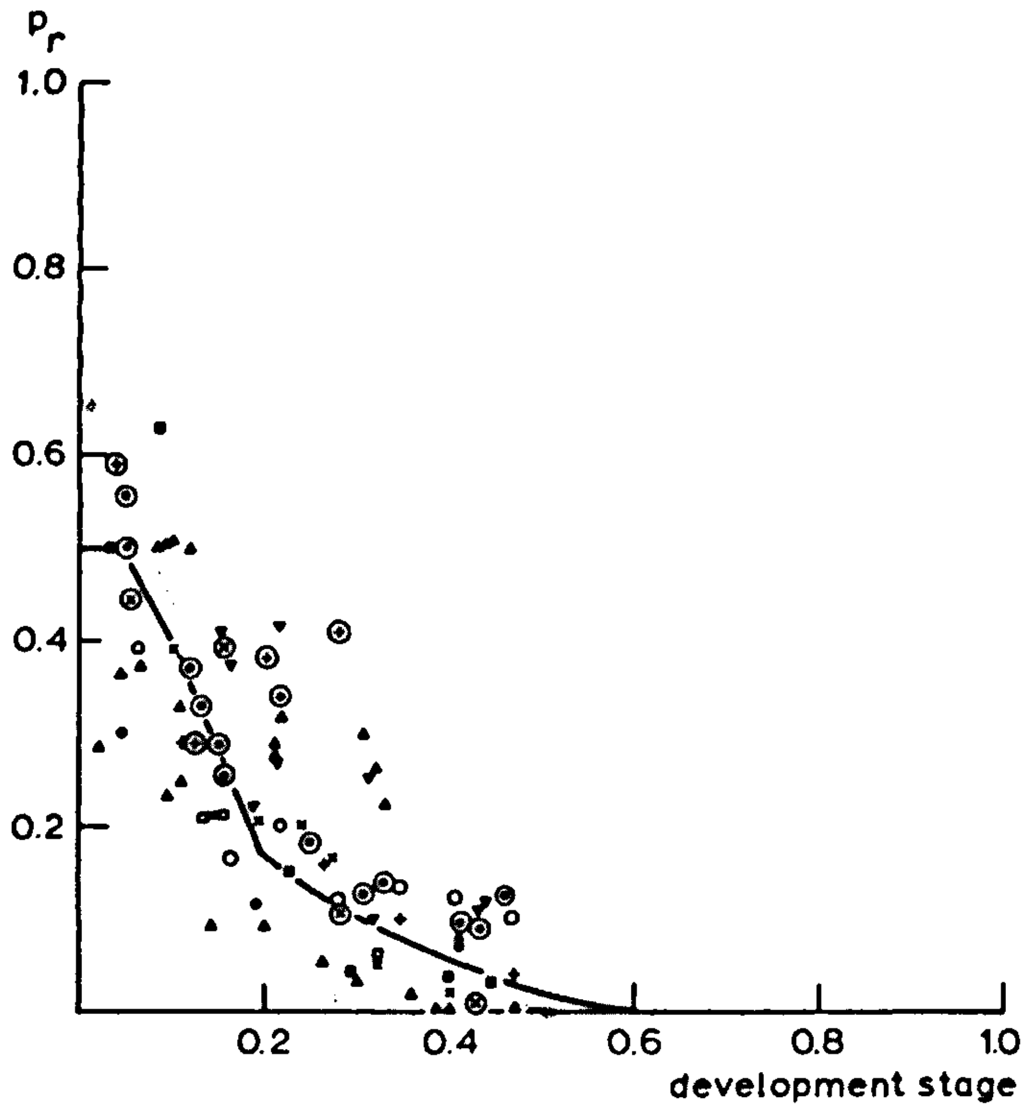

Figure 11. Fraction of current assimilate partitioned to the roots, p_r, as a function of development stage of the crop.
▵ Jonker, 1958 (Table 5); × Jonker, 1958 (Table 4); + van Dobben, 1962a; ⊙ Strebeyko et al., 1963; ○ Rawson & Hofstra, 1969; ▾ Schuurman & Knot, 1970; ⊕ MacDowall, 1972a; · Welbank et al., 1974; ⊗ Campbell et al., 1977b; ■ Gregory et al., 1978; ▿ Campbell & Davidson, 1979a; ▵ Campbell et al., 1983; □ Fischer, 1983. (For details see Table 8).

dure used to derive the values of p_r from the reported data are given in Table 8. Figure 11 shows a rather high investment in the root system in the early stages of growth, gradually declining to zero at anthesis (s_o = 0.5). There is considerable scatter in the data, which may be due to different cultivars, different growing conditions and different measuring techniques that were employed. The eye-fitted curve in Figure 11 which is used in the model, represents the general pattern that emerges from the data.

Data for p_l, the fraction of current assimilate allocated to the leaf blades are summarized in Figure 12 and Table 9. Again, there is considerable scatter between individual points, which may originate from the factors referred to above. The basic pattern that emerges is as follows: as the proportion of assimilate allocated to the roots declines, the proportion allocated to the leaves increases. Around floral initiation, stem extension begins and an increasingly larger proportion of assimilates is diverted to that sink. Leaf and stem growth cease at about anthesis, when the flag leaf has reached its final size.

The fraction allocated to the stems, p_s, is illustrated in Figure 13, details being given in Table 10. The data plotted in Figure 13 refer to the total weight

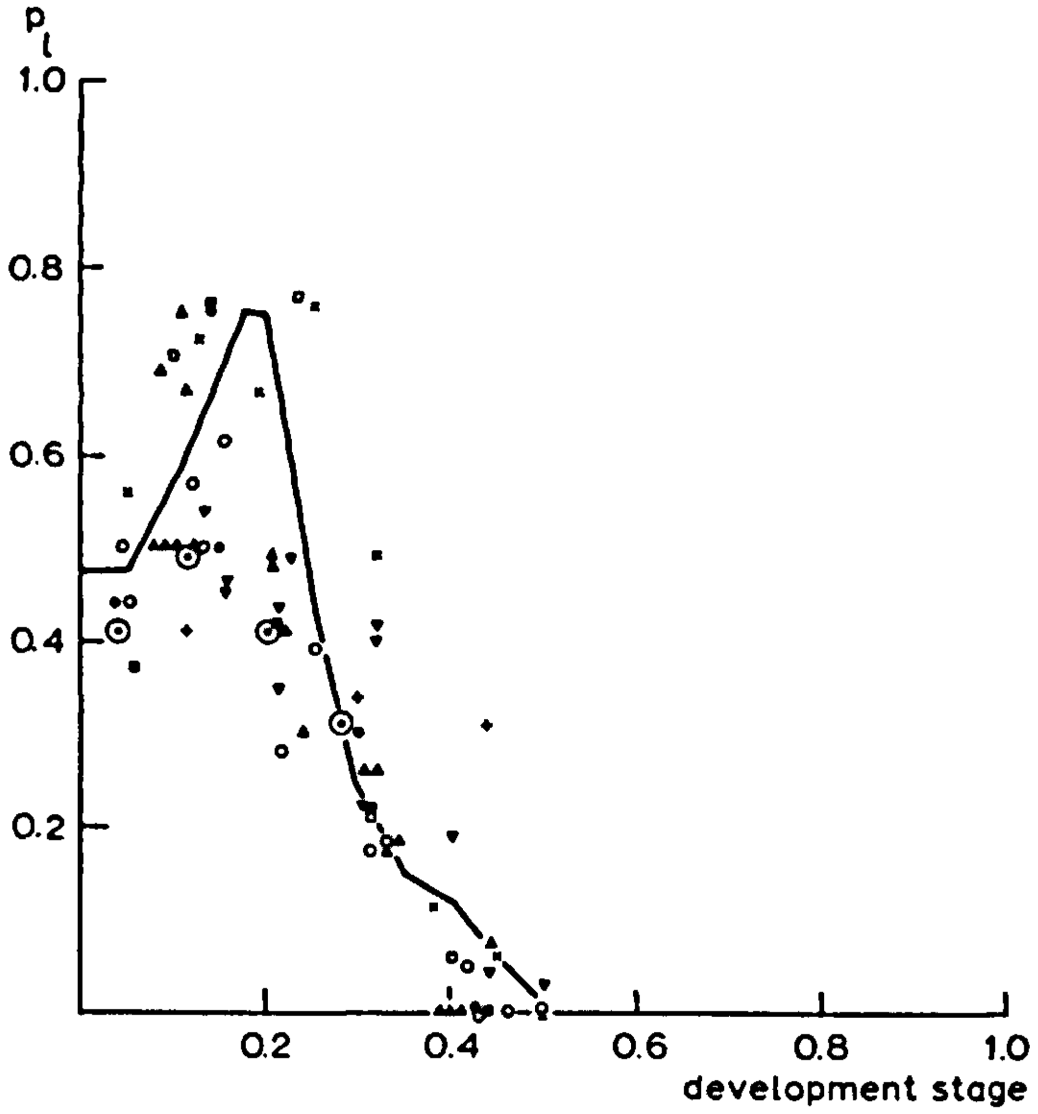

Figure 12. Fraction of current assimilate partitioned to leaf blades, p_l, as a function of development stage of the crop.
□ Boatwright & Haas, 1961; ○ Strebeyko et al., 1963; ▲ McNeal et al., 1966; • Puckridge & Donald, 1967; × Rawson & Hofstra, 1969; + Khan & Tsunoda, 1970d; ■ Spratt & Gasser, 1970; ⊙ MacDowall, 1972a; ▽ Campbell & Davidson, 1979a; ▼ Fischer, 1983; △ Campbell et al., 1983. (For details see Table 9).

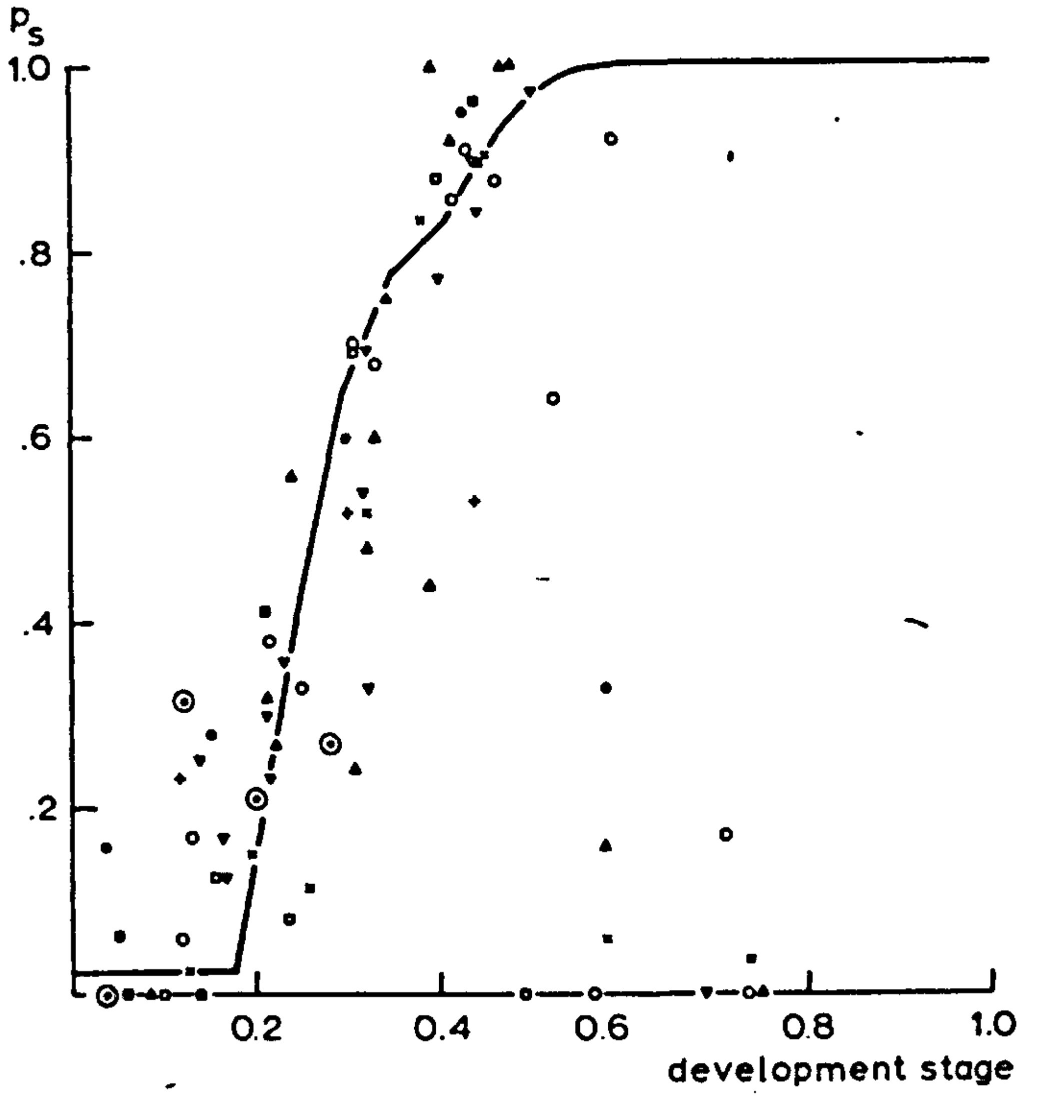

Figure 13. Fraction of current assimilate partitioned to stem plus reserves, p_s, as a function of development stage of the crop.
□ Boatwright & Haas, 1961; ○ Strebeyko et al., 1963; ▲ McNeal et al., 1966; • Puckridge & Donald, 1967; × Rawson & Hofstra, 1969; + Khan & Tsunoda, 1970d; ■ Spratt & Gasser, 1970; ⊙ MacDowall, 1972a; ▽ Campbell & Davidson, 1979a; ▼ Fischer, 1983; △ Campbell et al., 1983 (For details see Table 10).

of the stem, including the unused reserves that may accumulate there. In the model, where we distinguish between structural stem weight and non-structural carbohydrates stored in the stem, the fraction allocated to stem tissue is the difference between p_s as given in Figure 13 and p_e as given in Figure 10.

After cessation of ear formation a number of non-reproductive tillers may persist in the canopy (Section 3.5). In the model it is assumed that these tillers do not increase in size after that moment. Hence, these tillers only use assimilates necessary for their maintenance, while the remainder of their assimilates is assumed to be translocated to the reproductive tillers (Lupton & Pinthus, 1969; Bunting & Drennan, 1966), and is thus included in P_n.

Table 8. Fraction dry matter allocated to the roots (p_r) as a function of development stage (s_o)

Source	s_o	p_r	Details
Jonker, 1958 (Table 4)	0.10	0.39	heading (Feekes scale 10.1) assumed s_o = 0.4; other values of s_o calculated from measured temperatures, applying the relation of Figure 1. Points then situated midway between two measuring dates
	0.148	0.21	
	0.197	0.21	
	0.24	0.20	
	0.28	0.165	
	0.32	0.05	
	0.40	0.02	
Jonker, 1958 (Table 5)	0.02	0.285	
	0.045	0.36	
	0.06	0.37	
	0.09	0.23	
	0.14	0.09	
	0.20	0.09	
	0.26	0.05	
	0.30	0.03	
	0.36	0.02	
Welbank et al., 1974	0.0475	0.305	emergence estimated one week after sowing. Temperature assumed to be: 7.5 °C, 15 °C and 20 °C for April, May and June, respectively. Values of s_o calculated applying the relation of Figure 1.
	0.19	0.116	
	0.41	0.07	
van Dobben, 1962a	0.11	0.29	emergence estimated five days after sowing. s_o calculated as ratio of day number between successive samplings and flowering date
	0.27	0.16	
	0.35	0.10	
	0.42	0.14	
	0.47	0.04	
Gregory et al., 1979	0.035	0.50	anthesis from Figure 1 (Gregory et al, 1979). Values of s_o calculated using average temperatures (Gregory et al., 1981) and the relation of Figure 1 (winter wheat).
	0.09	0.63	
	0.16	0.21	
	0.295	0.04	
	0.44	0.03	

Table 8. (continued)

Source	s_o	p_r	Details
Schuurman & Knot, 1970	0.19	0.22	date of emergence given, s_o calculated from Figure 1, using average temperatures.
	0.42	0.0375	
Rawson & Hofstra, 1969	0.06	0.39	s_o calculated as ratio of number of days of measurement to days of anthesis; points situated midway between observations.
	0.156	0.165	
	0.219	0.20	
	0.281	0.12	
	0.343	0.135	
	0.406	0.12	
	0.469	0.10	
Fischer, 1982	0.137	0.21	Figure 1, s_o calculated as ratio of number of days to measurement and number of days to anthesis.
	0.226	0.15	
	0.315	0.06	
	0.40	0.04	
Strebeyko et al., 1963 1960-exp.	0.045	0.50	s_o calculated as ratio of number of days to measurement and number of days to anthesis
	0.13	0.33	
	0.25	0.28	
	0.33	0.14	
	0.415	0.095	
	046	0.125	
1961-exp.	0.05	0.555	
	0.12	0.37	
	0.155	0.26	
	0.215	0.34	
	0.31	0.125	
	0.43	0.09	
Campbell et al., 1977b	0.055	0.44	s_o calculated as ratio of temperature sum to measuring date and temperature sum to anthesis; data for wet high N treatment
	0.16	0.39	
	0.28	0.105	
	0.43	0.01	
Campbell et al., 1983	0.08	0.5	emergence estimated at five days after sowing; 27/12 °C treatment
	0.11	0.25	
	0.21	0.275	
	0.31	0.30	
	0.39	0.	
	0.09	0.5	22/12 °C treatment
	0.11	0.33	
	0.21	0.29	
	0.32	0.26	
	0.39	0.	
	0.095	0.5	27/12 °C treatment
	0.13	0.5	
	0.22	0.32	
	0.33	0.22	
	0.41	0.08	
	0.47	0.	

Table 8. (continued)

Source	s_0	p_r	Details
Campbell & Davidson, 1979a	0.16	0.40	s_0 derived from ratio of number of days at measurement and number of days to anthesis; Low stress/high N treatment, 22/12 °C
	0.22	0.42	
	0.32	0.10	
	0.43	0.11	
	0.16	0.38	27/12 °C temperature regime
	0.21	0.27	
	0.32	0.225	
	0.44	0.12	
McDowall, 1972a	0.04	0.59	high light treatment
	0.11	0.29	
	0.20	0.38	
	0.28	0.425	

Table 9. Fraction dry matter allocated to the leaves (p_l) as a function of development stage (s_0)

Source	s_0	p_l	Details
Rawson & Hofstra, 1969	0.05	0.56	s_0 calculated as ratio of number of days at measurement and number of days to anthesis. Points situated midway between successive harvests.
	0.13	0.725	
	0.195	0.67	
	0.255	0.76	
	0.32	0.39	
	0.38	0.11	
	0.45	0.06	
	0.5	0.	
Puckridge & Donald, 1967	0.035	0.44	Emergence estimated at 10 days after sowing. Average temperatures assumed from Doyle & Fischer, 1977. Values for 'normal' density. Fraction to roots estimated from Figure 11.
	0.15	0.50	
	0.30	0.30	
	0.425	0.005	
Khan & Tsunoda, 1970d	0.115	0.41	Average values for the two spring wheat varieties. Growth temperature estimated at 15 °C (Khan & Tsunoda, 1970c).
	0.30	0.34	
	0.44	0.31	
McNeal et al., 1966	0.0875	0.69	Figure 2, average of five varieties. Measured increase after June 28 partitioned: 50% to leaf blades, 50% to sheaths. Fraction to roots estimated from Figure 11.
	0.24	0.30	
	0.3425	0.185	
	0.4425	0.075	

Table 9. (continued)

Source	s_o	p_l	Details
Spratt & Gasser, 1970	0.0575	0.37	s_o calculated as ratio of number of days to measurement and anthesis day. Average of high N-treatments. Fraction to root estimated from Figure 11.
	0.1425	0.76	
	0.21	0.42	
	0.3125	0.22	
	0.4375	0.	
Fischer, 1982	0.137	0.54	s_o calculated as ratio of number of days to measurement and anthesis day.
	0.226	0.49	
	0.315	0.40	
	0.40	0.19	
	0.50	0.03	
Strebeyko et al., 1963 1960-exp.	0.045	0.50	s_o calculated as ratio of number of days to measurement and anthesis day. Curves smoothed before interpolation.
	0.13	0.50	
	0.25	0.39	
	0.33	0.18	
	0.415	0.05	
	0.46	0.0	
1961-exp.	0.05	0.445	
	0.12	0.57	
	0.155	0.615	
	0.215	0.28	
	0.31	0.175	
	0.43	0.	
Boatwright & Haas, 1961	0.10	0.71	s_o calculated as ratio of number of days to measurement and anthesis date. Fraction to roots estimated from Figure 11.
	0.235	0.77	
	0.31	0.21	
	0.40	0.06	
	0.495	0.02	
Campbell et al., 1983	0.08	0.5	emergence estimated at five days after sowing. 27/22 °C treatment
	0.11	0.75	
	0.21	0.48	
	0.31	0.26	
	0.39	0.	
	0.09	0.5	22/12 °C treatment
	0.11	0.67	
	0.21	0.39	
	0.32	0.26	
	0.39	0.	
	0.095	0.5	17/12 °C treatment
	0.13	0.5	
	0.22	0.41	
	0.33	0.18	
	0.41	0.	
MacDowall, 1972a	0.04	0.41	s_o estimated from Figure 1; high light treatment
	0.11	0.39	
	0.20	0.41	
	0.28	0.305	

Table 10. Fraction dry matter allocated to the stem (p_s) as a function of development stage (s_o)

Source	s_o	p_l	Details
Rawson & Hofstra, 1969	0.05	0.065	see Table 9
	0.13	0.025	
	0.195	0.15	
	0.255	0.115	
	0.32	0.52	
	0.38	0.835	
	0.45	0.90	
	0.58	0.06	
	0.74	0.04	
Puckridge & Donald, 1967	0.035	0.16	see Table 9. For period after anthesis total production estimated by assuming constant leaf weight; difference between ear weight and grain weight added to stem weight
	0.15	0.28	
	0.30	0.60	
	0.425	0.95	
	0.58	0.33	
Khan & Tsunoda, 1970d	0.115	0.23	see Table 9
	0.30	0.52	
	0.44	0.53	
McNeal et al., 1966	0.0875	0.	see Table 9. For period after anthesis total production estimated by assuming constant leaf weight
	0.24	0.56	
	0.3425	0.75	
	0.4425	0.89	
	0.58	0.16	
	0.75	0.	
Spratt & Gasser, 1970	0.0575	0.	see Table 9. Leaf weight assumed constant for calculation of total production after anthesis.
	0.1425	0.	
	0.21	0.415	
	0.3125	0.695	
	0.4375	0.96	
	0.575	0.24	
	0.745	0.	
Fischer, 1982	0.14	0.25	see Table 9. For period after anthesis spike weight added to stem weight.
	0.23	0.36	
	0.315	0.54	
	0.40	0.77	
	0.50	0.97	
	0.69	0.	
Strebeyko et al., 1963 1960-exp.	0.045	0.	see Table 9.
	0.13	0.17	
	0.25	0.33	
	0.33	0.68	
	0.415	0.855	
	0.46	0.875	
	0.59	0.92	
	0.71	0.17	
	0.74	0.	

Table 10. (continued)

Source	s_o	p_l	Details
1961-exp.	0.05	0.	
	0.12	0.06	
	0.155	0.125	
	0.215	0.38	
	0.31	0.70	
	0.43	0.91	
	0.525	0.64	
	0.57	0.	
Boatwright & Haas, 1961	0.10	0.	see Table 9.
	0.235	0.08	
	0.31	0.695	
	0.40	0.88	
	0.495	0.	
Campbell et al., 1983	0.08	0.	emergence estimated at five days after sowing. 27/22 °C treatment
	0.11	0.	
	0.21	0.245	
	0.31	0.44	
	0.39	1.0	
	0.465	1.0	
	0.09	0.	22/12 °C temperature regime
	0.11	0.	
	0.21	0.32	
	0.32	0.48	
	0.39	1.0	
	0.46	1.0	
	0.095	0.	27/12 °C temperature regime
	0.13	0.	
	0.22	0.27	
	0.33	0.60	
	0.41	0.92	
	0.47	1.0	
Campbell & Davidson, 1979a	0.16	0.13	s_o derived from ratio of number of days at measurement and number of days at anthesis. Low stress/ high N treatment; 27/12 °C temperature regime
	0.22	0.23	
	0.32	0.69	
	0.43	0.90	
	0.16	0.17	22/12 °C temperature regime
	0.21	0.30	
	0.32	0.33	
	0.44	0.84	
MacDowall, 1972a	0.04	0.	high light
	0.11	0.32	
	0.20	0.21	
	0.28	0.27	

3.4.3 Dry matter production

Non-grain tissue

The assimilates allocated to the various sinks are in the form of primary photosynthetic products i.e. a mixture of carbohydrates and nitrogenous compounds. These primary products have to be converted into structural plant material. Although the assimilate supply, P_n, is designated 'net' assimilation, the energy required for the conversion of these primary products into structural plant material has not yet been taken into account. The magnitude of growth respiration depends on the chemical composition of the material being formed (Penning de Vries et al., 1974; Penning de Vries, 1974). In the present formulation the latter is defined in terms of proteins and carbohydrates only, as these constitute the major part of the plant material. The proteins are assumed to be formed from nitrates only, so that the costs of reduction have to be taken into account.

The rate of increase in dry weight of leaves, stems and roots, w_x, is thus obtained from:

$$w_x = \epsilon_{cx} \cdot P_{nx} \tag{56}$$

where

ϵ_{cx} is efficiency of conversion of primary photosynthates (carbohydrates) into structural dry matter for each organ (kg kg^{-1})
P_{nx} is carbohydrate supply to the organ (kg ha^{-1} d^{-1})

The conversion efficiency is calculated as:

$$\epsilon_{cx} = \gamma_x \cdot \epsilon_{pr} + (1-\gamma_x)\, \epsilon_{ch} \tag{57}$$

where

γ_x is fraction of proteins in the vegetative tissue of the organ, equal to 6.25 n_{ax}
ϵ_{pr} is efficiency of conversion for proteins (kg kg^{-1})
ϵ_{ch} is efficiency of conversion for structural carbohydrates (kg kg^{-1})

It should be noted that in this formulation the tissues formed on a particular day are regarded as equal in composition to the existing tissues. The growing material generally has a higher protein concentration than the average of all material, so that the calculated efficiency would be too high, if not for the fact that part of the proteins for synthesis of new tissue originates from translocation. For that fraction nitrate reduction does not have to be taken into account.

Dry matter accumulation in the grain

The rate of dry matter accumulation in the grain may be limited by the supply of assimilates (source) or by the potential rate of accumulation in the grains (sink). From various studies it appears that the rate of dry weight accumulation in the grains is fairly constant during a substantial part of the grain filling period (Vos, 1981; Sofield et al., 1977a; Spiertz, 1977; to cite only a few references). This is possibly because of the relatively massive accumulation of reserve carbohydrates that normally occurs around anthesis, mainly in the stem (Figure 10).

On the basis of the foregoing reasoning, dry matter accumulation in the grains is described by:

$$w_g = \min (w_p, w_a) \tag{58}$$

where

w_g is rate of accumulation of dry matter in the grains (kg ha^{-1} d^{-1})
w_p is potential rate of dry matter accumulation in the grains (kg ha^{-1} d^{-1})
w_a is limiting rate of assimilate supply to the grains expressed in terms of dry matter (kg ha^{-1} d^{-1})

The potential rate of dry matter accumulation is obtained from:

$$w_p = g \cdot w_r \tag{59}$$

where

g is number of grains set
w_r is potential rate of dry matter accumulation per individual grain (kg d^{-1})

The potential rate of dry matter accumulation per grain is a function of temperature, as illustrated in Figure 14, which is derived from various sources. This potential rate could be a species characteristic as suggested for instance by

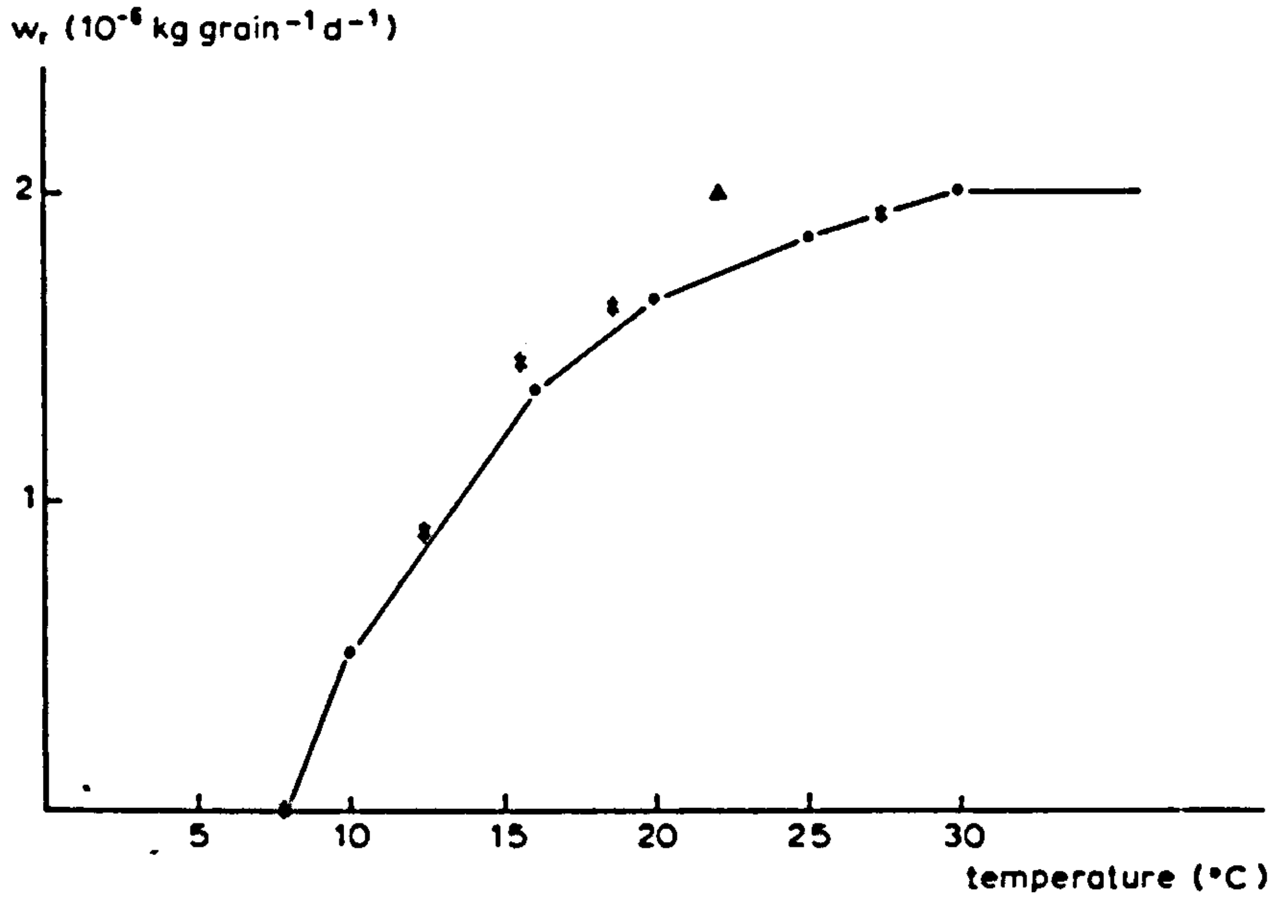

Figure 14. Potential growth rate of individual grains, w_r, as a function of canopy temperature.
* Sofield et al., 1977a; ▲ Waters et al., 1980.

Stamp & Geisler (1976), but it could well be that differences observed between cultivars are related to grain numbers, rather than to the inherent potential of individual grains for dry matter accumulation.

The total assimilate supply to the grain, is calculated as:

$$P_{ng} = (1 - c_r) \cdot W_{rs}/\tau_{tr} \tag{60}$$

where,

P_{ng} is rate of carbohydrate supply to the grains (kg ha^{-1} d^{-1})
c_r is residual non-remobilizable concentration of non-structural carbohydrates in the plant (dimensionless)

The rate of dry matter increase that can be sustained by this carbohydrate supply equals:

$$w_a = P_{ng} \cdot \epsilon_{cg} \tag{61}$$

where

ϵ_{cg} is efficiency of conversion of primary photosynthates into grain dry weight

The efficiency is calculated in the same way as for the other organs:

$$\epsilon_{cg} = \gamma_g \cdot \epsilon_{prg} + (1 - \gamma_g) \cdot \epsilon_{ch} \tag{62}$$

where

γ_g is fraction of proteins in the grains, calculated as $\gamma_g = 5.7\ n_{ag}$
ϵ_{prg} is conversion efficiency of plant protein into grain protein

3.5 Nitrogen balance in the crop

3.5.1 Nitrogen uptake

Uptake of nitrogen is dependent on the demand for nitrogen by the plant and its availability in the soil. Nitrogen is needed in the plant for the synthesis of new tissue, so that as the plant grows the demand for nitrogen increases, but with the accumulation of more structural carbohydrates, the ratio of nitrogen to total biomass of each of the plant parts falls (van Dobben, 1962b; 1960) even when nitrogen is available in surplus (Vos, 1981; Seligman et al., 1976; Dilz, 1964; van Burg, 1962). Initially the total nitrogen concentration in the leaves is that of young leaf tissue (around 0.07) and towards maturity it falls to around 0.01 when nitrogen supply is non-limiting (Table 11; Figures 15, 16 and 17). Under similar conditions, the nitrogen concentration in stem tissue falls from around 0.05 at the onset of stem elongation to about 0.003 at maturity (Table 12, Figures 15, 16 and 17). Maximum nitrogen concentrations in the root are much more variable than in the shoot and appear to be much higher

Table 11. Optimum nitrogen concentration in the leaves (n_l) as a function of development stage (s_o)

Source	s_o	n_l	Details
Boatwright & Haas, 1961	0.20	0.0487	s_o calculated as ratio of days to observation and days to anthesis plus ratio days from anthesis to days to maturity; leaves include leaf sheaths; data from NP treatment.
	0.27	0.0425	
	0.355	0.0256	
	0.45	0.0206	
	0.66	0.0143	
	1.0	0.0100	
McNeal et al., 1966	0.175	0.0451	s_o calculated as in previous example; leaves include leaf sheaths; average of 5 cultivars
	0.30	0.0405	
	0.385	0.0395	
	0.50	0.0313	
	0.66	0.0273	
	1.0	0.0189	
van Dobben, 1961	0.125	0.0550	s_o calculated as ratio of temperature sums. First two samplings only leaf tissue; Figure 2; Figure 1.
	0.19	0.0440	
	0.22	0.0530	
Campbell et al., 1977a	0.11	0.0549	s_o calculated as ratio of temperature sum to observation date to that at anthesis. Assumed first two samplings leaf blades only
	0.205	0.0473	

Table 12. Optimum nitrogen concentration in the stem (n_s) as a function of development stage (s_o)

Source	s_o	n_s	Details
Boatwright & Haas, 1961	0.355	0.0197	s_o calculated as ratio of days to observation and days to anthesis plus ratio days from anthesis to days from anthesis to maturity; stems do not include sheaths, but do include chaff; data from NP treatment
	0.45	0.0133	
	0.66	0.0096	
	1.0	0.0034	
McNeal et al., 1966	0.30	0.0216	s_o calculated as in previous example; stems without sheaths, chaff not clear; average of 5 cultivars.
	0.385	0.0200	
	0.50	0.0131	
	0.66	0.0113	
	0.84	0.0082	
	1.0	0.0056	

Table 13. *Optimum nitrogen concentration in the roots (n_r) as a function of development stage (s_o)*

Source	s_o	r	Details
Campbell et al., 1977b	0.11	0.0172	s_o calculated as ratio of temperature sum till observation date to temperature sum at anthesis. n_r calculated from tables 3 and 4 for wet, high N treatment.
	0.205	0.0217	
	0.36	0.0153	
	0.50	0.0105	
	1.0	0.0110	
Bosemark, 1954	0.08	0.0360	s_o calculated from relation in Figure 1
van Dobben, 1960	0.215	0.0267	s_o calculated from temperature data and day of anthesis.
	0.32	0.0237	
	0.38	0.0228	
	0.44	0.0218	
	0.50	0.0204	

in water culture than in sand and peat substrate (Table 13, Figure 19). Appropriate values under conditions of surplus supply from the soil would be about 0.035 at seedling emergence to 0.005 at maturity.

The nitrogen demand of any plant part at any point in time is defined as the difference between the maximum amount attained under optimum N-supply and the actual amount in the tissue at that moment. When nitrogen supply is non-limiting, there is a negative linear relationship between the nitrogen concentration of plant organs, n_{xx}, and the development stage of wheat (Figs. 15-19; Table 14). The limiting nitrogen concentration of the mature tissues is attained approximately at the end of the grain filling stage. Hence,

$$d_x = W_x (n_{xm} - n_{ax}) \tag{63}$$

$$n_{xm} = n_{yx} \cdot \max(0, (s_{eg} - s_o)/s_{eg}) + n_{mx} \tag{64}$$

where

d_x is nitrogen demand (or nitrogen deficiency) of the plant or organ (kg ha^{-1})
W_x is weight of plant or organ (kg ha^{-1})
n_{xm} is maximum nitrogen concentration at the current development stage
n_{ax} is current nitrogen concentration in the plant or organ
n_{yx} is the range in nitrogen concentration between young tissue of plant or organ and mature tissue
n_{mx} is nitrogen concentration in mature tissue of plant or organ
s_o is current development stage of the plant or organ (Section 3.2)
s_{eg} is development stage at the end of grain fill

The total nitrogen demand of the plant or the canopy, d_t, is then the sum

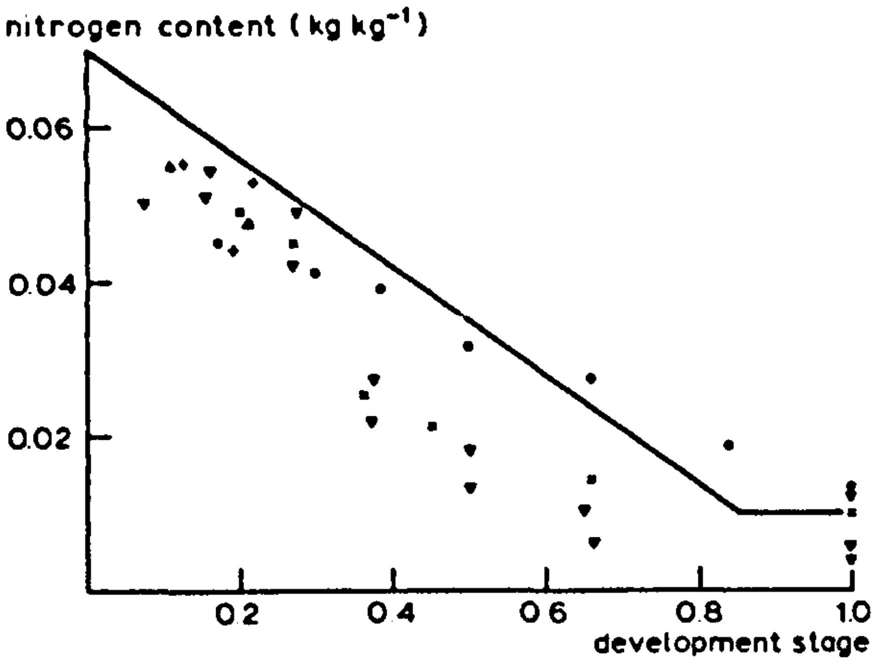

Figure 15. Maximum nitrogen content in leaf blades as a function of development stage of the crop. Solid line used in the model. x Boatwright & Haas, 1961; + van Dobbem, 1962a; ● McNeal et al., 1966; ▲ Campbell et al., 1977; ▼ Campbell & Davidson, 1977a. (For details see Table 11).

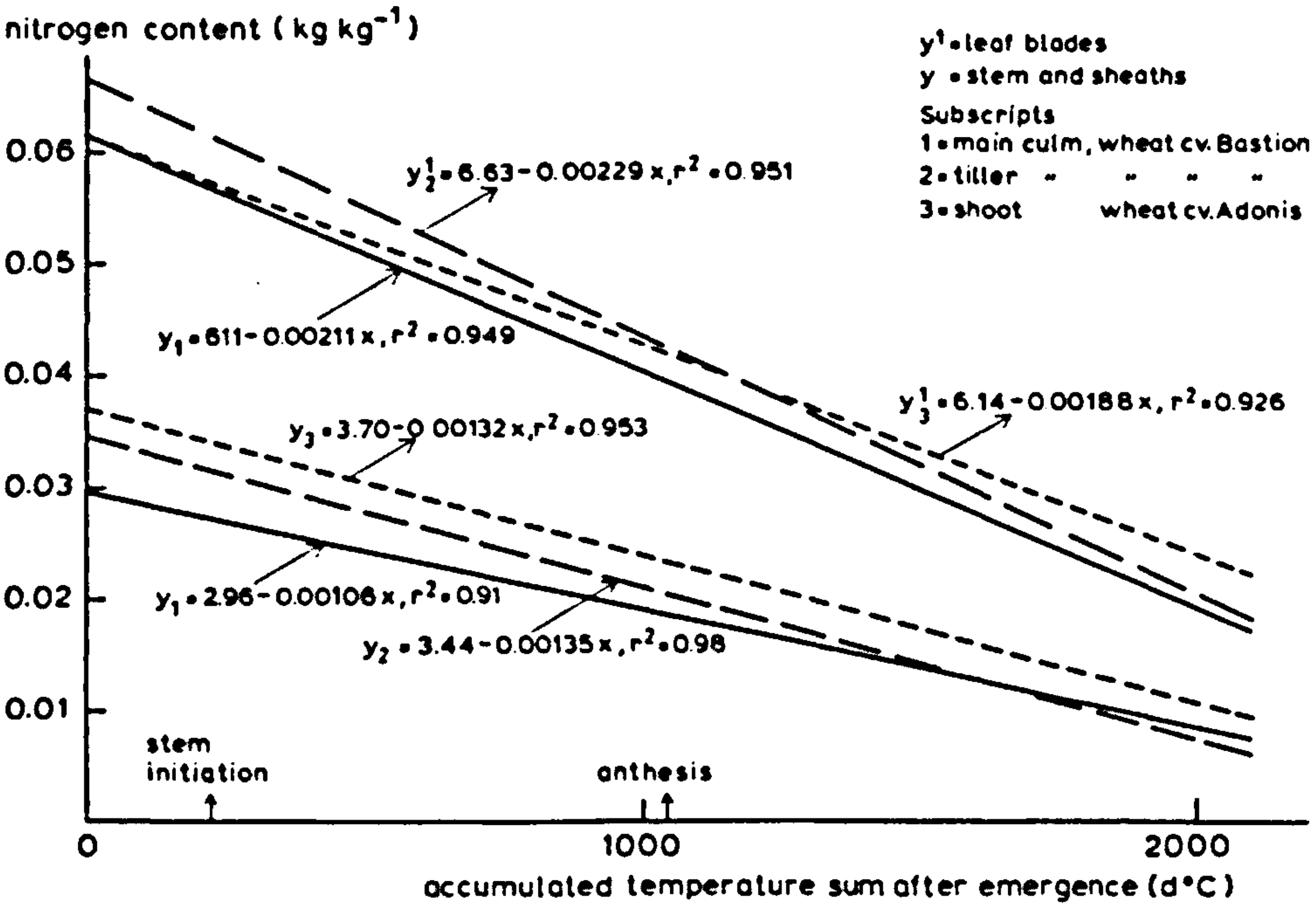

Figure 16. Relation between temperature sum after emergence and nitrogen content in leaf blades and (stems + sheaths) of wheat (Source: Vos, 1981).

of the nitrogen demands of the component parts or organs. In the present model, this is the sum of the nitrogen demand of the leaves, the 'stem' and the roots. Grain nitrogen is supplied by translocation from the vegetative organs and so does not contribute directly to nitrogen demand.

Availability of nitrogen to the plant depends both on the amount present in the soil and on the extent and density of the plant's root system (van Keulen et al., 1975). In the wheat crop, root density is generally relatively high, (i.e. greater than 1 cm root length cm^{-3} soil, e.g. Gajri & Prihar, 1985; Alston,

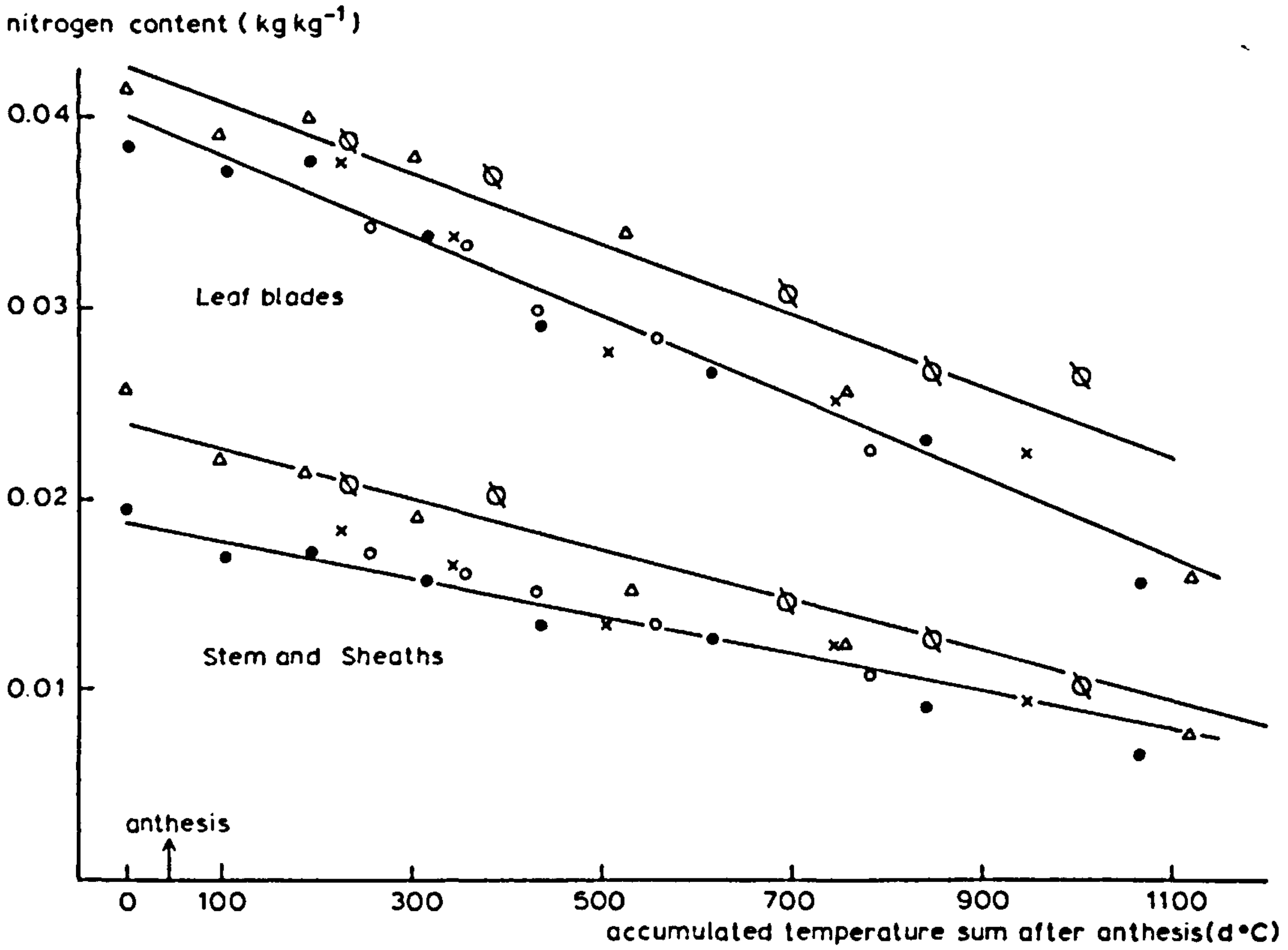

Figure 17. Relation between temperature sum after anthesis and nitrogen content in leaf blades and (stem + sheaths) of wheat (Source: Vos, 1981).

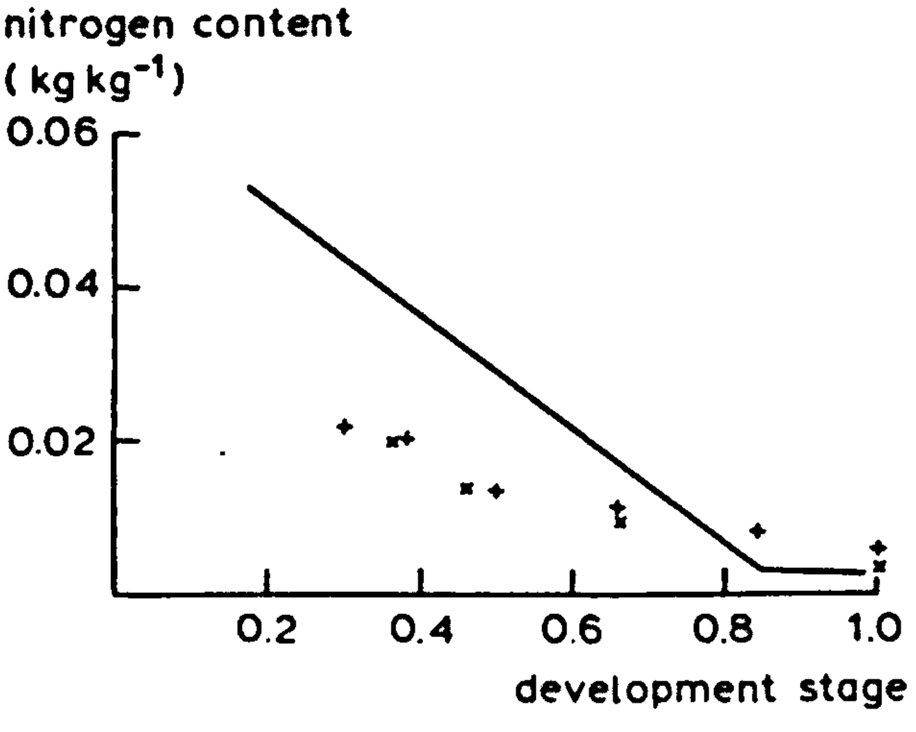

Figure 18. Maximum nitrogen content in stem + sheaths tissue as a function of development stage of the crop. Solid line used in the model. × Boatwrigth & Haas, 1961; + McNeal et al., 1966. (For details see Table 12).

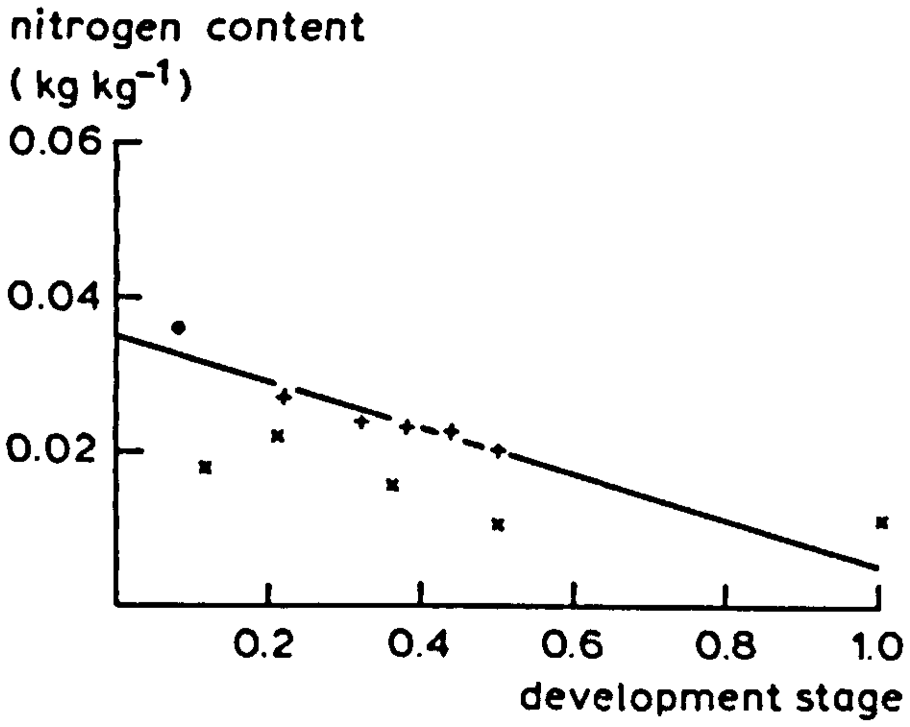

Figure 19. Maximum nitrogen content in roots as a function of development stage of the crop. Solid line used in the model.
x Campbell et al., 1977; · Bosemark, 1954; + van Dobben, 1960. (For details see Table 13).

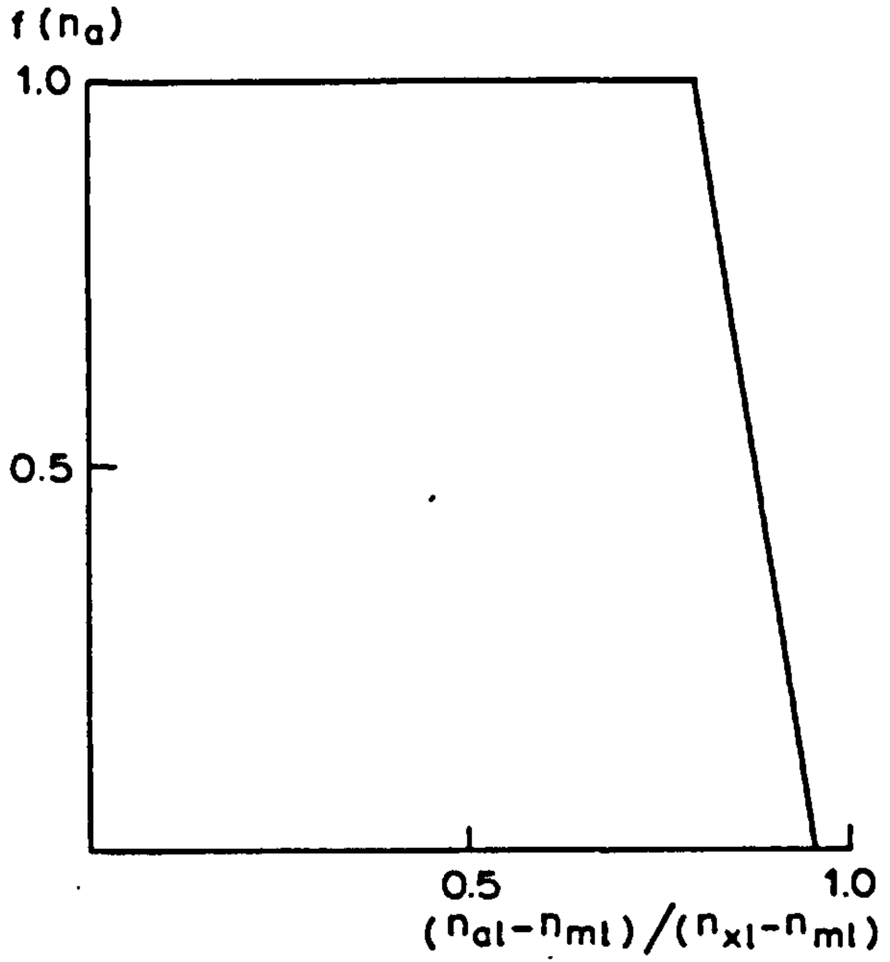

Figure 20. Relation between relative nitrogen concentration in live leaf blade tissue and in dying leaf blade tissue.

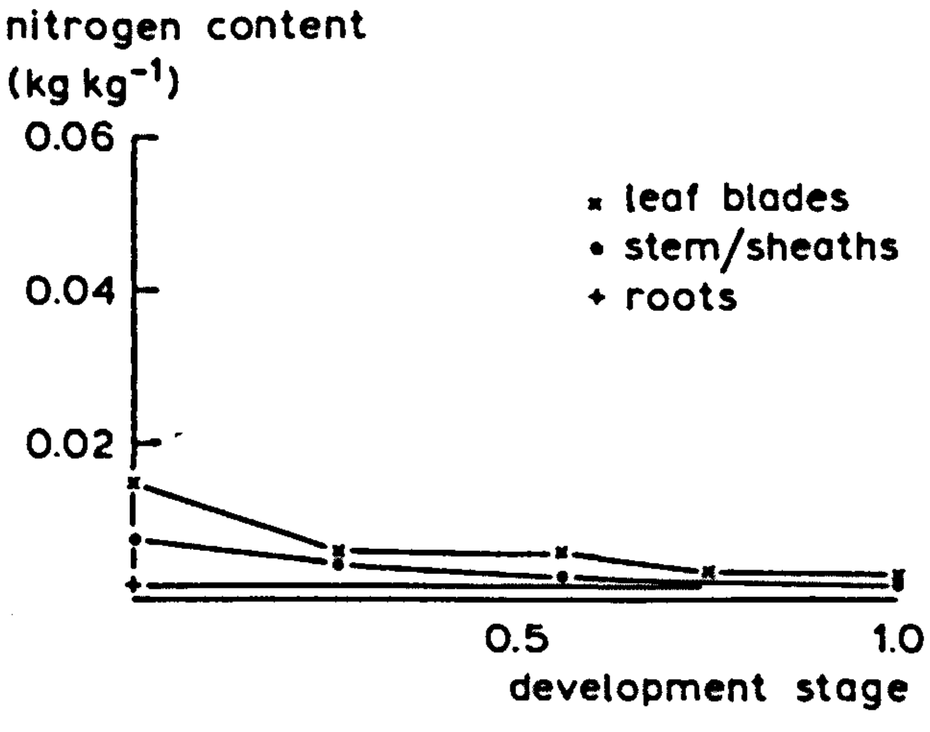

Figure 21. Residual nitrogen content in leaf blades, stem + sheaths and roots as a function of development stage of the crop.

1976; Lupton et al., 1974; Schultz, 1974; Baldy, 1973), and so would make most of the mineral nitrogen in the rooted zone available for uptake within one day and almost all within two days, provided that all or the greater part of that nitrogen is present in the form of nitrates. In that case, the surplus demand of the crop, above that supplied by mass flow can be supplied by diffusion, even when mass flow is very low. Early in the season, before the root system of the plant or crop is fully expanded horizontally, some of the soil nitrogen, even within the rooted depth may be unavailable. This cannot be simulated directly without horizontal subdivision of soil layers. Instead, it is approximated by a maximum uptake rate, u_x, which is determined by the extent of the root system. This presumably would be related to plant cover, which is then used as a measure of horizontal root extension. Nitrogen uptake, u_n, can thus be defined as:

$$u_n = \min (d_t/\tau_u,\ N_s/\Delta,\ u_x) \qquad (65)$$

where

d_t	is total nitrogen demand of the crop (kg ha^{-1} d^{-1})
τ_u	is time constant for nitrogen uptake, between 1 and 2 days
N_s	is available mineral nitrogen in the rooted zone (kg ha^{-1})
Δ	is the time step of integration (1 day in the present model)
u_x	is maximum uptake rate, limited by the translocation capacity of the root system (kg ha^{-1} d^{-1})

The formulation of Equation 65 implies that u_n cannot exceed d_t, so that if demand is satisfied, further uptake of nitrogen is actively prevented, i.e. excess nitrogen reaching the root surface by the transpiration stream is excluded. This phenomenon occurs in experiments with plants grown on nutrient solutions, where total uptake levels off beyond a certain concentration of nitrogen in the solution even though transpiration continues (cf. Alberda, 1965). This also occurs in the field where uptake by the vegetation levels off at high application rates (cf. Prins et al., 1981). This would not be the case if all the nitrogen in the soil solution was passively taken up during transpiration.

The maximum uptake rate is defined by:

$$u_x = u_c\ (1\text{-}e^{(-0.5(W_l + W_s)/f_c)}) \qquad (66)$$

where

u_c	is potential uptake rate of a closed canopy (kg ha^{-1} d^{-1})
W_l, W_s	is dry weight of live leaves and stems, respectively (kg ha^{-1})
f_c	is a factor that converts weight to relative area.

The parameter f_c can be estimated by setting $W_l + W_s$ equal to the minimum shoot weight necessary for attaining the maximum uptake rate. If $W_l + W_s$ equals 1000 kg ha^{-1}, $u_c = 6$ kg ha^{-1} d^{-1} and $u_x = 5.99$ kg ha^{-1} d^{-1}, then $f_c = 78$ kg ha^{-1}. When $u_x = 5.9$, then f_c would be 122. In the present model,

f_c is set at 100.

3.5.2 *Distribution of nitrogen in the plant*

The current uptake of nitrogen is distributed among the various vegetative plant organs, leaves, stems and roots, in proportion to their relative demands. When supply is limited, roots do not have first priority despite their closeness to the source (van Keulen, 1981b; van Dobben, 1963).

When the leaves die, some of their nitrogen can be transferred to other tissues, where an unsatisfied demand for nitrogen exists. The nitrogen concentration in the dying leaf tissue depends on the current concentration in the live leaf tissue, i.e.

$$r_{nl} = r_{dt} \cdot (n_{al} - (n_{al} - n_{ml})) \cdot f(n_a) \qquad (67)$$

where

r_{nl} is rate of nitrogen loss from live leaf tissue (kg ha^{-1} d^{-1})
r_{dt} is rate of decline in live leaf weight (kg ha^{-1} d^{-1}); Eqn. 98
n_{al} is current nitrogen concentration in life leaf blade tissue
n_{ml} is residual non-remobilizable nitrogen concentration in live leaf blade tissue

$$n_a = (n_{al} - n_{ml})/(n_{xl} - n_{ml}),\ 0 \leq n_a \leq 1 \qquad (68)$$

where

n_{xl} is maximum concentration of nitrogen in live leaf blades, function of development stage.

The function $f(n_a)$ is illustrated in Figure 20.

The unavailable level of nitrogen in the leaves, stems and roots is a function of the development stage of the vegetation (Figure 21), as younger parts die with a higher residual N content (Seligman, unpubl. data; Dilz, 1964). Some of the translocatable N of dying leaves can be used to satisfy the N demand of other organs, primarily the stem. In this way the stem serves as temporary store for N before translocation to the grain. Indications of an increase in stem N during early grain fill have been noted in the data used for calibration of the present model (Chapter 5). When tillers die, only a residual level of N remains in the dead stem, n_{ms}, the other part being translocated to the live leaf and stem tissue. Leaves on dying tillers are treated like any other leaves.

3.5.3 *Translocation of nitrogen to the growing seed*

Seeds receive most of their nitrogen in a reduced form, generally as amino acids that are translocated from the roots, leaves and stems (Donovan & Lee, 1978; Nair et al., 1978; Beevers & Hageman, 1969). From various studies, it appears that the rate of nitrogen accumulation in the grains is fairly constant during the linear phase of grain growth (Vos, 1981; Donovan & Lee, 1978; Sofield et al., 1977b). The actual rate of accumulation at any moment may be limited by the potential rate of accumulation in the grain (Donovan & Lee, 1978; 1977) or by the supply rate from the vegetative parts. The rate of nitrogen depletion from the vegetative parts of the plants is fairly constant as long as the nitrogen concentration in the tissue is above a threshold level of around 0.01 (Dalling et al., 1976; 1975). As the amount of nitrogen in the vegetative parts declines and the concentration approaches the residual level, the rate of depletion drops (Dalling et al., 1976; 1975). The rate of transfer and the uptake rate by the seeds are dependent on temperature (Vos, 1981; Spiertz, 1977) with a Q_{10} value of around 2 (Vos, 1981). The constant rate of depletion can be interpreted as withdrawal from a turning-over pool of amino acids (Hanson & Hitz, 1983) that is maintained at a more or less constant level, when calculated on an integrated daily basis. As the amino acids are transferred to the grain, storage or relatively stable proteins, like RuBPcase are mobilized (Friedrich & Huffaker, 1980). This is effected by a rise in proteolases at the onset of grain growth and nitrogen depletion. The level of proteolase stays relatively high and drops only as the grain approaches maturity (Dalling et al., 1976). This process of nitrogen depletion in the vegetative parts and translocation to the grain can be represented as follows:

$$v = \min(v_e, v_p) \tag{69}$$

where

v is rate of nitrogen transfer from the vegetative parts to the developing grains (kg ha^{-1} d^{-1})

v_e is current maximum rate of export of nitrogen from the vegetative parts (kg ha^{-1} d^{-1})

v_p is potential rate of nitrogen accumulation in the grains (kg ha^{-1} d^{-1})

$$v_e = f_t \cdot N_e \cdot e \tag{70}$$

where

f_t is relative rate of nitrogen turnover in the vegetative plant parts (d^{-1})

N_e is available nitrogen in the vegetative plant parts (excluding the residual sequestered mainly cell wall nitrogen) (kg ha^{-1})

e is fraction of labile nitrogen exported, function of n_v (derived from Dalling et al., 1976; Figure 22)

$$f_t = f_x \cdot q \cdot m \cdot r \tag{71}$$

$$n_v = N_e/(W_l + W_s + W_r) \tag{72}$$

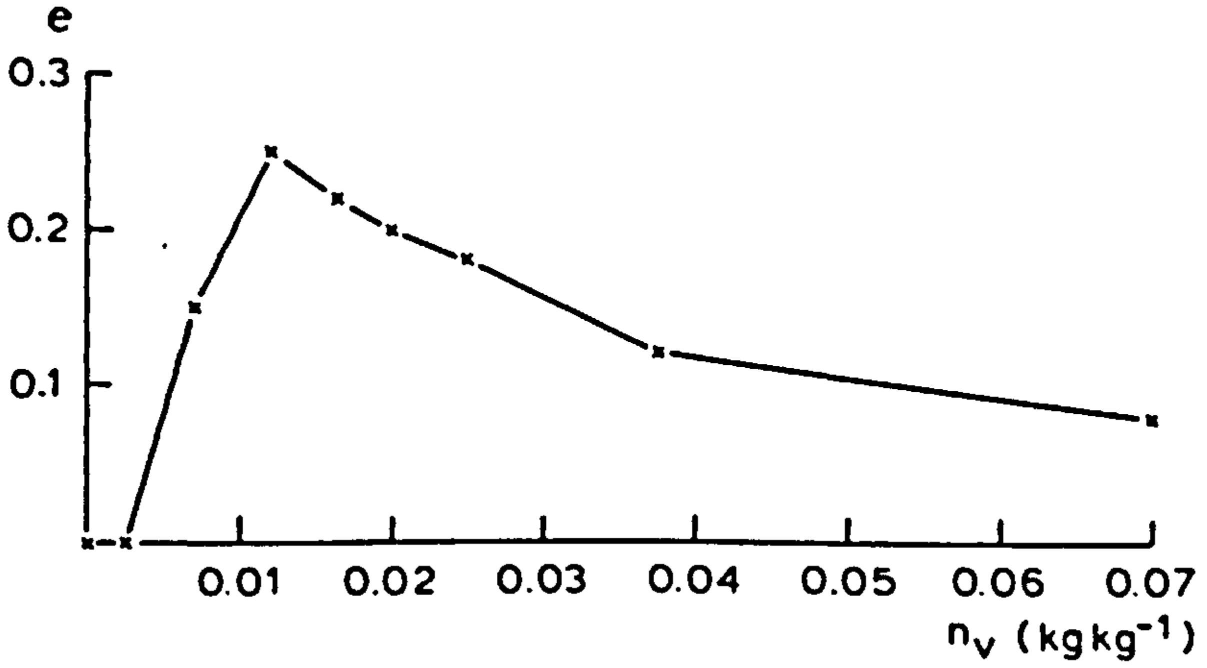

Figure 22. Fraction of labile nitrogen translocated, e, as a function of overall average content of available nitrogen in vegetative tissue.

where

f_x is basic relative rate of nitrogen turnover in vegetative tissue estimated at 0.25, at 20 °C
q is value of the temperature effect on nitrogen turnover
m is effect of water stress on nitrogen turnover
r is the effect of available carbohydrate reserves on nitrogen turnover. If the reserve pool is exhaused, the turnover rate is assumed to increase by a factor 1.2
n_v is overall average concentration of available nitrogen in the vegetative plant parts

The temperature effect is based on the relationship between translocation and temperature reported by Spiertz (1977).

The effect of water-stress on nitrogen turnover is difficult to disentangle from senescence. Under water-stressed conditions the nitrogen concentration of the leaf at maturity is generally higher (Halse et al., 1969; Fischer & Kohn, 1966c; Asana & Basu, 1963), probably because rapid senescence reduces the period available for translocation. Yet as the tissues senesce due to water stress, protein breakdown is accelerated (Lal & Sharma, 1973) and rebuilding of proteins is suppressed (Brady et al., 1974). It is therefore assumed that when the transpiration rate is reduced to that of cuticular transpiration, nitrogen turnover increases. Thus:

$$m = \begin{matrix} 1, & t > t_c \\ 1.2, & t \leq t_c \end{matrix} \qquad (73)$$

where

t_c = cuticular transpiration (mm d^{-1})

The available nitrogen in the vegetative plant parts is:

$$N_e = (N_l - W_l \cdot n_{ml}) + (N_{st} - W_s \cdot n_{ms}) + (N_r - W_r \cdot n_{mr}) \tag{74}$$

where

N_l, N_{st}, N_r	is amount of nitrogen in live leaves, stems and roots, respectively (kg ha^{-1})
W_l, W_s, W_r	is dry weight of live leaves, stems and roots, respectively (kg ha^{-1})
n_{ml}, n_{ms}, n_{mr}	is concentration of residual nitrogen in the tissue of leaves, stems and roots, respectively

The potential rate of accumulation of nitrogen in the grains is calculated from:

$$v_p = g \cdot v_r \tag{75}$$

where

g = number of grains set
v_r = potential rate of nitrogen accumulation per individual grain (kg d^{-1})

The latter value is a function of mean daily canopy temperature, largely derived from data of Sofield et al. (1977b), as illustrated in Figure 23.

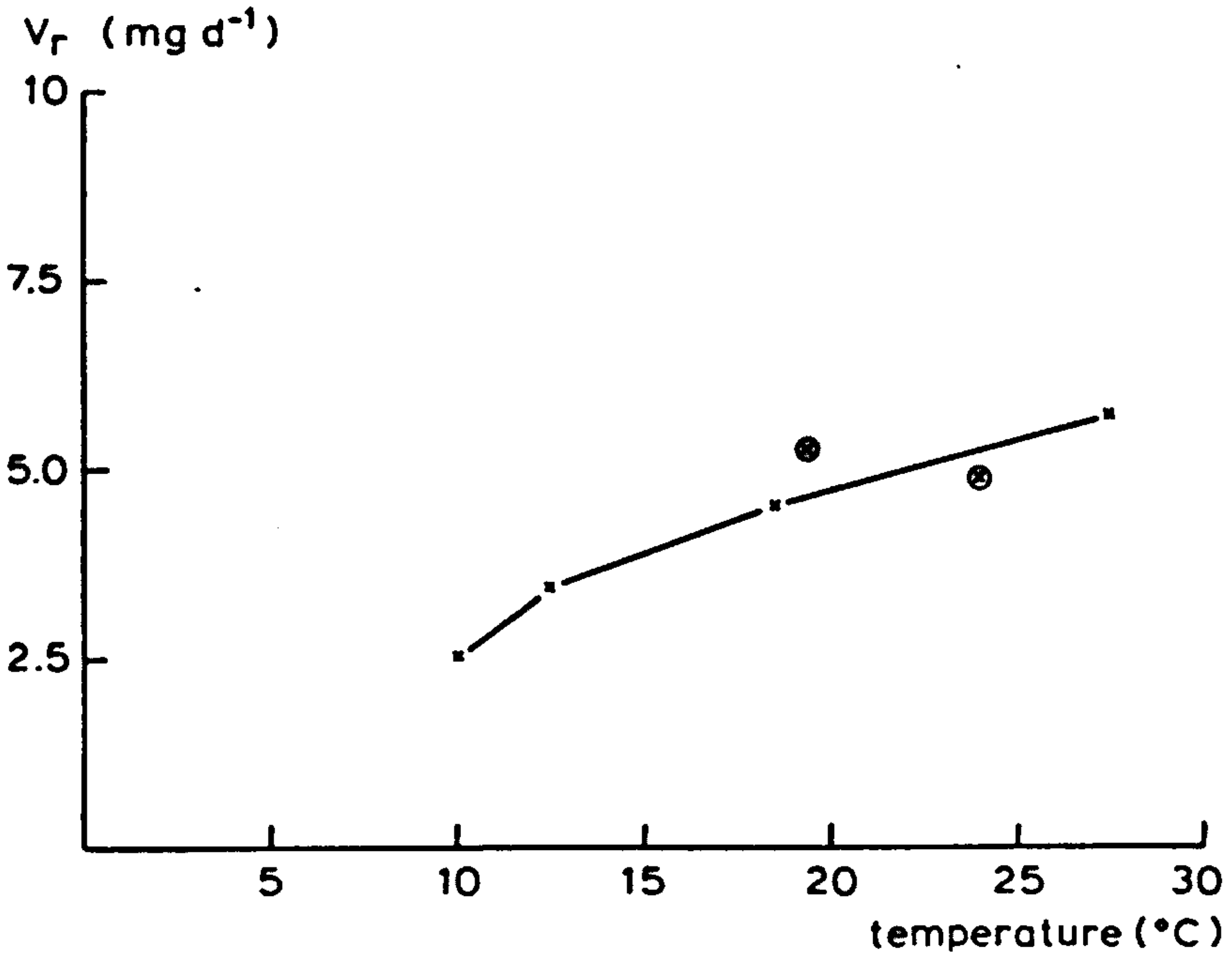

Figure 23. Potential accumulation rate of nitrogen per grain, v_r, as a function of canopy temperature. x Sofield et al., 1977b; ⊗ Donovan & Lee, 1977; ⊕ Donovan & Lee, 1978.

3.6 Plant morphogenesis

3.6.1 Rate of organ formation

Wheat yields, in terms of mass per area either of grain or total dry matter may be estimated without necessarily determining the population density of the component organs, or even of the yield components. Such estimates are either statistically derived functions, based on a set of data appropriate to the region in question (Zaban, 1981; Neghassi et al., 1975; Baier & Robertson, 1968; Williams & Robertson, 1965) or are based on the source approach where all sink-effects are completely ignored (van Keulen & de Milliano, 1984; van Keulen, 1980). Such models generally have a limited number of parameters and can be effectively applied to the region from where the data were derived or to which the model was calibrated. They are useful for determining environmentally dictated yield estimates for a region and are indeed used for that purpose (van Keulen & de Milliano, 1984; Zaban, 1981). Physiologically based growth models that are designed to analyze the effects of specific agrotechnical manipulation, cultivar characteristics or environmental conditions on the crop as a whole, need to account for yield components, especially when the crops that are simulated grow under fluctuating, sub-optimum, conditions. The increased error, introduced through the necessarily greater complexity could well offset some of the advantages of greater detail, but there should be a net advantage in better understanding of the interrelationships between factors that determine yield.

At different stages of ontogenetic development, the main constituent organs of the wheat plant that are important in determining final grain yield, are leaves and stems, tillers, spikes or ears, spikelets, florets and grains. The number of grains per unit area is highly correlated with yield (Spiertz & van Keulen, 1980; Fischer, 1979; Darwinkel, 1978; Fischer, 1973). Grain number is determined in a series of processes from tillering to grain set. Many studies have concerned themselves with the effects of environmental and endogenous factors on the number of organs formed. In most cases no attention was paid to the rates of organ development, but rather to the final result, so that it is often difficult to derive quantitative dynamic relationships. The available evidence on the effects of environmental factors on the development of various organs has been reviewed by Evans et al. (1975) and is summarized in Table 15 (p. 81).

The effects of radiation and day length directly influence the flow of carbohydrates to the active meristem at any moment during organ development. Shading before anthesis reduces the number of competent florets (Fischer & Stockman, 1980; Fischer, 1979). Moisture and nutrient supply also affect carbohydrate flow, although in addition they may have a specific influence on the rate of organ development. Some studies have shown that when the effects of carbohydrate flow and nutrient flow were separated, the effect of nutrient supply was negligible (Pinthus & Millet, 1978). Nutrient supply, especially nitro-

Table 14. Relationship between development measured as accumulated day-degrees and nitrogen concentration of spring wheat cultivars growing under conditions of non-limiting nitrogen supply. (Data from Vos, 1981; see Figure 11A)

Cultivar Bastion					
Experiment	Plant organ		slope	Nitrogen concentration	
		r^2	x 10^4	emergence	maturity
II 15, 20, 25	Leaf blade-main culm	0.95	-0.211	0.061	0.017
phytotron	Leaf blade-tiller	0.95	-0.229	0.066	0.018
full nutrient	Stem & sheath-main culm	0.91	-0.106	0.030	0.007
culture	Stem & sheath-tiller	0.98	-0.135	0.034	0.006
(hydroponic)	Roots	0.79	-0.203	0.060	0.018
Cultivar Adonis					
III N3-16, 22					
Sand and peat	Leaf blades	0.93	-0.188	0.061	0.022
in pots	Stem and sheath	0.95	-0.132	0.037	0.009
Greenhouse	Roots	0.17	-0.022	0.0225	0.018

Note: Emergence to anthesis – 0 to 1045 day °C
Anthesis to maturity – 1045 to 2100 day °C
Data cover 45 d °C before anthesis to maturity.
Nitrogen concentrations at emergence calculated by extrapolation.

gen supply appears to be important in tiller development (Yoshida & Hayakawa, 1970; Puckridge, 1968; Aspinall, 1961), as does moisture stress. In this respect, tillers respond like leaves. Increasing temperature accelerates the rate of ontogenetic development and so shortens the period during which organ formation can take place (Section 3.2; Evans et al., 1975; Friend et al., 1963). However, it also leads to an increased rate of organ formation (Halse & Weir, 1974; Rawson, 1970), so that some compensation may occur. In the model a direct effect of temperature on the rate of grain set is introduced, based mainly on the work by Hoshikawa (1960; 1959a & b). Effects of low night temperatures causing sterility in rice are well documented (Yoshida, 1983). To mimic that effect the rate of grain set in the model is affected by the minimum temperature. Indirect effects of temperature through its effect on CO_2 assimilation and respiration are expressed in the carbohydrate flow.

Genetic differences in the number of component organs in wheat are probably related to differences in the maximum size and numbers that a given organ can attain, as well as to differences in the rates of organ initiation (Rawson, 1970). In terms of carbohydrate flow, genetic differences could be expressed as differences in the minimum carbohydrate flow needed to initiate and maintain one organ. That would determine a ceiling number that can be maintained by a given flow of carbohydrate, and would contribute to determining the rate at which organ formation would proceed.

The model of organ formation that is elaborated here is based on carbohydrate flow and on temperature effects. A model of tiller development in Rhodes grass (*Chloris gayana*, Kunth) based on the same principle gave satisfactory results (Dayan et al., 1981). In some cases, the specific modifying effects of nutrient supply and water stress have been taken into account. The approach adopted is admittedly simplistic, but can account for much of the variation reported for organ initiation rates.

In general:

$$P = B + \int_{t_i}^{t_e} (F\text{-}A)\,dt \tag{76}$$

where

P is organ density (number ha^{-1})
B is initial organ density (number ha^{-1})
F is rate of organ formation (number ha^{-1} d^{-1})
A is rate of organ attrition (number ha^{-1} d^{-1})
t_i, t_e beginning and end of organ formation phase, respectively

As a rule, B equals zero. However, when the processes are described from some point in time after germination, generally from emergence, the initial number of tillers is already determined, usually by a relatively constant proportion of the seeding density. Also, the initial number of ears initiated is basically the same as the number of established seedlings. Germination and establishment, which are largely dependent on the utilization of a fixed amount of carbohydrate stored in the seed (Penning de Vries et al., 1979) are different processes, that do not lend themselves to the approach adopted here for the description of organ formation in the established shoot.

$$F = \begin{matrix} F_1, \; P<C \\ 0\;, \text{ otherwise} \end{matrix} \tag{77}$$

$$F_1 = \begin{matrix} \max(0, (X - P) \cdot H/T_f), \; s_b \leq s_{vr} \leq s_e \\ 0 \qquad\qquad\qquad\qquad\qquad , \text{ otherwise} \end{matrix} \tag{78}$$

where

C is ceiling number of organs possible (number ha^{-1})
X is number of organs that can be maintained by the current supply of carbohydrates to the sites of organ formation (number ha^{-1})
T_f is time constant for organ formation (d)
H is rate reduction factor due to moisture or nutrient deficiency
s_{vr} is development stage of the vegetation in either the pre-anthesis or post-anthesis phase (s_v or s_r)
s_b, s_e is development stage of the vegetation at the beginning and the end of the specific organ formation phase, respectively.

In some cases, the ceiling number of organs is not predetermined and is set by the process of organ formation itself: this could be the case with tiller formation. Uniculm cultivars could be simulated by setting the ceiling number of ears equal to the seedling density. That would imply that the character is genetically determined. It could also be simulated by increasing the carbohydrate requirement for tiller formation (see W in Eqn. 80). In other cases the ceiling is set by the existence of a finite number of precursor organs: thus in wheat the number of ears cannot be greater than the number of tillers (except in the case of a multiple eared wheat).

The time constant for organ formation, T_f, represents the time necessary for all the processes that need to be completed in order to form a new organ. It regulates the rate of organ formation by converting the potential increase in number of organs into an actual rate, which decreases as the number of organs present approaches the potential number, X. (An alternative formulation could be a constant rate of increase dependent on temperature, dropping suddenly to zero, when $P = X$. The asymptotic value, X, would be the same, but the rate at which it was attained would be different). The time constant is influenced by the number of precursor organs. The assumption is that the greater the number of precursor organs, the longer the time constant for organ formation primarily because organ formation in the plant is a serial process. This description produces a compensatory effect by increasing the rate of organ formation when precursor organs are few and vice versa.

The effect of temperature is also mediated through the development rate of the crop and through that on its development stage. The stages which delimit the formation phase for a particular organ, s_b and s_e, can be adequately described as a function of accumulated day degrees (Section 3.2), so that at lower temperatures, the organ formation phase is longer.

The reduction factor, H, can account for other effects, not accounted for by carbohydrate availability and temperature. Nutrient and moisture stress would be the most important factors, but the exact nature of the relationship between the degree of deficiency and the effect on organ formation would have to be derived empirically, since the interaction with carbohydrate supply is difficult to unravel from available data in the literature.

$$X = h/v_c \tag{79}$$

$$v_c = W \cdot r_p/z \tag{80}$$

$$z = s_e - s_b \tag{81}$$

where

h is carbohydrate flow to the vegetative above-ground organs of the plant (kg ha^{-1} d^{-1})

v_c flow of carbohydrate needed to initiate one viable organ (kg $organ^{-1}$ d^{-1})

W is minimum amount of carbohydrate needed to grow and maintain one viable organ (kg organ^{-1}) estimated by dividing the dry weight of an average viable organ by the conversion efficiency
r_p is development rate of the crop (d^{-1})
z is length of the organ development stage in development stage units.

The carbohydrate supply, h, is basically that part of the current assimilate supply available for increase in shoot weight (Section 3.4) including the proportion going to the reserves.

For the length of the formation phase of any particular organ, from t_1 when $s_{vr} = s_b$ to t_2 when $s_{vr} = s_e$, it holds:

$$\int_{t_1}^{t_2} r_p \, dt = s_e - s_b = z \qquad (82)$$

so that over the whole period:

$$\int_{t_1}^{t_2} v_c \, dt = W \qquad (83)$$

This description assumes that an organ needs a certain minimum size to be viable (Rawson & Bagga, 1979; Dougherty et al., 1975). Whether this size varies among cultivars cannot be judged on the basis of available information, but that could well be possible. Cultivar characteristics could thus be expressed by different values for W.

The number of organs that can be formed is inversely proportional to r_p, so that the lower the temperature during the organ formation phase, the higher the number of organs, X, that can be maintained and the longer the period available for their formation. This is what happens in fact (Evans et al., 1975; Halse & Weir, 1970; Friend et al., 1963) but whether the representation is quantitatively accurate is not yet clear. The parameters applied in the description of organ formation and their numerical values are summarized in Table 16 (p. 112).

Table 15. Factors that have been found to have significant effects on organ formation in wheat (Evans et al., 1965)

Environmental factor	Tiller	Ear	Spikelet	Floret	Grainset
level of irradiance	+	+	+	+	+
daylength		+		+	
temperature	+	+			+
moisture status			+	+	+
nutrition	+		+		+
cultivar	+	?	?	?	

Organ attrition is sometimes a prolonged process, proceeding at a low but persistent rate, A, as is the case with tillers (Evans et al., 1975, Figure 5.2) or it can be a residual effect, due to viable organs not developing to the following phase as is the case where spikelets do not develop into fertile florets. Where the dying organs have an important effect on other plant growth processes, as in the case of tillers, it should be accounted for. A logistic function is used:

$$A = \begin{matrix} A' \cdot P' \, (1 - P'/P'_m), \; s_v \leq s_\eta \\ 0 \qquad\qquad\qquad\qquad , \text{otherwise} \end{matrix} \tag{84}$$

where

A	is death rate of tillers (number ha^{-1} d^{-1})
A'	is relative rate of increase in dead tillers (d^{-1})
P'	is total number of dead tillers (number ha^{-1})
P'_m	is maximum number of dead tillers, determined as the number of non-fertile tillers when $s_v = s_{fl}$ (number ha^{-1})

The representation of organ proliferation as incorporated in the present model does not cover the whole range of possibilities. For instance, a moisture stress period at the beginning of spike formation followed by adequate water supply during the next of the growth period can cause a second phase of tillering (Hochman, 1978), possibly because of a large surplus of assimilates compared to the available sinks (or because apical dominance is broken). These tillers were small and did not develop ears, but diverted a fair amount of assimilates to non-reproductive organs. In some stress situations the second wave of tillers can produce the main part of the grain yield.

Tiller attrition is largely due to competition for light and nutrients. When the leaf area is low, tiller attrition is probably slower than when the canopy is dense, so that tiller attrition, A', could be related to canopy cover:

$$A'_e = A \bullet (1 - e^{-0.5q_a}) \tag{85}$$

3.6.2 *Leaf area dynamics*

Leaf area increases with assimilate flow to the leaf, subject to phenological stage and to nutrient and water deficiency. If leaf area expansion and associated leaf weight is limited by nutrient or water deficiency, then the excess available carbohydrate can be diverted to root growth and to the reserve carbohydrates.

Leaf area of a fully expanded leaf is very closely related to leaf weight. The ratio between the two, the specific leaf area, generally varies between narrow bounds around 20 m^2 kg^{-1} dry matter (Aase, 1978; Spiertz & Sibma, 1982). Leaf area increase, d_l, is defined as follows:

$$d_l = w_l \bullet s_l \tag{86}$$

where

w_l is rate of increase in dry weight of the leaf blades (kg ha^{-1} d^{-1}) (Equation 56, with l substituted for x)

s_l is specific leaf area (m^2 kg^{-1})

Leaves formed early in the growth cycle of the plant are usually thinner. Therefore s_l is higher at emergence and drops to the standard value when s_v reaches s_{sf}. It could well be that a more appropriate representation would be to relate specific leaf area to temperature (Friend et al., 1965).

Influence of water shortage

One of the most conspicuous effects of water shortage during development of the wheat crop is on the green leaf area (Gallagher et al., 1979; Fischer, 1973). Reduced moisture supply to the plants results in closure of the stomata, loss of turgidity, reduced expansion rates of the leaf blades, wilting of green leaves and finally senescence and leaf fall. These responses are all adaptations that minimize water use. Because of the relative constancy of s_l (Equation 86), the check in leaf area expansion follows from the reduction of leaf weight under water stress.

The check in leaf expansion already occurs at mild levels of water stress and is related to the level of water potential in the plant (Gallagher et al., 1979; Boyer & McPherson, 1975). In the present model, leaf water potentials are not simulated, so the increase in leaf area cannot be directly related to this parameter. However, the relative transpiration deficit, d_{rt}, is related to the degree of dehydration of the plant and so can be used to modify the rate of both leaf area expansion and leaf weight increase. Thus:

$$r_w = f(d_{rt}) \tag{87}$$

where

r_w is a factor accounting for the influence of water stress on growth of leaf blades (Figure 24)

Prolonged or very severe moisture stress leads to a rapid decline in green area (Boyer & McPherson, 1975; Fischer, 1973). Quantitative data relating the rate of green area decline to the actual level of moisture stress in the plant are scarce. In the model, leaf death due to water shortage, depends on the balance between water loss and water uptake by the canopy. Water loss under moisture stress conditions would be mainly due to cuticular transpiration from leaves with closed stomata. Excess loss over uptake from the soil causes dehydration of the plant and subsequent death of the leaves. The actual death rate also depends on the buffering capacity of the vegetation which can be represented by a time constant. Thus,

$$r_{dw} = 10^4 \cdot (t_c - t) \cdot W_l/f_w \cdot W_l/(W_l + W_s)\tau_d \tag{88}$$

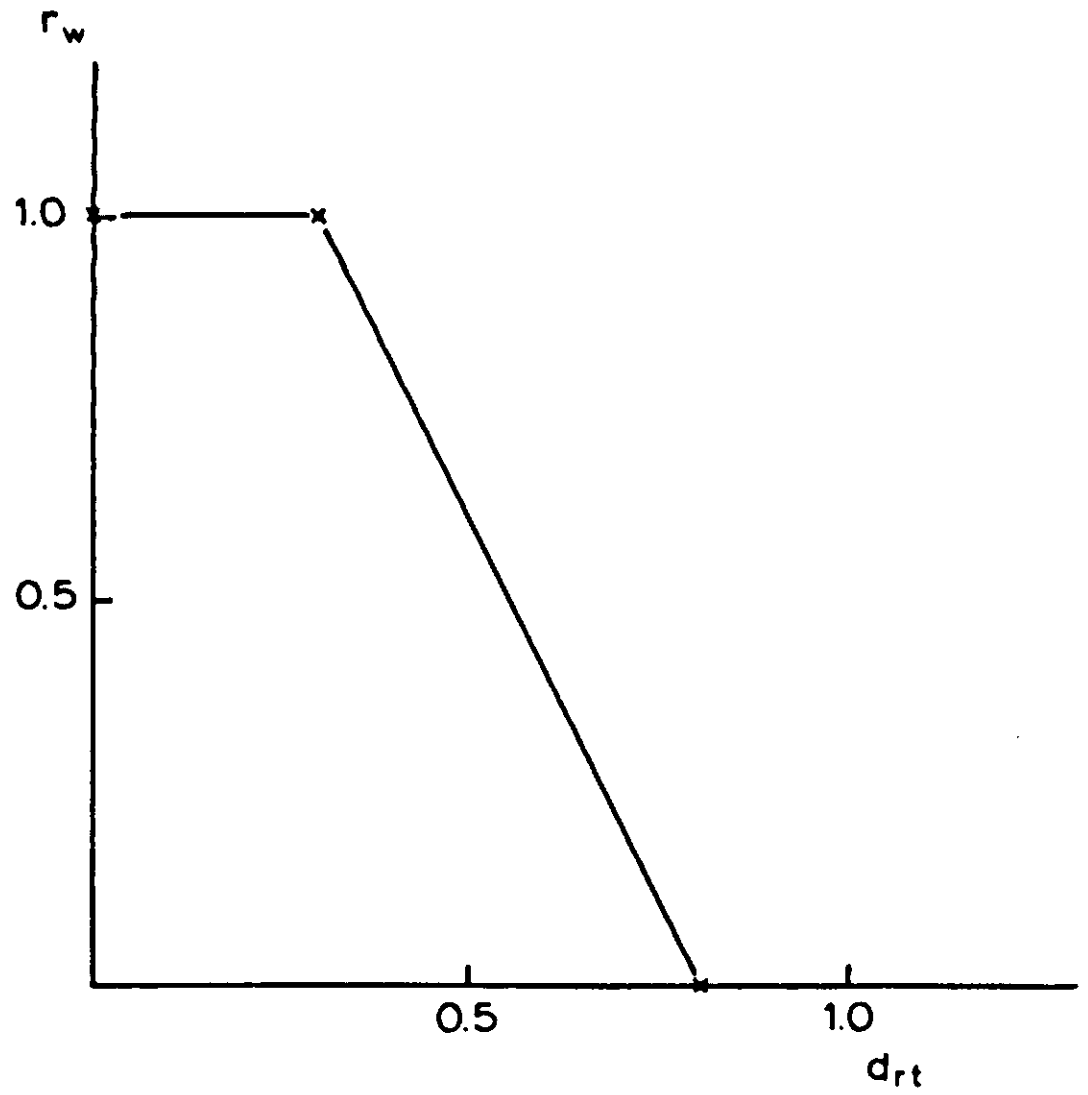

Figure 24. Reduction factor for leaf growth, r_w, as a function of relative transpiration deficit, d_{rt}.

where

r_{dw}	is rate of decline in leaf weight due to water shortage (kg ha^{-1} d^{-1})
t_c	is rate of cuticular transpiration (mm d^{-1})
t	is current rate of moisture uptake from the soil (mm d^{-1}) (10^4 converts from mm d^{-1} to kg ha^{-1} d^{-1})
W_l	is weight of the leaf blades (kg ha^{-1})
f_w	is fraction of water in the leaf blades that can be removed
W_s	is weight of the stem (kg ha^{-1})
τ_d	is time constant for leaf death due to water shortage (d)

Concurrently with the decline in leaf weight, leaf area is reduced. In order to maintain consistency between leaf area and leaf weight, daily leaf weight increments are monitored individually and in parallel with their specific leaf area at the time of formation and the accumulated temperature sum of each leaf increment. When leaves die for any reason (see senescence, d, below) the appropriate leaf area is decremented in parallel with the leaf weight, the oldest leaves dying first. Stem tissue can also die under the influence of water stress especially as the leaf sheaths are included in that compartment. This is implemented by replacing leaf weight by stem weight in Equation 88.

Influence of nitrogen shortage

The nitrogen status of the vegetation also influences the distribution of assimilates between the various organs of the plant (Section 3.4). Its effect on leaf area expansion is thus mediated wholly through the effect of reduced assimilate flow on leaf weight increase (see Equation 49):

$$r_n = f(n_{al}) \qquad (89)$$

where

r_n is reduction factor for leaf growth due to nitrogen stress
n_{al} is current nitrogen concentration in the leaf blades

The function used in the present model is derived from leaf expansion experiments on wheat, *Lolium rigidum* and *L. perenne* (Greenwood and Titmanis, 1966; Greenwood, 1966). It is illustrated in Figure 25. The measurements were done on the youngest expanding leaf. The relationship to total leaf nitrogen is roughly constant over the duration of the experiments (up to 58 days). However, whole canopy nitrogen concentration declines with plant development. As the nitrogen distribution within the live leaf mass is not defined in the model, the reduction of leaf expansion is defined as a function of the current leaf nitrogen concentration, n_{al}, the maximum nitrogen concentration of the leaves at a given development stage, n_{xl}, (Equation 64, where $n_{yx} = 0.06$ and $n_{mx} = 0.01$) and the minimum concentration of nitrogen in severely depleted leaves, n_{ml}.

Under conditions of prolonged nitrogen stress, part of the nitrogen in older tissue is mobilized and resynthesized for the formation of new organs. This nitrogen depletion eventually causes death of the older tissue. In the present

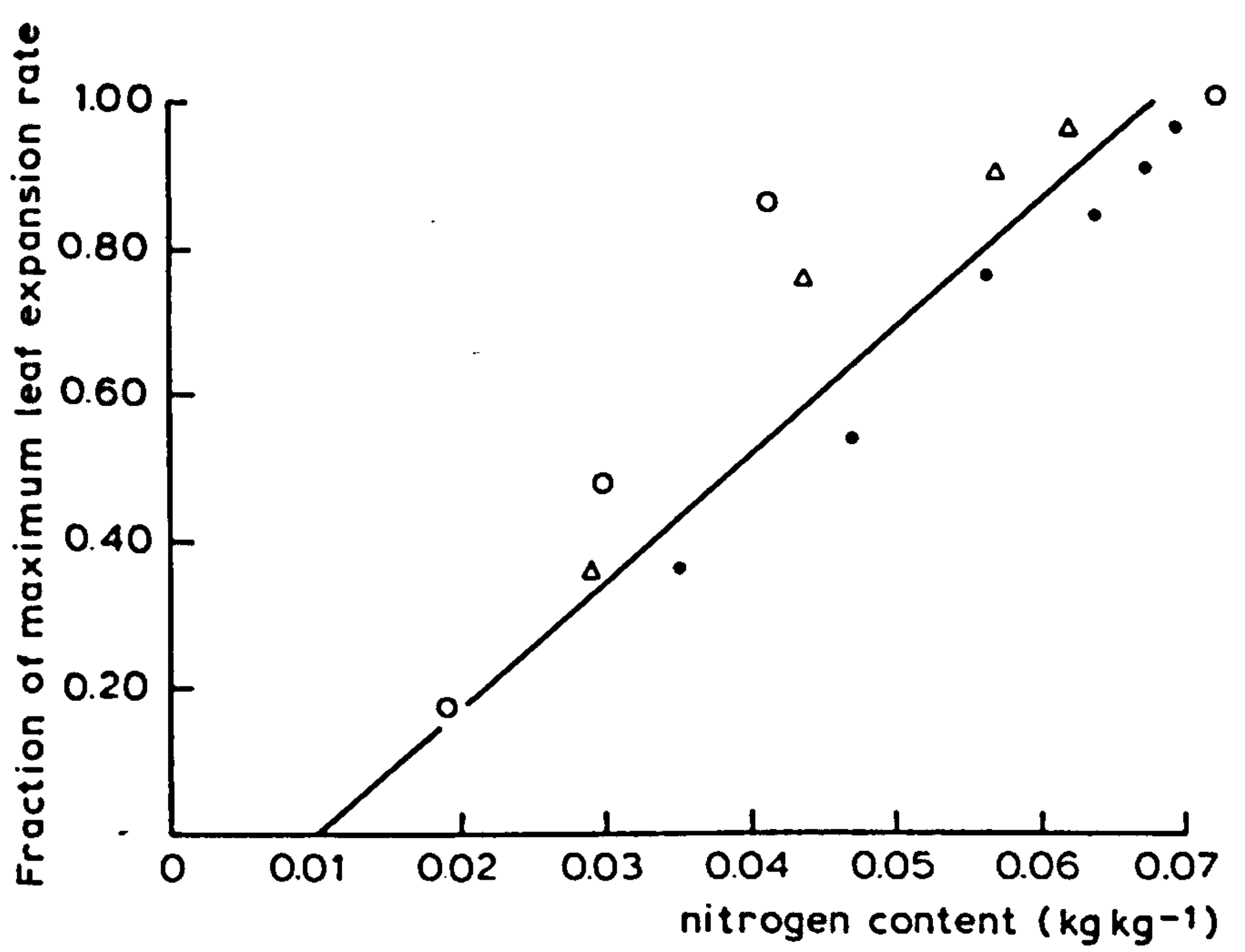

Figure 25. Fraction of maximum leaf expansion rate as a function of leaf nitrogen content. . *Lolium rigidum* (Greenwood & Titmanis, 1966); ▵ *Triticum aestivum* (Greenwood, 1966), o *Lolium perenne* (Wilson, 1975b).

model, where plant components are not subdivided into age compartments, the dying rate of leaves under the influence of nitrogen stress is related to the average nitrogen concentration in the leaf material, according to:

$$r_{dn} = r_{nr} \cdot W_l \tag{90}$$

$$r_{nr} = r_{nrm} \cdot f\,(n_a') \tag{91}$$

$$n_a' = (n_{al} - n_{ml})/(n_{mn} - n_{ml}) \tag{92}$$

where

r_{dn} is rate of decline in leaf weight due to nitrogen shortage (kg ha^{-1} d^{-1})
r_{nr} is relative rate of decline (d^{-1})
r_{nrm} is maximum relative rate of decline (d^{-1})
n_{al}, n_{ml}, n_{mn} are the current concentration of nitrogen in leaf tissue, the residual nitrogen concentration in leaf tissue and the nitrogen concentration for unrestricted growth, respectively
$f(n_a')$ is illustrated in Figure 26

Stem tissue also dies due to nitrogen shortage, particularly the leaf sheaths that are included in this compartment in the present model. The relative rate of decline in stem weight is obtained from Equation 90 by substituting a maximum value equal to one quarter of that of the leaf tissue.

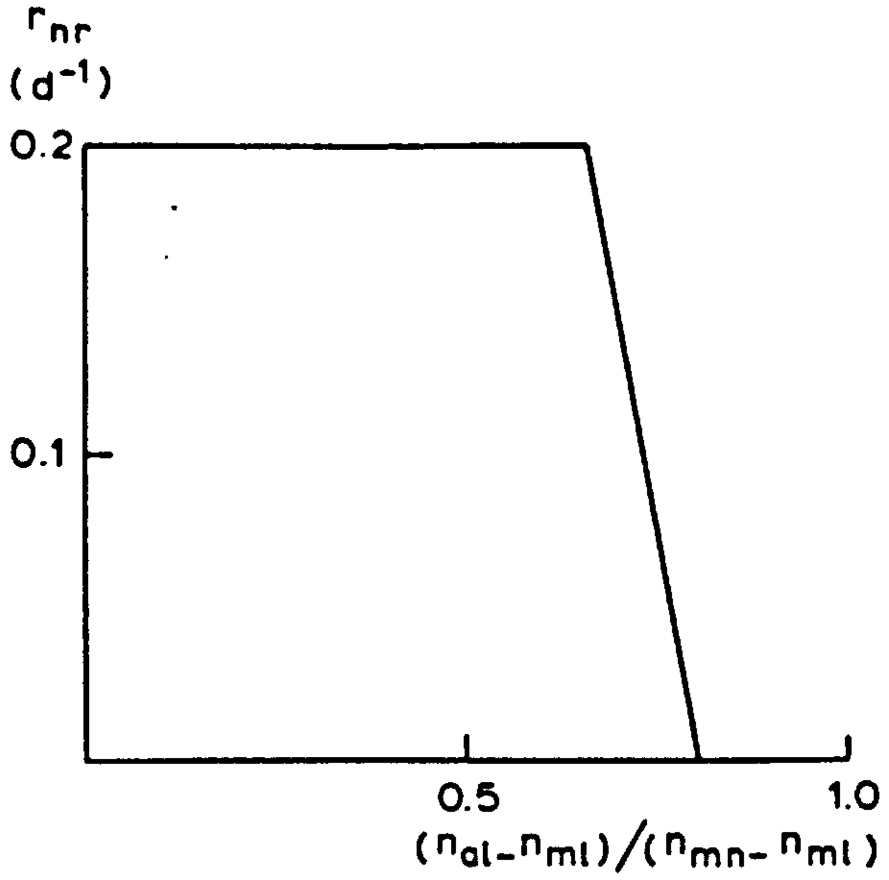

Figure 26. Relative death rate of leaf blades due to nitrogen deficiency, r_{nr}, as a function of its 'relative' nitrogen content.

Fate of non-reproductive tillers

Tillers that have not formed ears gradually disappear and reduce green area. In the model this is accounted for by determining the average leaf weight per tiller, w_{at}, at the moment ear formation ceases and calculating the loss of tiller leaf weight by multiplication with the death rate of tillers, A, as given in Equation 84. This is added to the overall death rate of leaf blades and the appropriate green area is decremented as explained above (item a in this section).

Influence of senescence

Leaves have a limited life span and eventually they begin to senesce and die. This process is accelerated by high temperatures, disease, water stress or nitrogen translocation from the leaves to the growing reproductive organ (Sinclair & de Wit, 1976). In the present model leaf death due to senescence is determined by assuming that leaves die when they have accumulated a fixed temperature sum (Ford & Thorne, 1975). Each daily leaf weight increment is monitored separately:

$$r_{ds} = \begin{matrix} w_{li}, T_i = T_{lf} \\ 0\ \ , \text{otherwise} \end{matrix} \qquad (93)$$

where

r_{ds} is potential death rate of the leaves due to senescence (kg ha^{-1} d^{-1})
w_{li} is growth rate of the leaves on day i (kg ha^{-1} d^{-1})
T_i is temperature sum since initiation of leaf increment i (d °C)
T_{lf} is average accumulated temperature sum needed for initiating senescense (d °C)

Leaf senescence may be accelerated in very dense stands, where the lower leaves are situated in an unfavourable light environment and lose much of their activity. This is accounted for in the model by assuming increased leaf death at high leaf area indices. The relative death rate due to mutual shading is linearly proportional to leaf area index above a value of 4, until a maximum value of 0.03 d^{-1} at an LAI of 8 and above (Puckridge & Donald, 1967). Hence:

$$r_{dl} = r_{lr} \cdot W_l \qquad (94)$$

$$r_{lr} = r_{lrm} \cdot (q_a - 4)/4,\ 0 \leq r_{lr} \leq r_{lrm} \qquad (95)$$

where

r_{dl} is rate of decline in leaf weight due to shading (kg ha^{-1} d^{-1})
r_{lr} is relative rate of decline (d^{-1})
r_{lrm} is maximum relative rate of decline (d^{-1})
q_a is leaf area index of the vegetation

Influence of reserve exhaustion

During grain filling, leaf death is assumed to increase as the reserve carbohydrate level is depleted below 0.05. When the reserve level drops to zero, relative death rate, r_{dcr}, reaches a maximum of 0.5 d^{-1}.

$$r_{dc} = r_{dcr} \cdot W_l \tag{96}$$

$$r_{dcr} = \begin{cases} r_{dcrm} \cdot P_n/(P_{gwr} - P_n), & P_n < 0 \\ 0 & \text{, otherwise} \end{cases} \tag{97}$$

where

r_{dc} is death rate of leaves due to carbohydrate exhaustion (kg ha^{-1} d^{-1})
r_{dcr} is current relative rate of decline due to carbohydrate exhaustion (d^{-1})
r_{dcrm} is maximum relative rate of decline (d^{-1})

The overall death rate of the leaves due to water, nitrogen or carbohydrate shortage or to shading is now defined as the maximum of:

$$r_{dt} = \max (r_{dw}, r_{dn}, r_{dc}, r_{dl}) \tag{98}$$

When leaves die from any of these causes, the oldest leaves will die first.

3.6.3 Total green area

In addition to the green area of the leaf blades, other green parts of the vegetation also contribute to the assimilatory capacity (cf. Marshall, 1978; Stoy, 1965; Boonstra, 1929).

In the model the total green area, used in the assimilation (and transpiration) calculation is therefore composed of area of leaf blades, area of stem and leaf sheaths and green components of the ear:

$$g_a = q_a + a_s + a_e \tag{99}$$

where

a_s is total green area of stem and leaf sheaths (m^2 m^{-2})
a_e is total green area of the ears (m^2 m^{-2})

It appeared difficult to quantify the contribution of the two latter components, so that approximate formulations are used. Green stem area is related to the weight of stem tissue and crop height:

$$a_s = 10^{-4} \cdot W_s/5000 \cdot h_c \cdot A_{sx} \tag{100}$$

where

W_s is weight of stem and sheath tissue (kg ha^{-1})
h_c is crop height (m)
A_{sx} is maximum green stem area (m^2 m^{-1})

To define the green area of the ears, basically data by Stoy (1965) have been elaborated.

$$a_e = 10^{-4} \cdot E_n \cdot a_{ea} \cdot a_f \tag{101}$$

where

E_n is number of ears (no. ha^{-1})
a_{ea} is maximum green area per ear (m^2)
a_f is factor accounting for the effect of age on ear yellowing, function of development stage.

4 Soil processes

Soil processes in the present model are related to root growth as well as to the water and nutrient balance. These processes are described separately for each soil layer and are then integrated over the relevant soil depth (de Wit & van Keulen, 1972). Each individual layer (or 'compartment') has constant thickness and is regarded as homogeneous. Not all compartments necessarily have the same properties, so that heterogeneity in the soil profile can be taken into account. In the present model the thickness of the compartments increases from 2 to 30 cm with increasing soil depth, since the steepest gradients, especially with respect to moisture content are near the soil surface. It is conceivable that finer subdivision of deeper soil layers may be necessary to simulate successfully water and nitrogen uptake in situations where depth of rooting is critical. In such cases, the thickness and number of soil layers can be adjusted as necessary (de Wit & van Keulen, 1972). All soil compartment integrals in such a new subdivision must be carefully initialised in order to ensure equivalence with the original subdivision over the whole profile.

4.1 Soil water balance

4.1.1 Infiltration and drainage

The amount of moisture available to the crop at any point in time is determined by the balance between input by rain, irrigation and run on and losses through run off, deep percolation, evaporation from the soil surface and transpiration by the vegetation. Run off can occur on sloping terrain when rainfall intensity exceeds the infiltration capacity of the soil. Infiltration capacity may change with the development of vegetative cover, as well as during storms when rain drop impact destroys the surface aggregates of soils and gradually forms a continuous crust (Morin & Benyamini, 1977).. In other situations a soil-water puddle may be formed at the soil surface, preventing escape of air from the profile, thus causing the build-up of above atmospheric pressures, which also hamper infiltration of additional water in the profile. This process may be aggravated by a hydrophobic layer formed by algae growing on the soil surface (Rietveld, 1978).

Mathematical modelling of these phenomena is possible, but such models require much more detailed information and time steps much smaller than 1 day (Rietveld, 1978; Stroosnijder et al., 1972; van Keulen & van Beek, 1971). Rainfall data are seldom available in sufficient detail and as a consequence, empirical functions are used, based on long-term average values for run off losses, in which run off is expressed as a function of daily rainfall and soil cover (Shanan & Schick, 1980) or of soil type (Stroosnijder, 1982). In each case, definition of the appropriate parameter values requires experimentation at the site of interest. In whole-season crop growth models, the infiltration rate is generally defined as the difference between daily amount of rainfall and the daily amount of run off. Distribution of moisture in the profile is based on the concept of 'field capacity', defined as the equilibrium moisture content of a volume of soil after allowing excess water to drain until drainage virtually ceases (Veihmeyer & Hendrickson, 1931). This moisture content is not uniquely defined for a given soil (Veihmeyer & Hendrickson, 1949), but is a function of the boundary conditions of the system. It is especially sensitive to the presence or absence of a water table. For practical purposes, the moisture content at pF 2.5, i.e. the one-third-atmosphere-point is a widely accepted measure of field capacity (Hillel, 1971; Slatyer, 1967; Colman, 1947). This value can be determined by standard techniques, provided that undisturbed soil samples are available for analysis. It is assumed in the model, that this equilibrium moisture content is reached instantaneously (i.e. within the time step of one day), whenever sufficient water enters a compartment. The rate of change in moisture content in the i-th compartment, due to infiltration, r_{zi}, is described by:

$$r_{zi} = \min(r_i, (z_{fi} - z_{ai})/\Delta) \qquad (102)$$

where

r_i is rate of water flow into compartment i from soil surface or from compartment i-1 (mm d^{-1})
z_{fi} is moisture content of the i-th compartment at field capacity (mm)
z_{ai} is current moisture content in the i-th compartment (mm)
Δ is time interval of integration (d)

The rate of inflow into the i-th compartment r_i is equal to infiltration from the soil surface or outflow from compartment i-1:

$$r_i = \max(0, r_{i-1} - (z_{f(i-1)} - z_{a(i-1)})/\Delta) \qquad (103)$$

The compartments in the profile are wetted till field capacity from the top one downwards until total infiltration is dissipated within the potential rooting zone. Water draining below that zone is simply:

$$d_r = \max(0, r_{zn} - (z_{fn} - z_{an})/\Delta) \qquad (104)$$

where

n is bottom soil layer, equivalent to the number of compartments in the potential rooting zone
d_r is rate of drainage (mm d^{-1})

The moisture distribution obtained in this way is a fair approximation of that calculated with process models of infiltration (Figure 27). Upward movement

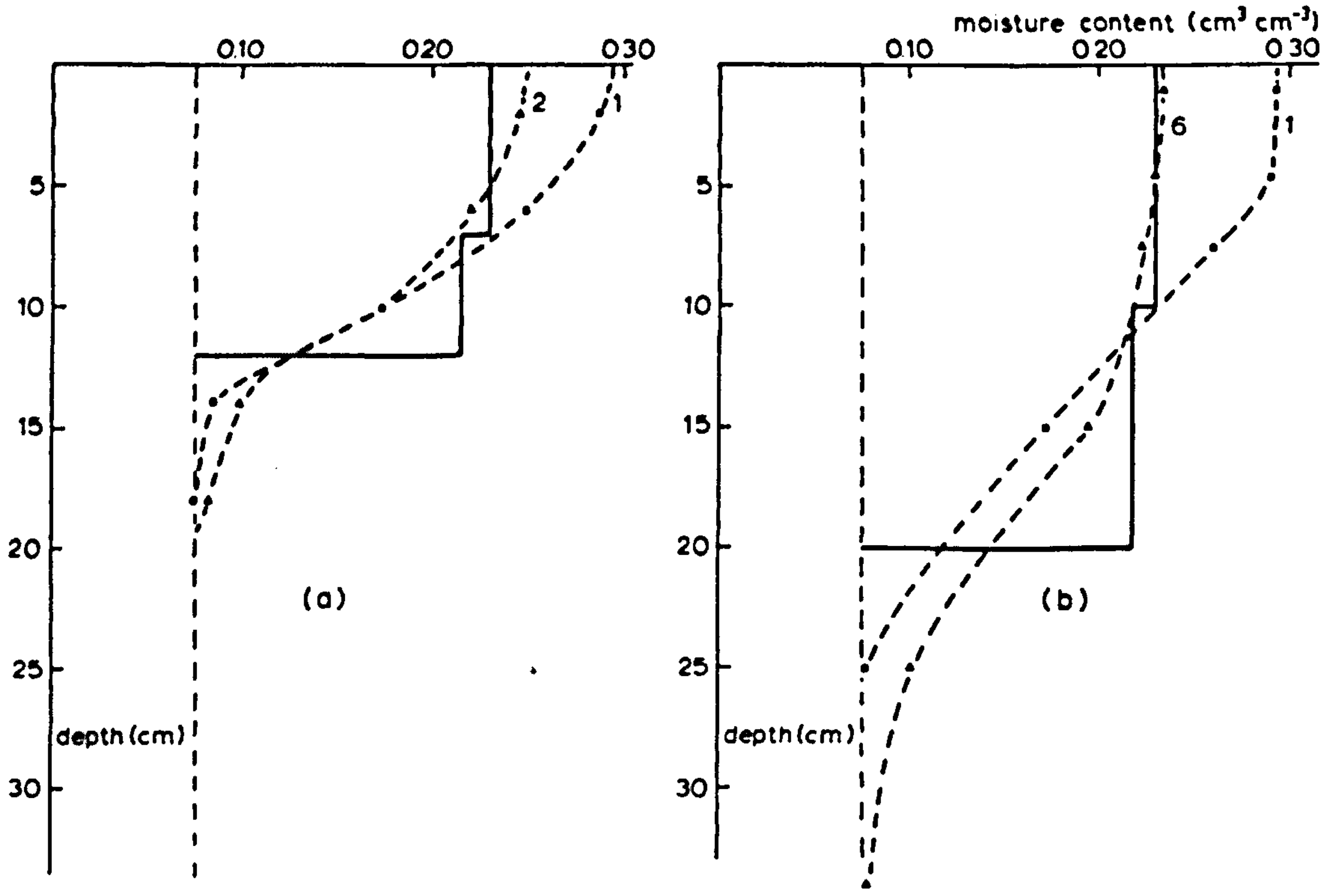

Figure 27. Comparison of soil moisture profiles calculated with a detailed simulation model and those obtained with the approximation used in the present model. Dashed vertical line represents initial moisture distribution. Dashed lines with symbols calculated with the detailed model, solid lines with the simplified procedure. Numbers next to the lines refer to days since rain. (a) moderate rain (18 mm) on dry soil; (b) heavy rain (30 mm) on dry soil (Source: van Keulen, 1975).

of water is ignored, but this is not of much importance in most dryland situations where the water table is at a considerable distance below the rooting zone. When necessary, however, this aspect can also be taken into account (Marletto & van Keulen, 1984; Massa & Lantinga, 1981). There are, of course, deviations which can be significant in themselves, but have only a small influence on the availability of water to the plant roots. Considerable experience with this formulation has shown it to be adequate for the type of model described here (van Keulen et al., 1980).

4.1.2 Bare soil evaporation

In arid and semi-arid environments a substantial proportion of the annual precipitation may be lost by evaporation from the soil surface, without contributing to the water consumption of the vegetation and hence to its productivity (van Loon & Wösten, 1979). The actual amount of moisture lost in this way depends mainly on the distribution and the timing of the precipitation in a particular year: A relatively large number of light rainfall showers, especially early in the growing season, when most of the soil is bare, results in the loss of a large proportion of this precipitation (van Keulen, 1975). For heavier rainfall events, where a large part of the infiltrated moisture penetrates to the deeper layers of the profile, the relative losses will be smaller.

A self-mulching effect can create a barrier to moisture transport in semi-arid conditions. To clarify the importance of this effect, a detailed model of soil evaporation (van Keulen, 1975) was run for a number of limiting situations, starting from moisture contents close to the actual wilting point of the soil type. The results indicate (Figure 28) that under constant conditions of evaporativity, such as those created in laboratory experiments, the ratio of actual evaporation to potential evaporation falls linearly with a decrease in soil water potential in the top soil compartment (taken as 2 cm here). When the top soil dries out sufficiently, evaporation drops to almost zero. This is accounted for by the factor b_s in Equation 105 below.

The amount of water lost by evaporation from the soil surface is estimated as follows:

$$E_a = E_p \cdot b_l \cdot b_s \qquad (105)$$

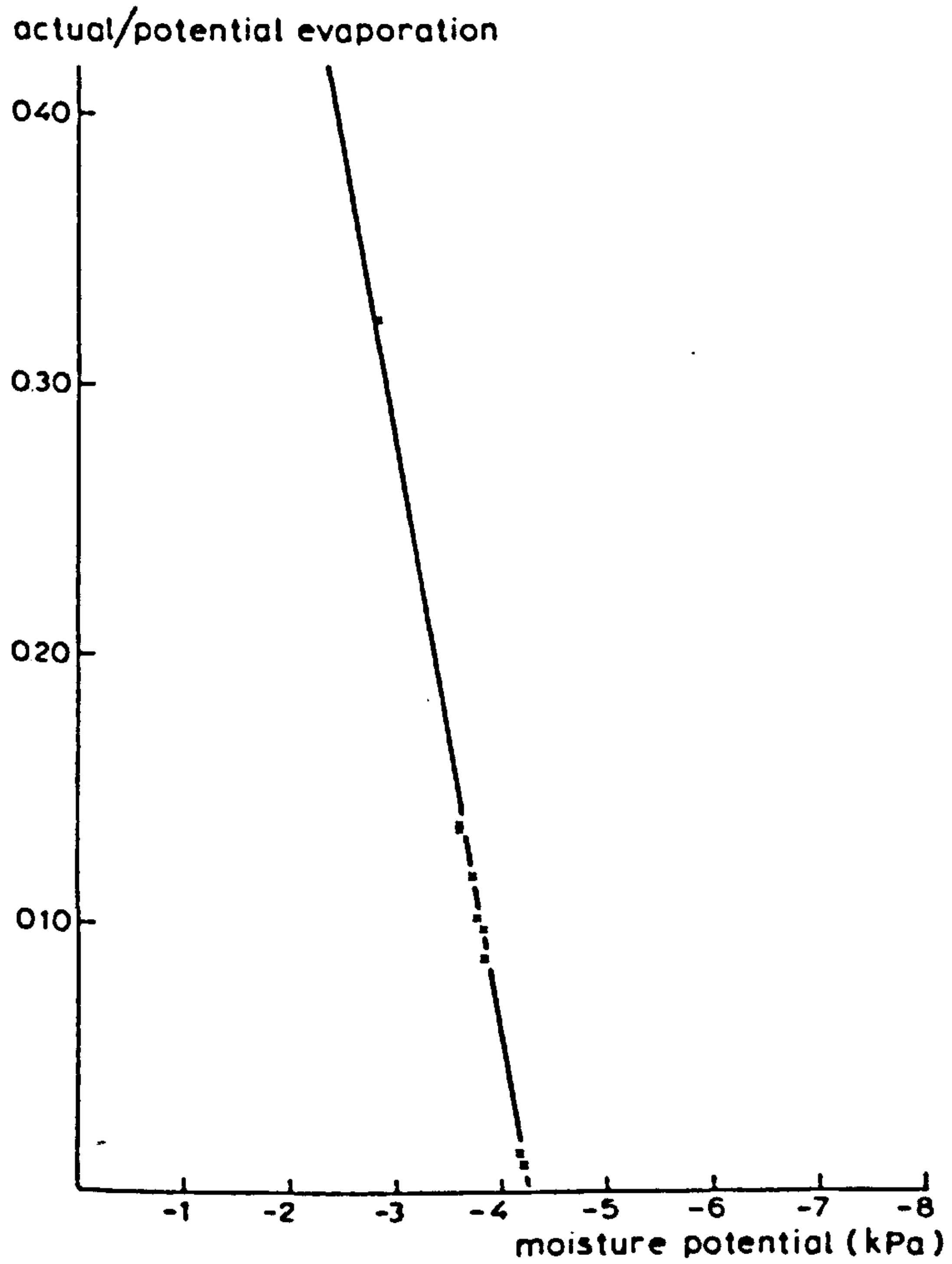

Figure 28. Relation between moisture potential expressed as equivalent water column in the top 2 cm of soil and ratio of actual to potential soil evaporation, calculated with a simulation model (Source: van Keulen, 1975).

where

E_a is actual rate of evaporation from the soil surface (mm d^{-1})
E_p is potential rate of evaporation from the soil surface (mm d^{-1}) calculated from environmental conditions applying a Penman-type equation
b_l is a reduction factor accounting for the effect of shading by the vegetation (dimensionless)
b_s is a reduction factor accounting for the influence of soil moisture content of the surface compartment (dimensionless)

The reduction in evaporation due to the presence of the vegetation accounts for the interception of energy, as well as for aerodynamic effects, resulting from decreased wind speeds at the soil surface. This reduction may be related to the leaf area index of the vegetation (Goudriaan, 1977; Ritchie, 1972; 1971) and is described in the model by:

$$b_l = e^{-k_s \cdot q_t} \qquad (106)$$

where

q_t is area index of both green and dead leaf tissue (dimensionless)
k_s is proportionality factor (dimensionless)

The proportionality factor, k_s, may vary for different crops mainly due to differences in geometrical properties. It is about 0.5 for very leafy crops like grass and about 0.6 for taller stemmy crops like wheat (Goudriaan, 1977).

The reduction factor b_s, is defined as a function of a dimensionless soil moisture number, z′, where:

$$z' = (\theta_l - \theta_a)/(\theta_f - \theta_a) \qquad (107)$$

where

θ_l is current volumetric moisture content of the top soil compartment ($cm^3\ cm^{-3}$)
θ_f is volumetric moisture content of the top soil compartment at field capacity ($cm^3\ cm^{-3}$)
θ_a is volumetric moisture content of the top soil compartment at air dryness ($cm^3\ cm^{-3}$)

The relation between z′ and soil water potential (Figure 29) is based on literature data (van Keulen & Stroosnijder, 1973; Stroosnijder & van Keulen, 1973; Hillel, 1968; Rijtema, 1969). A combination of these data with those shown in Figure 28 yields a direct relation between the dimensionless moisture number z′ and the reduction factor for evaporation, b_s, as shown in Figure 30. Although this procedure should be a generally applicable description of evaporation from the soil surface, it is not adequate for all situations, as shown by Stroosnijder (1982) for a semi-arid summer rainfall region. The reason for

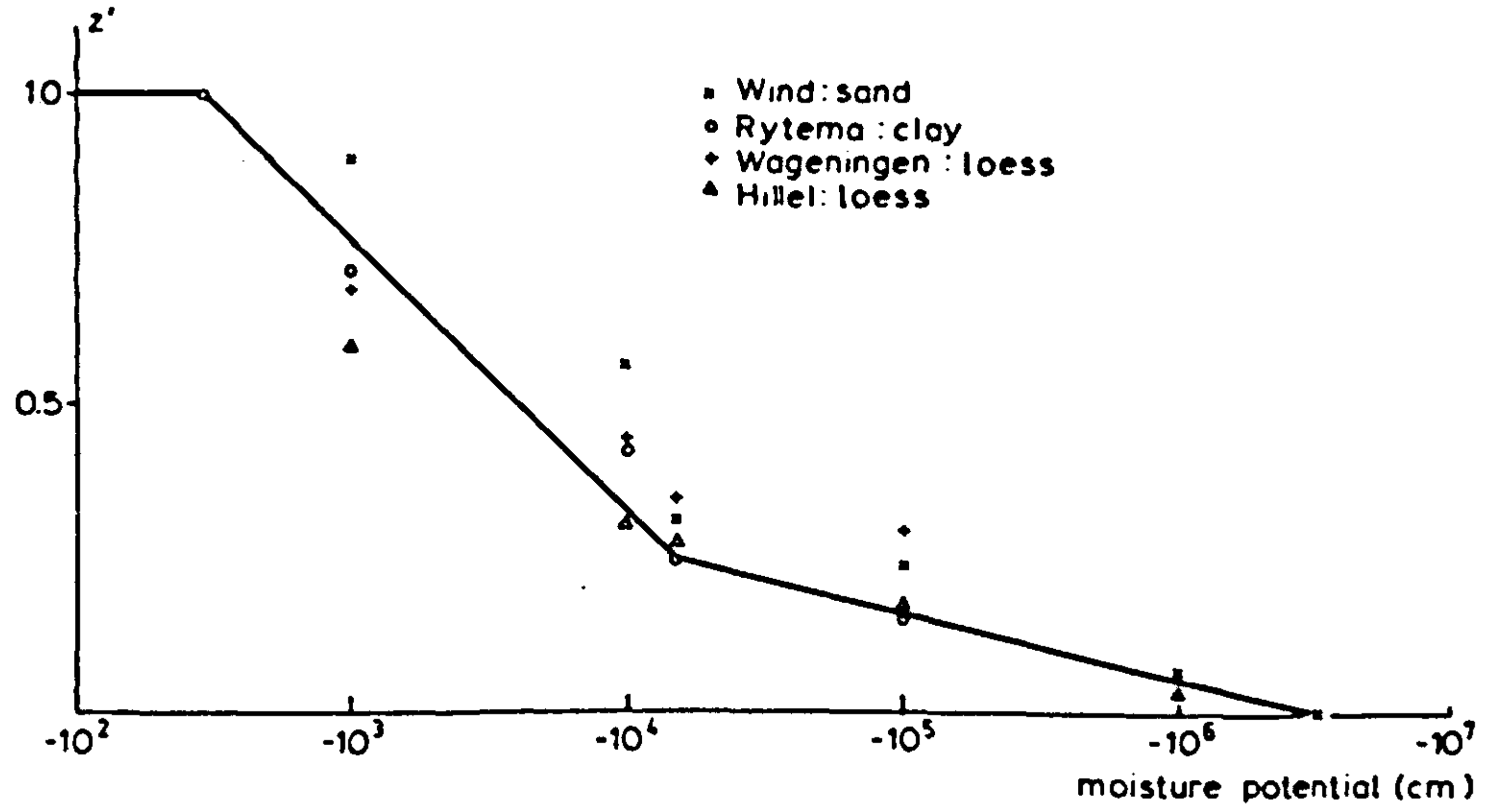

Figure 29. Relation between dimensionless moisture content, z', and moisture potential in various soil types (Source: van Keulen, 1975).

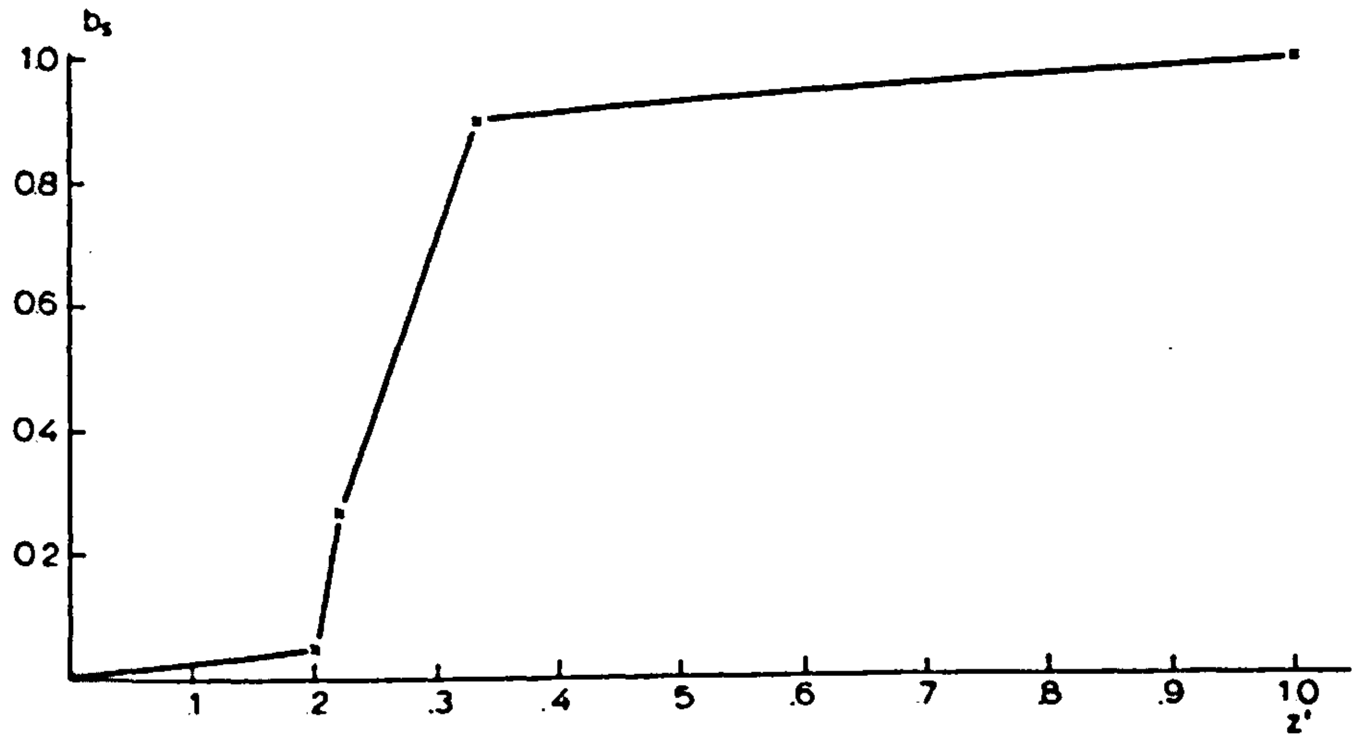

Figure 30. Relation between dimensionless moisture content in the uppermost soil compartment, z', and reduction factor for soil surface evaporation, b_s.

the inadequacy is not clear.

Using the present function for b_s improved the prediction of evaporation during a dry spell in a field of natural pasture in the northern Negev, Israel. With the previous function for b_s (van Keulen, 1975), evaporation during that period was significantly overestimated.

A good approximation of the moisture dynamics in the top soil layer is necessary because evaporation is dependent on its moisture content. Since flow between compartments, resulting from developing potential gradients, cannot be taken into account in the present model, the total amount E_a is withdrawn from the various compartments by means of a distribution factor, m_i:

$$E_i = m_i \cdot E_a \tag{108}$$

where

E_i is rate of moisture withdrawal by evaporation from the i-th compartment (mm d^{-1})

The distribution factor, m_i, is calculated from the current moisture distribution in the profile and an exponential decay function, dependent on soil type:

$$m_i = (d_i \cdot Y_i) / \sum_{i=1}^{n} (d_i \cdot Y_i) \tag{109}$$

$$Y_i = \max(0, (\theta_{li} - \theta_{ai})) \cdot e^{-k' \cdot l_i} \tag{110}$$

where

d_i is thickness of the i-th soil layer or 'compartment' (mm)
k' is extinction coefficient for moisture withdrawal (dimensionless)
l_i is depth of the centre of the i-th compartment below the soil surface (mm)
θ_{li} is actual volumetric moisture content of the i-th compartment (cm^3 cm^{-3})
θ_{ai} is volumetric moisture content of the i-th compartment at air dryness (cm^3 cm^{-3})

The soil-specific k' values can be derived from a detailed process model of soil evaporation (van Keulen, 1975). For the loess soils of the northern Negev a value of 0.015 fit the data best; for a sandy soil in a laboratory column a value of 0.005 gave good results.

4.1.3 Water uptake by the roots

Extension growth of the root system

It is assumed that root density is always adequate to explore the rooted soil volume completely, (Subsection 3.3.2). Moisture availability to the crop therefore depends mainly on the rooting depth. It is assumed that at emergence the length of the roots is 0.08 m and that extension growth continues until a maximum rooting depth is reached, set either by plant or cultivar characteristics. Extension growth also ceases when either an impermeable layer in the profile is reached or when the root tip reaches a soil compartment with a moisture content at or below wilting point (Salim et al., 1965). When the supply of assimilates to the root system is halted (Subsection 3.4.2) extension growth of the roots also comes to a standstill.

Finally it is assumed, that when growth of the above ground parts of the vegetation is restricted due to water or nitrogen deficiency, the unused assimilate is diverted to the root system. Extension growth increases up to double the current rate as leaf and stem growth cease.

Hence,

$$E_r := E_{rm} \cdot (r_f + (1 - f_{ws})),\ p_r > 0;\ z_{ap} > z_{wp} \quad (111)$$

where

E_r	is extension rate of the root system (mm d^{-1})
E_{rm}	is maximum extension rate the root system (mm d^{-1})
r_f	is basic multiplication factor for root extension rate (dimensionless)
f_{ws}	is reduction factor for shoot growth due to water or nitrogen shortage (dimensionless)
p_r	is partitioning factor for assimilate to the root system
z_{ap}, z_{wp}	current moisture content and moisture content at wilting point for compartment in which the root tip is situated

Water uptake by the root system

Transpiration by the vegetation (Section 3.3) must be balanced by water uptake from the soil. Water uptake depends on the difference in potential between the water in the plant and in the soil, and on the resistance to transport of moisture from the soil to the atmosphere. Numerous experimental and theoretical studies have been conducted to determine the relative importance of the various components of the total resistance (Newman, 1969a,b; Andrews & Newman, 1969; Cowan, 1965; Slatyer & Gardner, 1965; Gardner, 1960). The general consensus is that the major resistance to moisture transport is in the plant when soil moisture potential is low and in the soil when soil moisture potential is high. Up to a point, water potential in the plant can be adapted so as to maintain potential transpiration. At what soil moisture potential the transition from potential transpiration to a transpiration deficit takes place, is difficult to quantify in terms relevant to this model, because most experimental data are based on soil moisture status defined in terms of an average moisture content or moisture potential in the rooting zone (c.f. Fischer & Turner, 1978; Stanhill, 1957). In the model each soil compartment is treated separately. Compensatory effects can be accomodated, so that when part of the root system is in dry soil compartments, those parts that are in wetter compartments, will take up more water (cf. Lawlor, 1973).

On the basis of these considerations, water uptake by roots in each soil compartment, i, is described in the model as follows:

$$r_{ui} = r_{up} \cdot f_{sm} \cdot f_{so} \cdot l_{ri} \cdot e_f \quad (112)$$

where

r_{ui}	is current rate of moisture uptake per unit of effective depth of root penetration (mm mm^{-1} d^{-1})
r_{up}	is potential rate of moisture uptake per unit of effective depth of root penetration (mm mm^{-1} d^{-1})

f_{sm} is a reduction factor for water uptake, function of available soil moisture in compartment i
f_{so} is a reduction factor accounting for the effect of osmotic potential in the soil
l_{ri} is root penetration into a soil compartment (mm)
e_f is root activity coefficient calculated as a function of soil moisture content (dimensionless)

Potential uptake by the roots per unit of effective root penetration, r_{up}, is defined by:

$$r_{up} = t_o/L_{re} \tag{113}$$

where

t_o is potential rate of transpiration of the vegetation (mm d^{-1})
L_{re} is total effective root length (mm)

The effective root penetration depth in mm, L_{re}, is obtained by:

$$L_{re} = \sum_{i=1}^{n} (l_{ri} \cdot e_f) \tag{114}$$

The root penetration depth, l_{ri}, is defined as the vertical extension of the root into a compartment and can vary thus between 0 and the thickness of that compartment. It should be noted that partial penetration of the roots into a given compartment can only limit the *rate* of water uptake from a soil compartment in which the roots have not yet penetrated to the bottom of the compartment. It cannot limit the total amount available. That would involve subdividing the compartment into thinner layers (de Wit & van Keulen, 1972). Root density is considered adequate throughout the profile to meet the demand for unrestricted water uptake (van Keulen et al., 1975). There are situations, however, where this assumption does not hold. In heavy soils, where roots at greater depth do not penetrate the structural elements, a much higher root density would be needed to withdraw water till wilting point (Harmsen, 1984). This effect could be taken into account by using a different values for wilting point with increasing depth.

The root activity coefficient, e_f, varies between 0 and 1 and is inversely related to available soil moisture (Figure 31). The effect of this factor is to decrease the potential uptake per unit depth of root penetration for that part of the root system that is in dry soil compartments, thus allowing increased uptake by roots in wetter compartments.

The reduction factor f_{sm} is defined as a function of the relative amount of available moisture in a soil compartment (Figure 32). Root water uptake is not limited by soil moisture status until about seven-tenths of the available moisture has been depleted, after which a rapid decline follows (Veihmeyer & Hendrickson, 1955; 1950).

The effect of osmotic potential is included to account for situations where excessive concentrations of nitrate develop, especially in heavy fertilized soils

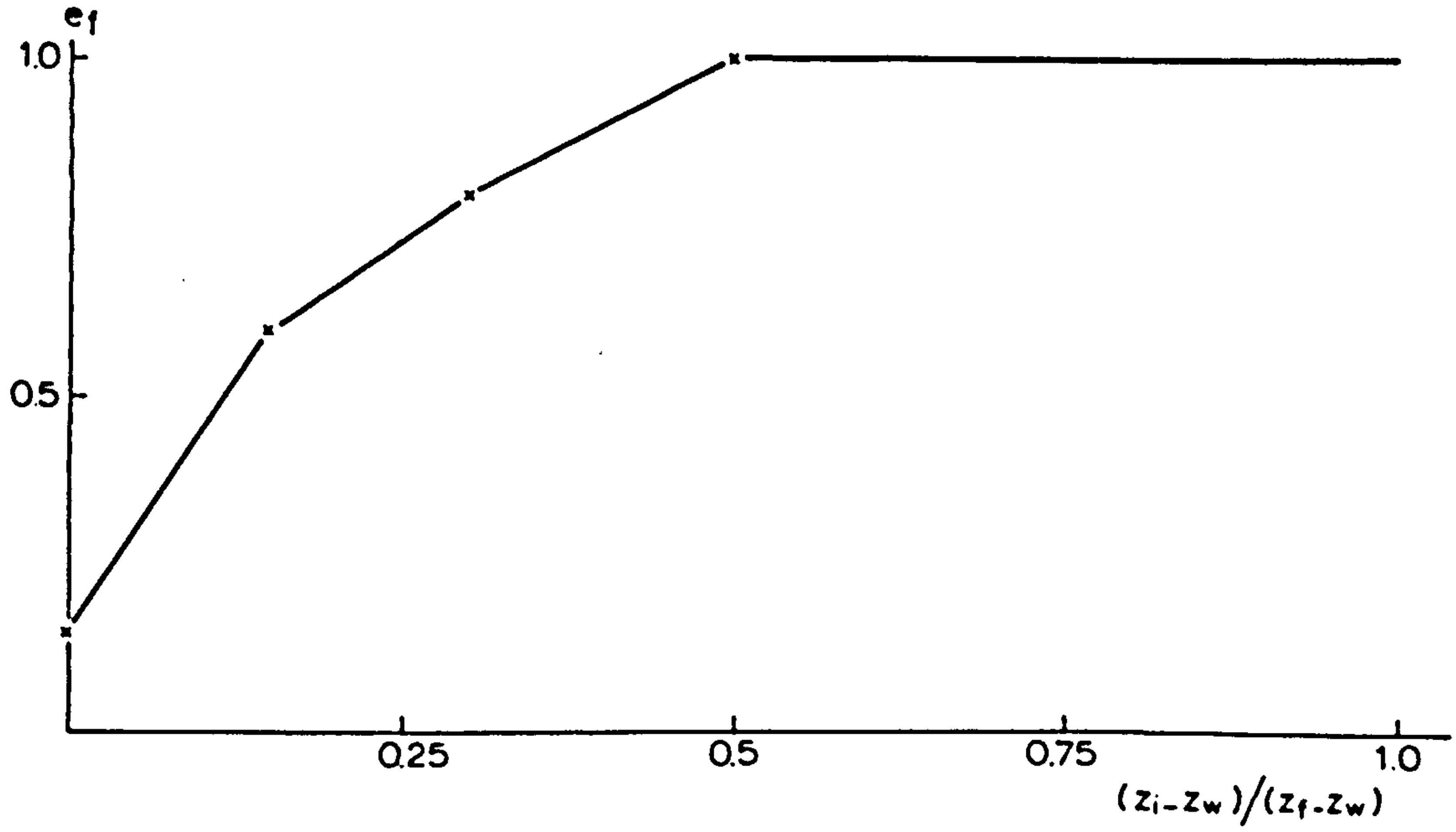

Figure 31. Relation between relative amount of available water in a soil compartment and root activity coefficient, e_f.

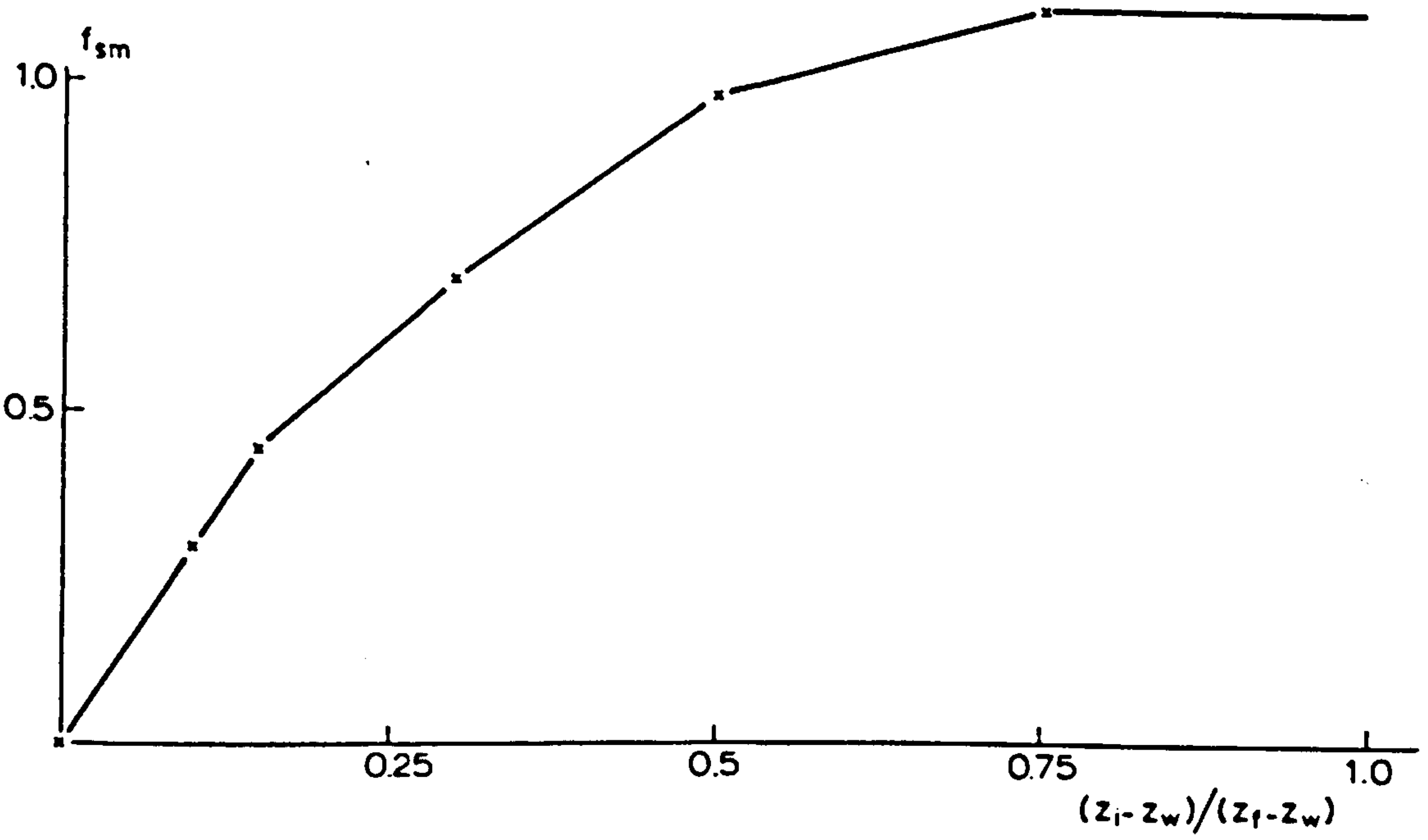

Figure 32. Relation between relative amount of available water in a soil compartment and reduction factor for water uptake by roots, f_{sm}.

as soil moisture is depleted by evaporation. This is an unusual situation and probably occurs only seldom. The effect of salinity is not covered by this function as no other salts besides nitrates are included in the model.

Potential moisture uptake by the crop then follows from summation of water uptake from the various soil compartments:

$$t_p = \sum_{i=1}^{n} r_{ui} \tag{115}$$

Soil temperature also influences the uptake of water from the soil through its effect on both the conductivity of the root system and on the viscosity of the water (Kuiper, 1964). The former effect is most likely related to the fact that maintenance of root conductivity is an active process. In the model, this effect is accounted for by first calculating the potential conductivity of the root system, C_p, as a function of root weight (de Wit et al., 1978) assuming an average age distribution of the root system:

$$C_p = W_r/r_c \tag{116}$$

where

W_r is weight of the roots (kg ha^{-1})
r_c is weight to conductivity ratio of the root system (kg ha^{-1} mm^{-1} d)

The effect of soil temperature is subsequently introduced by:

$$C_a = C_p \bullet f_{st} \tag{117}$$

where

C_a is actual conductivity of the root system (mm d^{-1})
f_{st} is a factor accounting for the effect of temperature on root conductivity (Figure 33)

Actual transpiration is consequently:

$$t = \min (C_a, t_p) \tag{118}$$

For each of the compartments the water balance is thus described by:

$$w_i = r_i - r_{i+1} - E_i - r_{ui} \tag{119}$$

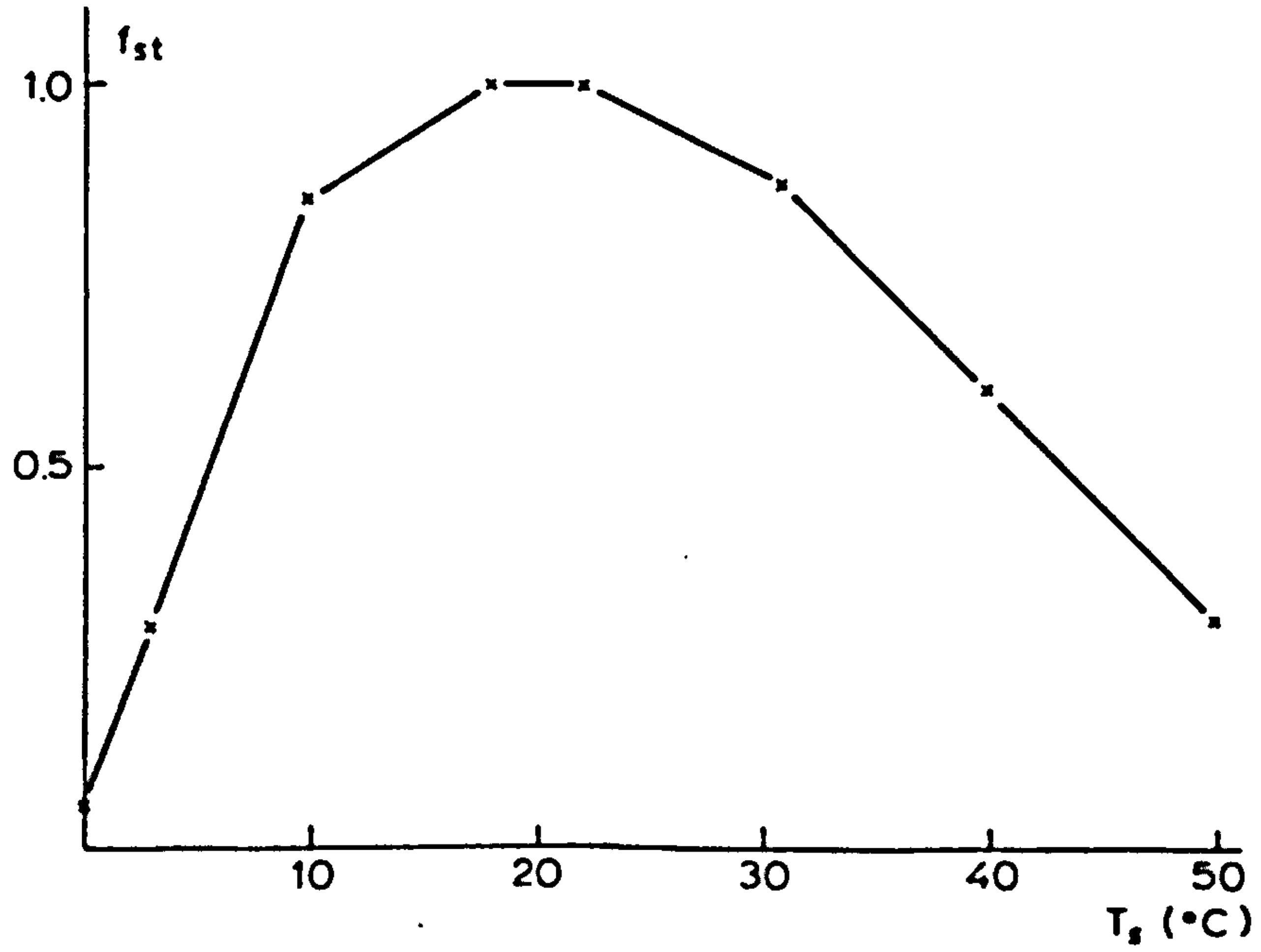

Figure 33. Effect of soil temperature, T_s, on reduction in root conductivity, f_{st}.

where

w_i is rate of change of moisture content in compartment i (mm d^{-1})
r_i is rate of moisture flow into the i-th compartment (mm d^{-1})
r_{i+1} is rate of moisture flow out of the i-th compartment (mm d^{-1})
E_i is rate of moisture withdrawal from i-th compartment for evaporation (mm d^{-1})
r_{ui} is rate of moisture uptake by the roots from the i-th compartment (mm d^{-1})

4.2 Soil nitrogen balance

4.2.1 Conceptual background

The importance of the nitrogen transformations in the soil for the supply of that nutrient to the vegetation has been long recognized and numerous studies on different aspects have been carried out (Bartholomew & Clark, 1965). Much of the accumulated knowledge has been used in recent years to develop detailed models of the soil nitrogen system (van Veen, 1977; Hagin & Amberger, 1974; Beek & Frissel, 1973). Despite all these efforts it is still difficult to simulate the major transformations of nitrogen in the soil to an acceptable degree of accuracy. Direct incorporation of these models or even parts of them in the present model is not possible both because of the small time constants that are used to describe the dynamics of the microbial population in the soil and the need for initializing soil and microbial parameters that are very difficult to measure. Instead, mass balances between sink and source have been used with time constants to moderate the rates of flow. The same approach was adopted to describe the water balance and for similar reasons. Such simplification is essential for tractability and manageability in models where large differences exist in the relaxation times between different component processes but where the central interest is in those processes with the longer relaxation times (de Wit, 1970).

In the present model, the soil nitrogen section is similar to that used for natural pasture (Seligman & van Keulen, 1981; van Keulen, 1981b), except for the fact that the microbial biomass is explicitly considered as a separate pool. The need for such a treatment appeared to arise from experimental data collected in the field, which showed fluctuations in the level of mineral nitrogen in the soil in the course of the year that could not be accounted for by the description previously used.

Total soil nitrogen is subdivided into four components: mineral nitrogen which includes NO_3^-, NH_4^+, NO_2^-; nitrogen in fresh organic material, from recent plant residues; nitrogen in stable organic material, which is the material that has undergone microbial transformations at least once and nitrogen in the microbial biomass.

The mineralization of organic nitrogen to NH_4^+ and the subsequent transformation to NO_3^- is treated in the model as one transformation, since no distinction is made between the two components. This simplification seems justified in the present context by the fact that in the well-aerated soils of the semi-arid winter rainfall region, neither environmental conditions nor lack of oxidizing organisms limit the transformation of NH_4^+ to NO_3^- and in general no accumulation of the former is found (van Veen, 1977). This assumption does not hold under all conditions, as may be deduced from data obtained in a semi-arid region with summer rainfall where significant accumulation of NH_4^+ was measured (Krul et al., 1982). This phenomenon could be related to the fact that in these regions high summer soil temperatures could cause partial soil sterilization with a consequent reduction in populations of nitrifying bacteria in the upper soil layers. This process is not treated in the present model even though there are indications that NH_4^+ accumulation could occur during the hot dry summer in a winter rainfall region (Benjamin, unpublished data).

Volatilization of ammonia may occur in soils having high pH values, especially when ammonical fertilizers are applied before the rains start. That process is treated, albeit very simplistically.

Denitrification is not considered in the present model as anaerobic conditions seldom occur under semi-arid conditions. However, when wet conditions during the rainy season are prolonged and localised anoxia due to intensive microbial activity can occur, denitrification might not necessarily be insignificant (Seligman et al., 1985; Feigenbaum et al., 1984).

4.2.2 Decomposition of organic material

The fresh organic material, roots and other components of last year's crop that have been incorporated into the soil, is divided into three fractions each with its own specific decomposition rate: easily decomposable constituents (proteins, sugars); moderately decomposable constituents (cellulose, hemicellulose); and constituents relatively resistant to decomposition (lignin). The exact composition can be given in dependence of pretreatment or other influences. Actual decomposition is influenced by environmental conditions, mainly soil temperature and soil moisture content through their action on microbial activity.

The stable organic material is assumed to have a constant C/N ratio of 10. It decomposes at a rate much slower than the fresh organic material, but is affected by environmental conditions in a similar way.

Soil microbial biomass growth may either be limited by nutrient (nitrogen) availability, by energy (carbon) availability or by the maximum growth rate of the microbial biomass. It appears that a central parameter in the description of the microbial biomass is its energy (or carbon) requirement for maintenance of existing structures. Reported data of this parameter, especially under field conditions, are scarce and vary widely (Anderson & Domsch, 1985; Anderson & Domsch, 1978; Clark, 1967).

The decomposition of fresh organic material in each soil compartment is described by:

$$d_{ci} = O_i \cdot d_{co} \cdot m_t \cdot m_s \cdot m_c \cdot m_b \tag{120}$$

where

d_{ci} is rate of decomposition of fresh organic material in the i-th compartment (kg ha^{-1} d^{-1})
O_i is amount of fresh organic material in i-th compartment (kg ha^{-1})
d_{co} is relative decomposition rate under optimum conditions of whatever component is currently decomposing (d^{-1})
m_t, m_s, m_c is set of factors accounting for the influence of temperature, soil moisture status and C/N ratio of the material, respectively
m_b is factor accounting for the influence of size of the microbial population on decomposition rate.

The relative rate of decomposition, d_{co}, is specific to each component of the organic material. The component that is being decomposed at any point in time is determined by assuming that easily decomposable material is decomposed first. Thus, progressively more resistant material is decomposed as the process continues and as the organic substrate disappears. Thus:

$$d_{co} = \begin{cases} d_{rp}, & O_i/O_i' > 1 - o_p \\ d_{rc}, & 1 - o_p \geq O_i/O_i' \geq 1 - (o_p + o_c) \\ d_{rl}, & O_i/O_i' < 1 - (o_p + o_c) \end{cases} \tag{121}$$

where

o_p, o_c is fraction of easily decomposable proteins (and carbohydrates) and cellulose (and hemicellulose) in the original material, the remainder being mainly lignin
O_i' is initial amount of fresh organic material in i-th compartment (kg ha^{-1})
d_{rp}, d_{rc}, d_{rl} are relative rates of decomposition of proteins, cellulose and lignin, respectively under optimum conditions (d^{-1})

The effect of soil temperature on the activity of the microbial biomass, m_t, is a function adapted from Beek & Frissel (1973). The relation between soil moisture status and the relative microbial activity, m_s, as given by Beek & Frissel (1973) allows for relatively intensive activity in the low soil moisture range. As there is conflicting evidence in the literature with respect to microbial activity in dry soil (cf. Stanford & Epstein, 1974; Robinson, 1957), the functions used in the present model were modified and are given in Figure 34.
The influence of the C/N ratio is accounted for by:

$$m_c = e^{-0.693(c_n - 25)/25} \tag{122}$$

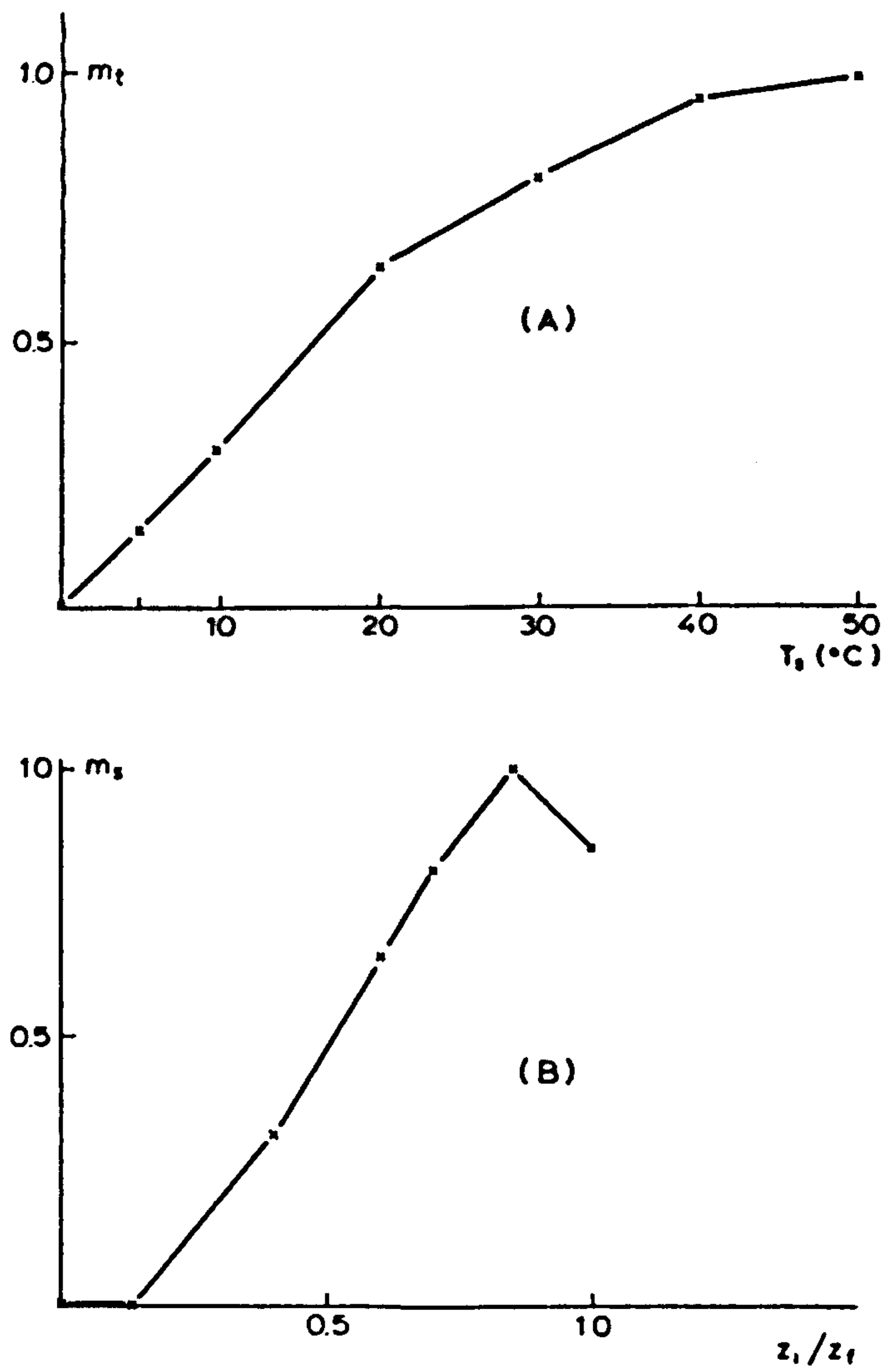

Figure 34. (A) Effect of soil temperature, T_s, on relative rate of decomposition of organic matter, m_t. (B) Effect of soil moisture conditions on relative rate of decomposition of organic matter, m_s.

where

c_n is the C/N ratio of the decomposing biomass which includes the mineral nitrogen present in the soil compartment (Parnas, 1975)

Decomposition of stable organic material is defined as:

$$d_{si} = S_i \cdot d_s \cdot m_t \cdot m_s \qquad (123)$$

where

d_{si} is rate of decomposition of stable organic material in i-th compartment (kg ha^{-1} d^{-1})

S_i is amount of stable organic material in i-th compartment (kg ha^{-1})

d_s is relative rate of decomposition under optimum conditions (d^{-1})

Some of the fresh organic material is eventually incorporated into the stable organic material. In the model this occurs when the C/N ratio in a compartment falls below 25, and carbon availability for microbial activity becomes increasingly limiting in relation to nitrogen availability. Mineral nitrogen is then released during decomposition, of which a fraction is incorporated, together with the carbon required to achieve a constant C/N ratio, into the stable fraction (van Veen, 1977). The fraction incorporated is taken as 0.2 in the present model, but its exact value is difficult to assess. There are indications that this value may be higher when the fresh organic material has a high C/N ratio (Seligman et al., 1985).

The mineralization of nitrogen is described as follows:

$$r_{nfi} = d_{ci} \bullet n_{fi} \tag{124}$$

$$r_{nsi} = d_{si} \bullet n_{si} \tag{125}$$

where

r_{nfi}, r_{nsi} is rate of release of mineral nitrogen during decomposition of fresh and stable organic material, respectively, in the i-th soil compartment (kg ha^{-1} d^{-1})

n_{fi}, n_{si} is concentration of nitrogen in fresh and stable organic material, respectively, in the i-th soil compartment

4.2.3 Growth of the microbial biomass

Decomposition of the organic components yields energy, carbon and nutrients which can be utilized for maintenance and growth of the microbial biomass. As the energy substrate is depleted and becomes insufficient to maintain the microbial biomass, some microbes will die and become available as substrate for respiration. If it is assumed that no more microbes will die than are necessary to maintain the remaining live biomass, then the death rate will be the product of the 'excess' biomass and the relative respiration rate of the live biomass. Thus,

$$m_{ni} = \begin{matrix} m_{bi} & , m_{bi} > 0 \\ m_{bi} \bullet m_r, & m_{bi} \leq 0 \end{matrix} \tag{126}$$

$$m_{bi} = (M_{xi}/c_{nx} - M_i)/\tau_b \tag{127}$$

where

m_{ni} is net rate of change of nitrogen in the microbial biomass (kg ha^{-1} d^{-1})

m_{bi} is nitrogen requirement or nitrogen 'surplus' in the microbial biomass (kg ha^{-1} d^{-1})

m_r is relative maintenance respiration rate of live microbial biomass (d^{-1})

M_{xi} is potential microbial biomass that can be maintained by available C or N (kg C ha^{-1})
c_{nx} is C/N ratio of the microbial biomass
M_i is nitrogen in the live microbial biomass (kg ha^{-1})
τ_b is time constant for change in the microbial biomass (d)

The potential microbial biomass, M_{xi}, is determined by availability of energy or nitrogen, whichever is lower or by the maximum relative growth rate of the microbial biomass.

$$M_{xi} = \min(M_{xni}, M_{xci}, M_{xri}) \tag{128}$$

The potential biomass that is limited by available nitrogen, M_{xni}, is determined by the existing biomass and the instantaneously available mineral nitrogen for further microbial growth at any point in time:

$$M_{xni} = (N_i + M_i) \cdot c_{nx} \tag{129}$$

where

N_i is the available mineral nitrogen in the i-th compartment (kg ha^{-1})

The potential microbial biomass, that is limited by energy availability from decomposing substrate, M_{xci}, follows from:

$$M_{xci} = (C_{di} - C_{gi})/m_r \tag{130}$$

$$C_{di} = 0.4\ d_{ci} + 10\ d_{si} \tag{131}$$

$$C_{gi} = \begin{matrix} m'_{ni} \cdot c_{nx}, & m_{bi} \leq 0 \\ m'_{ni} \cdot c_{nx}/\epsilon_{cb}, & m_{bi} > 0 \end{matrix} \tag{132}$$

$$\epsilon_{cb} = (0.25\ \epsilon_{pr} + 0.75\ \epsilon_{ch}) \tag{133}$$

where

C_{di} is carbon available from decomposition of fresh organic material (kg ha^{-1} d^{-1})
C_{gi} is carbon required for growth of the microbial population or carbon released as microbes die (kg ha^{-1} d^{-1})
m_r is the relative maintenance respiration rate for microbial biomass (d^{-1})
m'_{ni} is m_{ni} of the previous time step. This definition is an artefact necessary to avoid defining the growth rate as an instantaneous function of itself
ϵ_{cb} is the growth efficiency of the microbial biomass. This value is calculated by assuming a mean value of 25% proteins and 75% carbohydrates and fats. Energy requirement for mineral synthesis is negligible

The size of the microbial biomass may also be limited by the inherent capacity of the population to grow. This is expressed in the model by the value of M_{xri}:

$$M_{xri} = m_{ni} \cdot c_{nx} \cdot (1 + r_{mxb}) \tag{134}$$

where

M_{xri} is maximum size of the microbial biomass dictated by the maximum growth rate of the population (kg C ha^{-1})

r_{mxb} is maximum relative growth rate of the microbial population (d^{-1})

4.2.4 Uptake of mineral nitrogen by the roots

The uptake of nitrogen by the vegetation is in part governed by the availability of the element in the soil. It is assumed that nitrogen is being taken up in nitrate form and that the density of the fibrous root system of the wheat crop is high enough to allow for significant movement of nitrate ions towards the root by diffusion (van Keulen et al., 1975). All the mineral nitrogen present in the wet part of the rooted zone is thus available to the vegetation within a relatively short time. A time constant of 1.5 days for diffusion of soil mineral nitrogen to the root system is assumed (Dijkshoorn et al., 1968).

The uptake of nitrogen by roots from the soil in the model is treated along the following lines. First, the uptake by mass flow, n_{tr}, resulting from the transpiration flux is calculated by:

$$n_{tr} = \sum_{i=1}^{n} r_{ui} \cdot n_i \tag{135}$$

where

r_{ui} is mass flow of water to the roots in i-th compartment (mm d^{-1}) (Equation 112)

n_i is concentration of mineral N in i-th compartment (kg mm^{-1})

This amount is then compared to the total demand for nitrogen of the vegetation, d_t, (Section 3.6) to determine whether there is unfulfilled demand that could be met by diffusion, n_{rd}:

$$n_{rd} = \begin{matrix} \max(0,\ d_t - n_{tr})/\tau_{nd},\ s_o \leq 0.60 \\ 0 \qquad\qquad\qquad\qquad ,\ \text{otherwise} \end{matrix} \tag{136}$$

where

τ_{nd} is time constant for diffusion of soil mineral nitrogen to the roots (d)

This formulation assumes no leakage of nitrogen from the plant back to the soil. The specified condition assumes that shortly after the onset of grain fill, when translocation of carbohydrates to the root system has ceased, there is not enough energy available for active uptake of nitrogen or for reduction of nitrate in the plant and a gradient barrier can develop. This could account for the fact that in general very little nitrogen is taken up by the crop after anthesis. There are, however, cases where considerable amounts can be taken up (Ellen & Spiertz, 1980; Spiertz & Ellen, 1978; The permanent plot team, 1971).

The uptake due to diffusion to the root surface is then distributed among the various compartments in proportion to the amount of available nitrogen in each of them and to the depth of root penetration, according to:

$$n_{di} = \begin{matrix} n_{rd} \cdot N_i / N_s \cdot l_{ri} / d_i, & z_{ai} > z_{wi} \\ 0 & \text{, otherwise} \end{matrix} \qquad (137)$$

where

n_{di} is nitrogen supply by diffusion from the i-th compartment (kg ha^{-1} d^{-1})
N_i is amount of available nitrogen in i-th compartment (kg ha^{-1})
N_s is $\sum_{i=1}^{n} N_i$, when $z_{ai} > z_{wi}$
l_{ri} is depth of penetration of the root into the i-th compartment (mm)
d_i is thickness of the i-th compartment (mm)
z_{ai} is current moisture content in the i-th compartment
z_{wi} is moisture content at wilting point in the i-th compartment

Total uptake of nitrogen, n_t, cannot exceed a maximum uptake rate set by the capacity of the transport system of the plant, u_x (Section 3.4.1), or what is available in that part of the rooted zone where moisture content is above wilting point, N_s:

$$n_t = \min (n_{tr} + \sum_{1}^{-} n_{di},\ u_x,\ N_s/\Delta) \qquad (138)$$

The specified condition, which is a rough approximation of reality (van Keulen, 1981b) accounts for the fact that at low moisture contents in the soil ($z_{ai} < z_{wi}$) discontinuities in the water layer prevent effective diffusion towards the root surface.

If $n_t < (n_{tr} + \Sigma\, n_{di})$, n_{di} must be adjusted accordingly. The term l_{ri}/d_i prevents uptake in soil layers where there are no roots. But, if the deepest roots penetrate even a small fraction of the thickness of a soil compartment, all available mineral nitrogen in that compartment will be available to the root system, only at a much slower rate. When there is a large amount of available nitrogen in a thick layer, this may cause unrealistically high values for nitrogen uptake. Where such a possibility exists, a larger number of thinner soil compartments should be defined.

4.2.5 Transport of mineral nitrogen in the soil

The mineral nitrogen balance in each soil compartment is completed with the description of transport between soil compartments. Models have been developed to describe the transport of ions in soils (Frissel & Reiniger, 1974; de Wit & van Keulen, 1972), but these are not relevant to the present model because of the small time constants used to describe the transport processes. As the dominant influences on movement of mineral nitrogen in the soil under dryland conditions are those due to mass transport, uptake by the plants and microbial biomass and gaseous losses, redistribution in the soil profile by diffusion is ignored as is adsorption on negatively charged soil particles. Only downward transport of nitrogen in the soil is considered:

$$s_n = s_{ni} - s_{no} \tag{139}$$

$$s_{ni} = n_{i-1} \bullet r_i \tag{140}$$

$$s_{no} = n_i \bullet r_{i+1} \tag{141}$$

where

s_n is rate of change of nitrogen content in i-th compartment by transport (kg ha^{-1} d^{-1})
s_{ni} is rate of inflow of nitrogen in i-th compartment (kg ha^{-1} d^{-1})
s_{no} is rate of flow of nitrogen out of i-th compartment (kg ha^{-1} d^{-1})
n_i, n_{i-1} is nitrogen concentration in the appropriate compartment (kg. ha mm^{-1})
r_i, r_{i+1} is rate of water flow into the appropriate compartment (mm d^{-1})

For each compartment, the nitrogen concentration is calculated as:

$$n_i = (N_i + s_{ni} \bullet \Delta)/(z_{ai} + r_i \bullet \Delta) \tag{142}$$

where

N_i is amount of mineral nitrogen in the i-th compartment (kg ha^{-1})
z_{ai} is current moisture content in the i-th compartment (mm)
Δ is time step of integration.

Thus, all nitrogen present in the compartment and that flowing into it, is mixed with all the moisture associated with it to calculate an average nitrogen concentration. Under dryland conditions, this description represents the transport dynamics of nitrogen in the soil fairly well. Diffusion *per se* along developing concentration gradients, which will generally result in downward movement, particularly in the case of fertilizer application, will be partly compensated for by upward movement of nitrogen with moisture evaporating from the soil surface. As is the case with water, the exact distribution of nitrogen in the profile will be different from that achieved with the detailed process models, but that will hardly effect its availability to the wheat root system which has access to mineral nitrogen over the whole rooted depth. Upward movement of nitrate from below the rooted depth to the root in dryland is unlikely to be an important source of plant nitrogen and can be ignored (Simpson, 1962).

The total mineral nitrogen balance for a soil compartment is now described by:

$$c_{ni} = s_i - s_{i+1} + m_{bi} + r_{nfi} + r_{nsi} - \boxed{r_{ui}} \bullet n_i - n_{di} \tag{143}$$

where,

c_{ni} is rate of change in nitrogen content in the i-th compartment (kg ha^{-1} d^{-1})

5 Performance of the model

5.1 Calibration and validation

5.1.1 Problems in crop model validation

Crop simulation models can never be 'general', in the sense that chemical or physical models are general, simply because a crop is not an isolated process, but an organisation of processes with a wide range of relaxation times (de Wit, 1970). The whole organisation, controlled by its specific genetic code with its context-related expression, can never be fully described in a model, not only because of lack of knowledge, but also because of the extreme complexity of the organisation and the range of resolution times. The rationale for attempting to simulate such an organisation is not based on the generality of the model in the physical-chemical sense as much as on the conservatism of the organization expressed as negative feedbacks that ensure a relatively predictable behaviour under a fairly wide range of operating conditions.

A crop model should therefore be capable of simulating such behaviour with a minimum of site specific adjustment. In the foreseeable future such a model can be used to test hypotheses, but it cannot replace experiment as the final arbiter of their validity. The performance of a crop model in relation to the behaviour of the real world system that is being simulated, can be evaluated by comparing the results obtained from the model in a well-defined situation with experimental data under identical conditions. During model development one (or more) sets of experimental data are generally used to test model behaviour. This involves a recurring cycle of model formulation, comparison of the model results with field data, reformulation of structure and/or adjustment of parameter values of the model. The calibration cycle is repeated until further possibilities for significant improvements are exhausted, given the conceptual constraints of the model and the accuracy of the available data.

While the agreement of the model results with this set (or these sets) of data can be of interest in itself, a critical evaluation, or validation, of the model requires a separate set of data that was not used during its development (van Keulen, 1976a). We will present both calibration and validation phases in some detail.

Validation of crop models presents a number of serious problems that arise from the fact that field data are seldom so definite that validation can be conclusive. The model parameters and driving variables, by definition, simulate a specific situation that is determined by a number of site and crop (or cultivar) characteristics. These are expressed in the initial conditions and in the dynamics of the forcing variables. Ideally, all of these characteristics should be measured and available. In practice, plant, soil and meteorological data for the study site are rarely precise, and often come from a nearby site which, almost by definition, is not identical. Often, parameters that are not routinely measured turn out to be important. Such parameters are then estimated by various means, some of them inherently arbitrary. As a result, the 'noise' in the model output increases. Measured characteristics also have their complement of 'noise' that derives from the heterogeneity of growing conditions in even the most homogeneous sites. Soil characteristics especially vary widely on a micro scale because of land preparation or the action of man or animals. Average sample values, even with small standard errors can be misleading because nonlinearity in the response of the crop to environmental variation can produce results that are different from those obtained with a model based on the assumption of environmental uniformity.

This situation also holds for crop data that reflect the heterogeneity of the soil and in addition variations in micro- and meso-environmental conditions throughout the growing period. These variations give rise to large standard deviations in the measured crop variables. A case in point is a carefully conducted field experiment on wheat in Australia, reported by Paltridge et al. (1972). In the introduction to their report it is stated that 'considerable effort was expended in an attempt to achieve an 'even' crop... and these efforts were highly successful'. Nevertheless, replicate samples of above ground dry matter on a particular date were different often by more than a factor of two; averages determined on consecutive dates, over rather short time intervals oscillated for no obvious reason except sampling error. The common solution to this situation is to fit a curve that smoothes the data. But then the curve is a special case, just as the model output is another special case. As a rule, the model results are regarded as satisfactory as long as they are within the standard error of the data but, in view of site variation, even that may be an excessive demand. A problem that derives from this criterion is that the 'noisier' the data, the easier it is to 'validate' the model! Eventually, the model validation may be so inconclusive because of the variation in existing field data that it may need careful custom-designed experiments to determine validity. That would be the case especially where the model predicts a response that is unexpected or that cannot be resolved from available information. In essence, the model is an hypothesis, but one that is difficult to test. Nevertheless, the consequences of the hypothesis can be interesting and even useful, as we hope to show in subsequent sections.

5.1.2 Migda 1979/1980

The model output will be evaluated by comparing it to a set of data obtained from spring wheat grown in the Northern Negev of Israel during the 1979/1980 season. The crop was part of a wheat fertilization experiment conducted at the Migda Experimental Farm as part of a joint Dutch-Israeli research project on

Table 16. Organ-formation parameters

	Units	Tillers	Ears	Spikelets	Florets	Grains
integral (P)	number ha^{-1}	TLN	EARN	NSPS	FFNR	CRN
Derivative –•output	number ha^{-1} d^{-1}	ZZ1060	REARF	RSPLF	RFFF	RGRN
R – development rate	d^{-1}	DVRV	DVRV	DVRV	DVRV	DVRR
DS – development stage	-	DVSV	DVSV	DVSV	DVSV	DVSR
DSB – DS at phase beginning	-	DVSTS	DVSSE	DVSSPS	DVSFS	DVSSGF
DSE – DS at phase end	-	DVSPRE	DVSPRE	DVSSPE	DVSFE	DVSEGF
P-current organ population density	number ha^{-1}	TLN	EARN	NSPS	FFNR	GRN
W-minimum viable organ weight	kg org^{-1}	CHFTB	CHFEB	CHFSB	CHFFB	
FCHN-carbohydrate flow to shoot	kg ha^{-1} d^{-1}	FCHLS	FCHLS	FCHLS	FCHLS	FCHLS
C-ceiling organ population density	number ha^{-1}	100*TLNI	TLN	25*EARN	4*NSPS	FFNR
TF-time constant for organ formation	d	TCTF	TCEF	TCSF	TCFF	TCGF
R-reduction factor for water and/or nutrient stress		FNC	1	1	1	RFT
F-organ formation rate	number ha^{-1} d^{-1}	GRNT	REAKF	RSPLF	RFFF	RGRN

pasture and crop productivity in arid regions (Van Keulen et al., 1983). Details on soil and climate are given by Hillel (1971b), van Keulen (1975) and Dan et al. (1976). The wheat (*T. aestivum* cv. Miriam) was sown on November 11, 1979 at a rate of 140 kg ha^{-1} and emerged between December 5 and 8 after rain at the end of November. Two treatments were selected for evaluation: one that received no nitrogen fertilizer in the year of the experiment ('low N') and one that received 100 kg ha^{-1} as urea ('high N'), broadcast and disked into the top 10 cm soil layer before sowing on October 28. Both plots received 45 kg ha^{-1} P given as granulated superphosphate (Benjamin et al., 1986), disked in at the same time as the urea.

From the end of December onwards, the two treatments were sampled approximately every fortnight by clipping ten to twenty 0.5 × 0.5 m quadrats, chosen at random. The samples were separated into stems, green leaves, dry leaves and ears, dried in a forced-draught oven at 70°C for 48 hours, and weighed · All plant samples were analyzed for total nitrogen by the micro-Kjeldahl method (Bremner & Keeney, 1963).

The soil was sampled down to 1.8 m after fertilizer application and before sowing. Soil moisture and mineral N content was determined for each of six 30 cm soil layers.

Weather data for running the model consisted of daily rainfall data from the Migda site and daily minimum and maximum temperature, dew point, wind run and radiation data from the meteorological station at the Gilat Regional Experiment Station, about 8 km SSE of the experimental site.

The initialization of the soil state variables was based mainly on measured data for the Migda site. Crop state variables were initialized on emergence, assuming an initial leaf weight of 5 kg ha^{-1}. This is much lower than the 140 kg sown, but appears to be a suitable value for initial green leaf as most of the seed reserves that are available before emergence appear to be invested in the roots, underground parts of the shoot and in respiration. All other plant characterisation parameters were set to standard values (Table 17).

The simulated growth, N uptake and N concentration in the shoot for the 'high N' runs are given in Figs. 35 to 37. On the whole, the simulated values for total shoot weight and green leaf weight are close to the observed values. The most glaring deviation is at the peak of the growing season (day 200), when the measured value is well above the simulated value. As subsequent measured values were close to the simulated ones, and as the sudden peak value occurs while leaves were rapidly senescing, it may well be that the observed value is an overestimate due to unintentional sampling bias.

The simulated time course for green leaf follows observed values quite closely, except for one deviant observed value. Senescence is triggered in the model by ageing of leaves (when each daily increment has accumulated 750 d°C, equivalent to a 'standard' life span of 50 days at 15°C), and also by increasing moisture stress.

The N uptake curve follows observed values quite closely till day 160, after

Table 17. Parameter values for 'standard' Migda 1979/1980 runs.

Parameter		Units	'standard' ('high N')
CULTP	– development rate factor, pre-anthesis phase	unitless	1.0
CULTM	– development rate factor, post-anthesis phase	unitless	1.0
AVLTLF	– leaf longevity	d (at 15°C)	50
CHFTB	– assimilate requirement, tiller formation	mg tiller^{-1}	700
CHFEB	– assimilate requirement, ear formation	mg ear^{-1}	1000
CHFSB	– assimilate requirement, spikelet formation	mg spikelet^{-1}	120
CHFFB	– assimilate requirement, floret formation	mg floret^{-1}	45
TRP	– moisture stress switch	unitless	1 (according to water status)
NGIFT	– N-fertilizer application	kg ha^{-1}	0
NAPDAY	– day of N-fertilizer application	d	0
IAS1	– mineral N in 0-2 cm soil layer	kg ha^{-1}	0
IAS2	– mineral N in 2-5 cm soil layer	kg ha^{-1}	2
IAS3	– mineral N in 5-10 cm soil layer	kg ha^{-1}	4
IAS4	– mineral N in 10-20 cm soil layer	kg ha^{-1}	7
IAS5	– mineral N in 20-30 cm soil layer	kg ha^{-1}	7
IAS6	– mineral N in 30-60 cm soil layer	kg ha^{-1}	20
IAS7	– mineral N in 60-90 cm soil layer	kg ha^{-1}	80
SOWD	– sowing date	d	60 (29 Nov.)
SWDF	– sowing density factor	unitless	1.0
TLNI	– initial plant density	plants m^{-2}	260

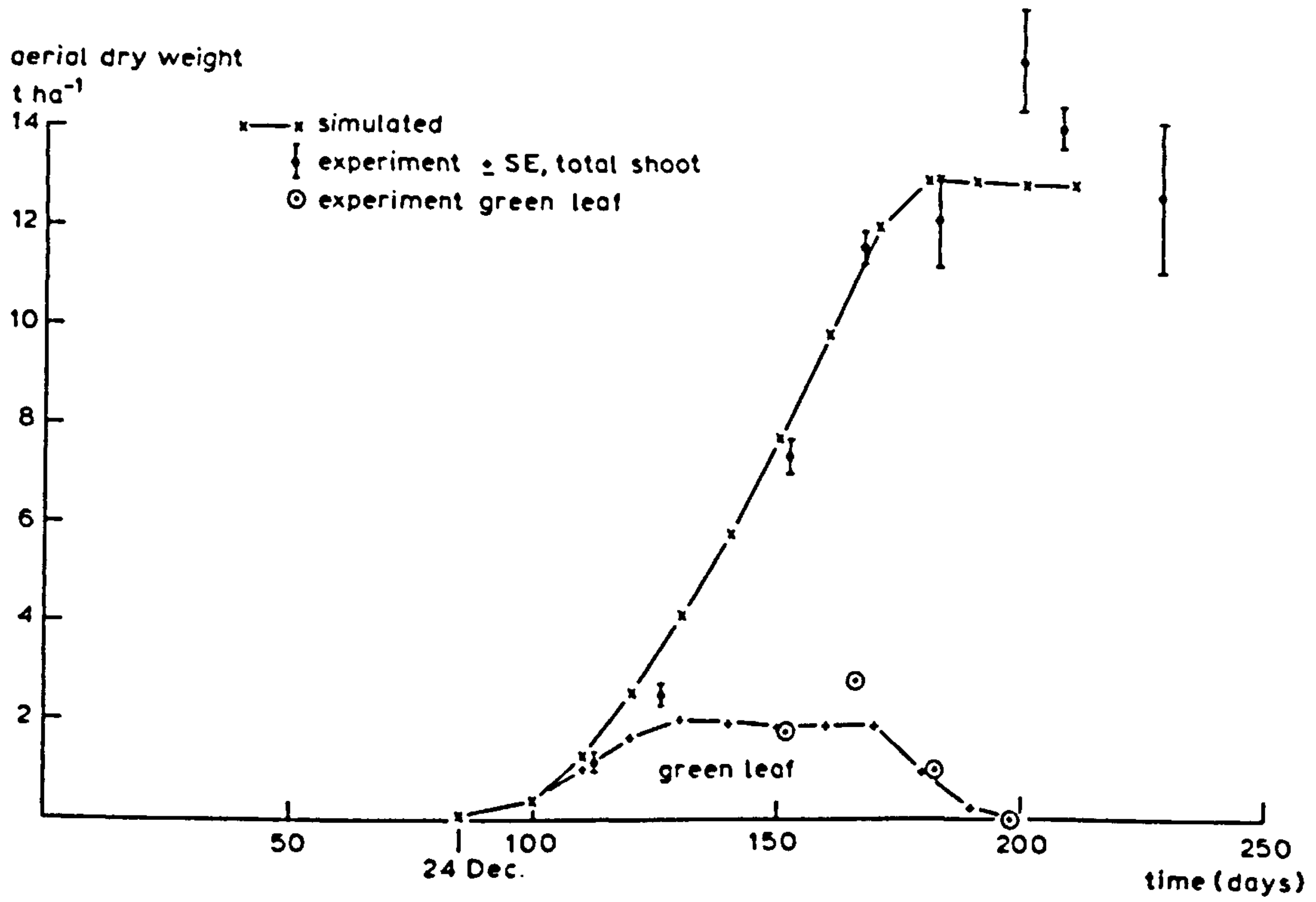

Figure 35. Comparison of measured and simulated time course of total aerial dry matter production for 'high N' treatment in Migda, Israel, 1979/1980.

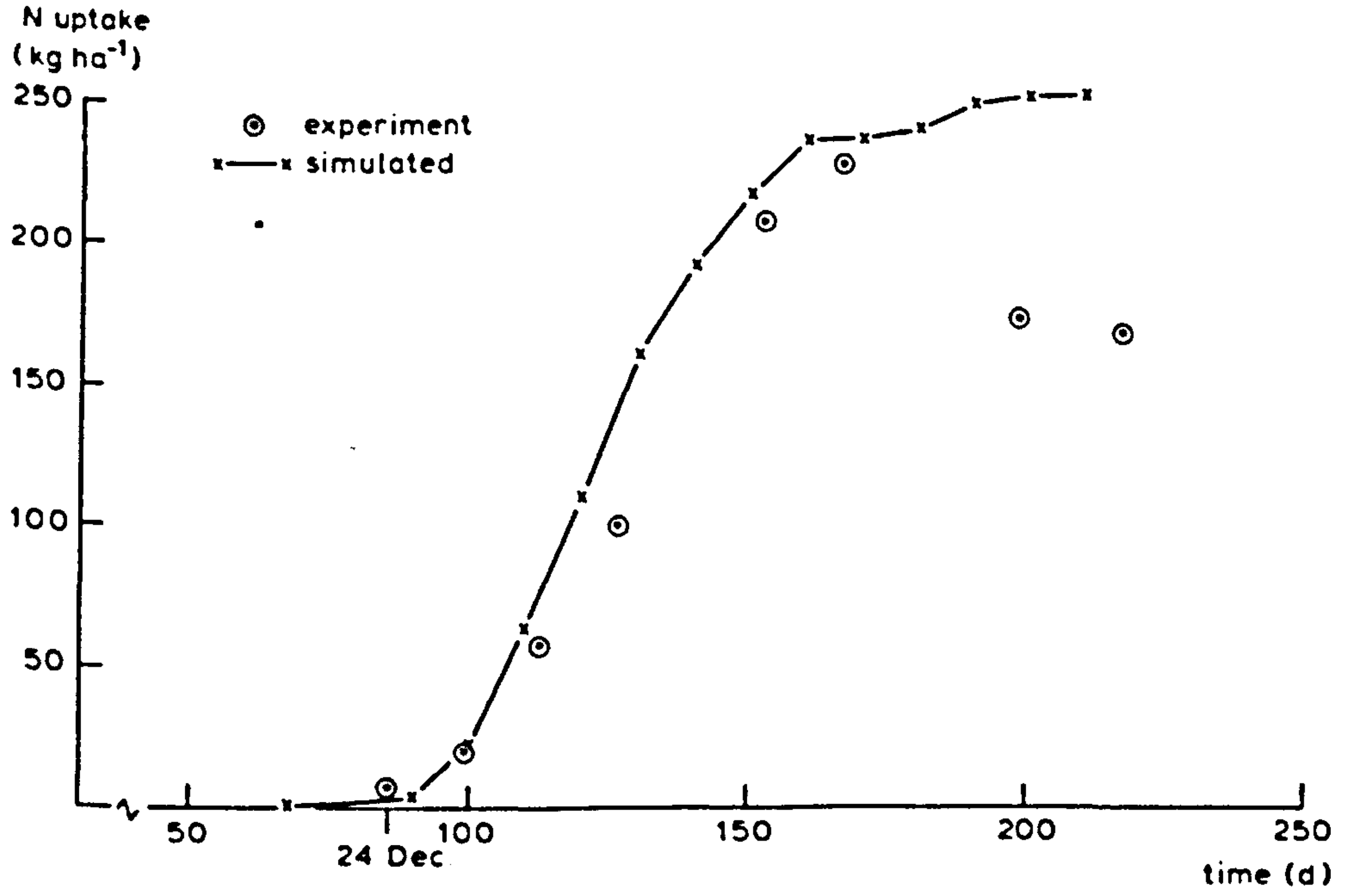

Figure 36. Comparison of measured and simulated time course of total aerial N uptake for 'high N' treatment in Migda, Israel, 1979/1980.

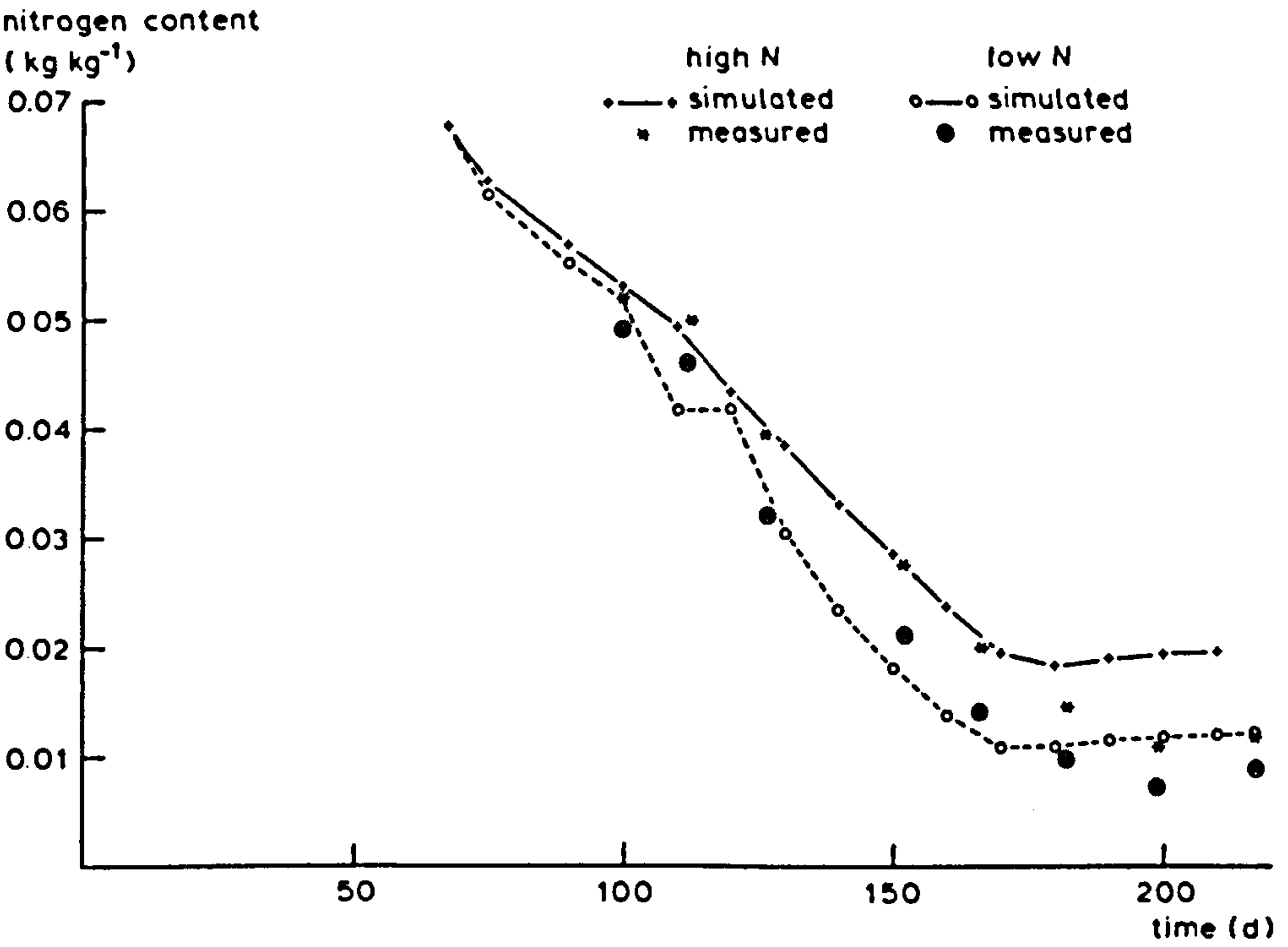

Figure 37. Comparison of measured and simulated time course of nitrogen content in aerial dry matter of 'high N' and 'low N' treatments in Migda, Israel, 1979/1980.

which, in the observations, massive amounts of N 'vanish' from the shoot. This could be sampling error again, but it is also a phenomenon that has often been reported (e.g. Puckridge and Donald, 1967; Spratt & Gasser, 1962; Boatwright and Haas, 1961). It is therefore not clear whether this loss is apparent or real, and if real, where all the N goes to. Loss by insects, leaching (Tukey, 1970), volatilization (Wetselaar & Farquhar, 1980), and other causes have been suggested, but most are speculative. Whatever the reason, it is not represented in the model and so the discrepancy will remain until resolved by careful experimentation. The course of N concentration in the shoot is close to observed for most of the life cycle of the crop. Towards the end, after day 170, the model overestimates N concentration in the shoot for the same reasons as those discussed above with regard to N uptake.

Final harvest statistics are compared to simulated values in Table 18. The problems associated with sampling are well illustrated in this table, where for the 'high N' field, combine-harvested yield of the whole field was 3080 kg ha^{-1} while hand sampled yields were between 3410 and 4020 kg ha^{-1}. Whereas it could be argued that the combine harvest is the only 'true' value, it should be noted that it includes all the irregularities, bare spots and weedy areas that are generally avoided during hand sampling. The model assumed a uniform crop canopy, a condition which is rare, especially under dryland conditions. Consequently, it would tend to predict higher values than combine-harvest yields. As the simulated grain yield falls within the range of the various observed values, it can be viewed at least with the same confidence one would

Table 18. Comparison of simulation results and observed data from field 3; Migda, Israel 1979/80.

Variable	Units	High N Observed	High N Simulated	Low N Observed	Low N Simulated
		X ± SE[(a)]		X ± SE[(a)]	
Combine harvest					
a. Grain yield, day 230	ton ha^{-1}	3.08	4.08	3.20	4.04
b. Grain weight, day 230	mg grain^{-1}	25.6 ± 0.3	35.2	30.0 ± 0.2	37.7
c. Grain density (a/b), day 230	number m^{-2}	$1.2*10^4$	$1.16*10^4$	$1.07*10^4$	$1.07*10^4$
d. Grain per ear, day 217	number ear^{-1}	31.1 ± 3.0	29.7	32.0 ± 3.1	33.4
e. Ear density (c/d), day 217	number m^{-2}	385	390	334	321
f. Spikelets per ear, day 217	number ear^{-1}	13.3 ± 1.0	10.4	12.2 ± 0.9	10.7
g. Spikelet density (e*f), day 217	number m^{-2}	$5.12*10^3$	$4.05*10^3$	$4.06*10^3$	$3.44*10^3$
h. N concentration grain	unitless	0.028	0.029	0.020	0.020
Hand harvest					
i. Grain yield, day 217	ton ha^{-1}	3.41 ± 0.18		3.75 ± 0.23	
j. Grain yield, day 230	ton ha^{-1}	4.02 ± 0.35		3.72 ± 0.27	
k. Ear density, day 217	number m^{-2}	500 ±35		390 ±35	
l. Spikelet density, day 217	number m^{-2}	$6.66*10^3$		$4.74*10^3$	
m. Grain density, day 217	number m^{-2}	$1.35*10^4$		$1.11*10^4$	
n. Tiller density, day 198	number m^{-2}	541 ±30	395	408 ±19	324

(a) Variables ±SE are observed values; these without SE are derived as indicated.

ascribe to the measured values which vary as a result of subtle interactions between plant characteristics and environment. Some of these characteristics can be simulated and will be discussed later (Section 5.2).

Most of the morphological characters of the plant, i.e. grain density, grains per ear and ear density are simulated fairly accurately; others less so, – particularly grain weight. Nitrogen concentration of the grain was simulated as 0.029 kg kg^{-1} compared to 0.028 observed at 'high N' (Fig. 38).

Summarizing the performance of 'high N', it can be said that the model simulated a recognizable wheat crop for the year and for the given growing conditions. That may not be much, but it is a minimum requirement for a model that is to be used for analysis of agronomic practice or of plant characteristics.

The 'low N' simulation and observed data are given in Figs. 37 to 40 and also in Table 18. The simulated growth curve (Fig. 39) compares less favourably with observed values than in the case of 'high N', especially during the early growth phase. On the other hand, the final simulated total dry matter production is quite close to observed. Green leaf which is accurately simulated during the early growth phase, tends to be overestimated towards the end of the growing season. The general overestimation of early growth is related to nitrogen availability to the crop which is apparently more abundant in the model than in reality, despite measured initial values of mineral soil nitrogen. In Fig. 40 we see that whereas at the end of the season, simulated and observed nitrogen uptake are close to each other, simulated nitrogen uptake after day 110 is grossly exaggerated. This illustrates the difficulty, often encountered, of monitoring nitrogen status of the soil in the field. Not only is the sampling variation large, but the dynamics of nitrogen in the soil are not understood well enough to ex-

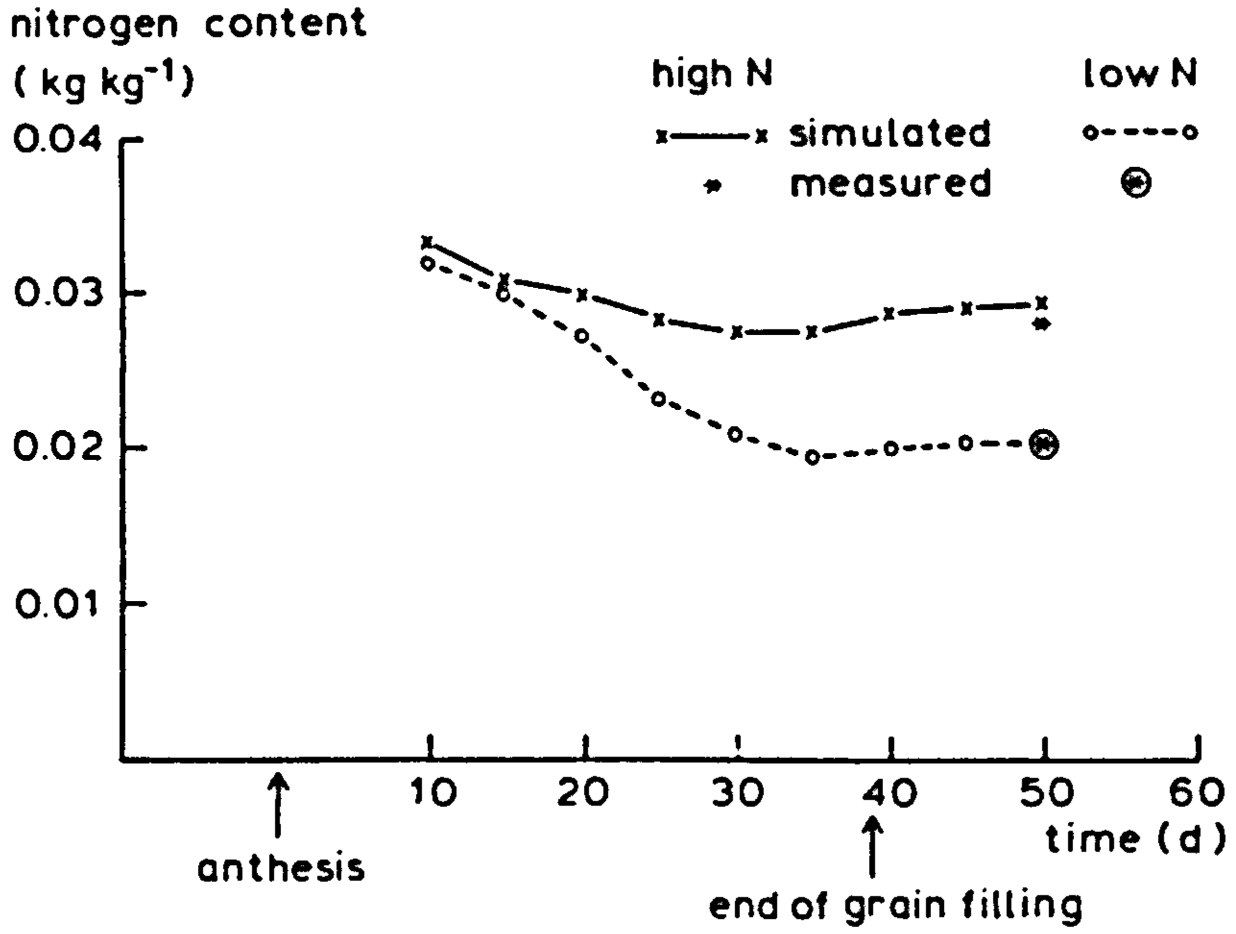

Figure 38. Comparison of measured and simulated nitrogen content in grain for 'high N' and 'low N' treatments in Migda, Israel, 1979/1980.

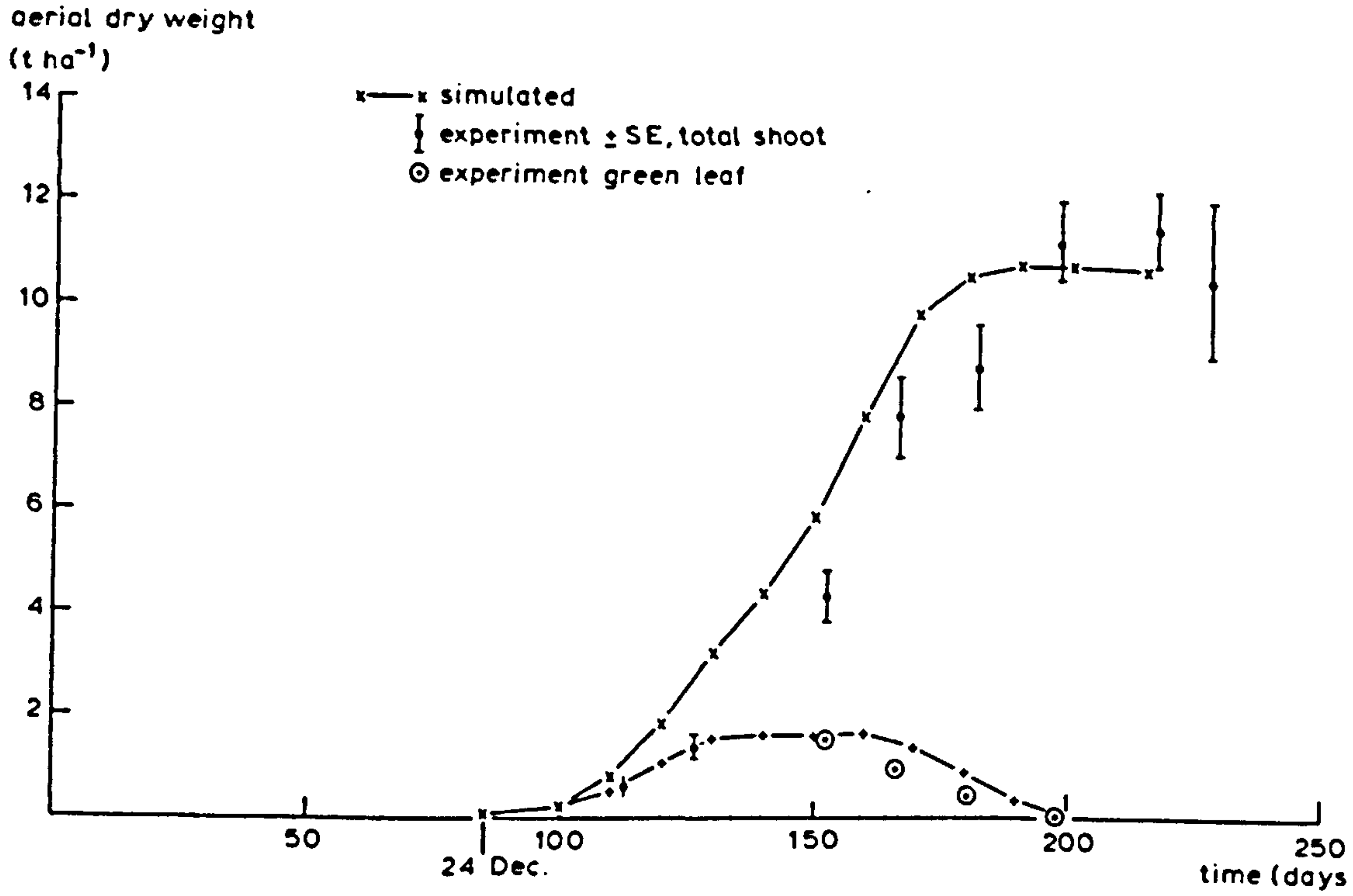

Figure 39. Comparison of measured and simulated time course of total aerial dry matter production for 'low N' treatment in Migda, Israel, 1979/1980.

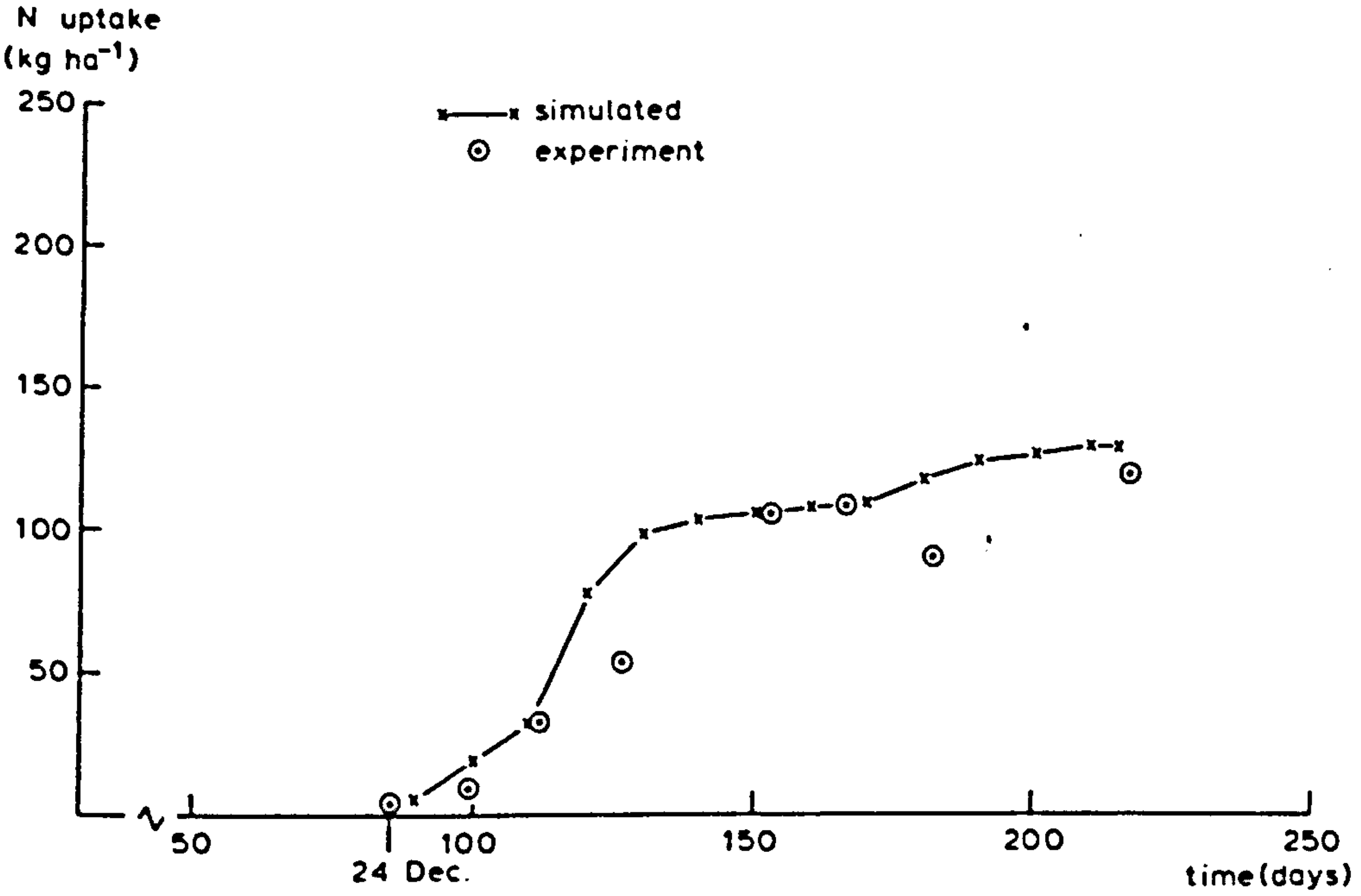

Figure 40. Comparison of measured and simulated time course of total N uptake in aerial parts for 'low N' treatment in Migda, Israel, 1979/1980.

plain anomalous behaviour. In the present case, it is fairly clear that the amounts of nitrogen measured in the soil at the beginning of the season in the 'low N' field, were not available during the early part of the season, but did become available later. Even though the model does try to mimic the activity of the microbial biomass in the soil and its role in immobilization and mineralization of nitrogen, it clearly did not succeed very well in the present case unless the unavailability of nitrogen to the crop was due to other unidentified causes. As a result, nitrogen uptake and consequently plant growth proceeded too rapidly. Had the release of nitrogen been more gradual in the model, uptake and plant growth would have been closer to reality. The problem is only partially due to the compartmentalization of the simulated soil into fairly thick layers, 30 cm each, below 30 cm depth.

The implications for crop performance, however, are not quite as serious as would be expected. The nitrogen concentration in the shoot is simulated quite well (Fig. 37), except for considerable deviation at the end of the growing season. Performance as measured by final harvest statistics is, surprisingly, better than in the case of 'high N'. Simulated grain yield is within the range of measured values, plant morphological characters are very close to observed and grain N-concentration is accurately simulated (Table 18; Fig. 38).

As in the case of 'high N' the simulated wheat crop does behave in a way that is recognizably similar to reality over a fairly wide and demanding range of criteria. True, some of the similarity must stem from the fact that the plant characteristics used to define the cultivar were adjusted to the observed crops. That would parallel the process of choosing a suitable variety for a given condition. But having defined that 'cultivar', further analyses of crop management under varying conditions and for different plant characteristics can be undertaken, as illustrated in the following section.

5.1.3 Sde Boker 1977/1978

A second experiment that was available for validation purposes was carried out also in the framework of the joint Dutch-Israeli research project (van Keulen et al., 1983) in Sde Boker in the central Negev Desert (30°51'N, 34°41' E). Details on the experiment are given by Hochman (1982; 1978), and so only general information is given here.

The experiment was designed to test the effect of water stress at different phenological stages on growth and yield of spring wheat. The site is suitable for such an experiment because rainfall in the region is low (long-term average 92 mm per season) and water supply can be regulated easily by irrigation. The soil is level and fairly homogenenous; and the incidence of weeds, pests and diseases is relatively low.

Spring wheat, cv. Lachish was sown on October 30, 1977, 25 mm of irrigation water was applied and germination was completed in about a week. Plant nutrients, N, P and K were applied at rates of 150, 90 and 10 kg ha^{-1}, respectively. Sowing rate was 140 kg ha^{-1} with commercial equipment.

Total dry matter was determined at regular intervals during the growing season by sampling two 0.25 m^2 quadrats in each of four replicate plots. The plant material was oven-dried at 80°C for 48 hours and weighed. Other parameters measured on the same day included total tiller number; soil moisture, which was determined gravimetrically in 20 cm layers till the depth of root penetration; phenological development, which was recorded, using Large's (1954) illustration of the Feekes scale. Leaf area was determined five times during the pre-anthesis phase by measuring leaf number and leaf area on five individual plants, and then calculating the plant leaf area per unit soil area. Detailed measurements on plant water status (leaf water potential and stomatal conductance) that are of less interest for the present study, were also carried out (Hochman, 1978).

When the model was run with the 'standard data set' and the Sde Boker environmental conditions for the non-stressed, fully irrigated treatment, growth and production was grossly underestimated. Therefore a number of parameter values was adapted:

- leaf area development suggested that the specific leaf area early in the season must have been substantially higher than the value of 20 m^2 kg^{-1} used in the standard run. This may be associated with the fact that average temperatures during the early stages of crop development were higher (November vs. December), a condition which generally induces thinner leaves (Friend, 1966). An initial specific leaf area value of 30 m^2 kg^{-1} was therefore introduced in the model, decreasing to the standard 20 at the onset of stem elongation.
- organ formation also appeared to be incorrectly simulated, probably because in this experiment a different cultivar was used than in the standard run. The minimum size for ears was changed to 900 mg ear^{-1} and that for florets to 35 mg (instead of 1200 and 45 for the standard cultivar, Table 17). Also the maximum growth rate of the individual grains, defined in the standard run as $2 * 10^{-6}$ kg $grain^{-1}$ d^{-1} at optimum temperatures was too low to achieve grain weights as measured in the field. This would thus indicate that there may be differences between cultivars in their capacity for starch accumulation as has been suggested by Stamp & Geisler (1976). The potential grain growth rate was therefore multiplied by a factor of 1.4.
- after anthesis the nitrogen concentration was substantially higher in the flag leaf than in the lower leaves. In the model nitrogen concentration is the average calculated for the entire leaf mass. As the flag leaf contributes most to assimilation after anthesis, gross assimilation may well be underestimated. To take the uneven distribution into account the average nitrogen concentration used to calculate maximum photosynthetic rate, was multiplied by 1.2. Preferential translocation of nitrogen from the lower leaves to the growing grain is a phenomenon that has also been observed in winter wheat (cf. Ellen & Spiertz, 1980).
- the simulated duration of the period between anthesis and the end of grain

fill was shorter than in reality. To account for this difference the cultivar-specific development rate parameter for post-anthesis development was set to 0.8.

- simulated growth rates were low especially towards the end of the growth period, possibly due to accelerated senescence following excessive N translocation to the grain. In order to enhance leaf activity in the later part of the season, N translocation was moderated by setting the basic relative turnover rate of nitrogen in the vegetative tissue to 0.10 instead of the 0.25 as in the 'standard' cultivar.

The results of the model after these parameter adaptations are closer to the measured data (Figs. 41, 42 and 43; Table 19). Dry matter accumulation is slightly overestimated at the beginning of the growing season, and the difference persists at practically a constant value throughout the growth cycle. Observed and simulated growth rates are very similar until about day 150, after which growth rate in the model decreases suddenly due to leaf senescence. The observed data shows that growth continues at a constant rate practically till maturity.

The simulated and observed course of leaf blade area are almost identical in the first half of the growing period. As no leaf area measurements were taken during the second part of the growing period it is not possible to say whether this difference in dry matter accumulation rates is caused by inaccurate description of leaf senescence. This possibility could be tested by increasing the parameter value describing leaf longevity (Section 5.2).

Comparison of measured and simulated soil moisture (Fig. 43) shows that total soil moisture in the potential rooting zone is overestimated in the first part of the growing season, but accurately simulated in the second part. The reason for the early discrepancy is not clear.

The simulated yield components are within 10 percent of the observed values (Table 19), the largest discrepancies occurring in grain weight and the associated grain yield.

It can be concluded from this comparison that the model can simulate high grain yields under optimum growing conditions, provided that the 'right' cultivar is used that can take full advantage of the favourable circumstances. It has also indicated that using an average concentration of nitrogen for leaves throughout the canopy may be an oversimplification under good growing conditions.

After these adjustments had been made for the unstressed treatment, the model was run to simulate other treatments in which the crop was stressed at three different phenological stages. All treatments were irrigated at establishment. In treatment 1 irrigation was withheld during the pre-anthesis phase; in treatment 2 around anthesis; and in treatment 3 during the grain filling stage. The results of the simulation runs compared to observed data are summarized in Figs. 44, 45 and 46 and Table 20.

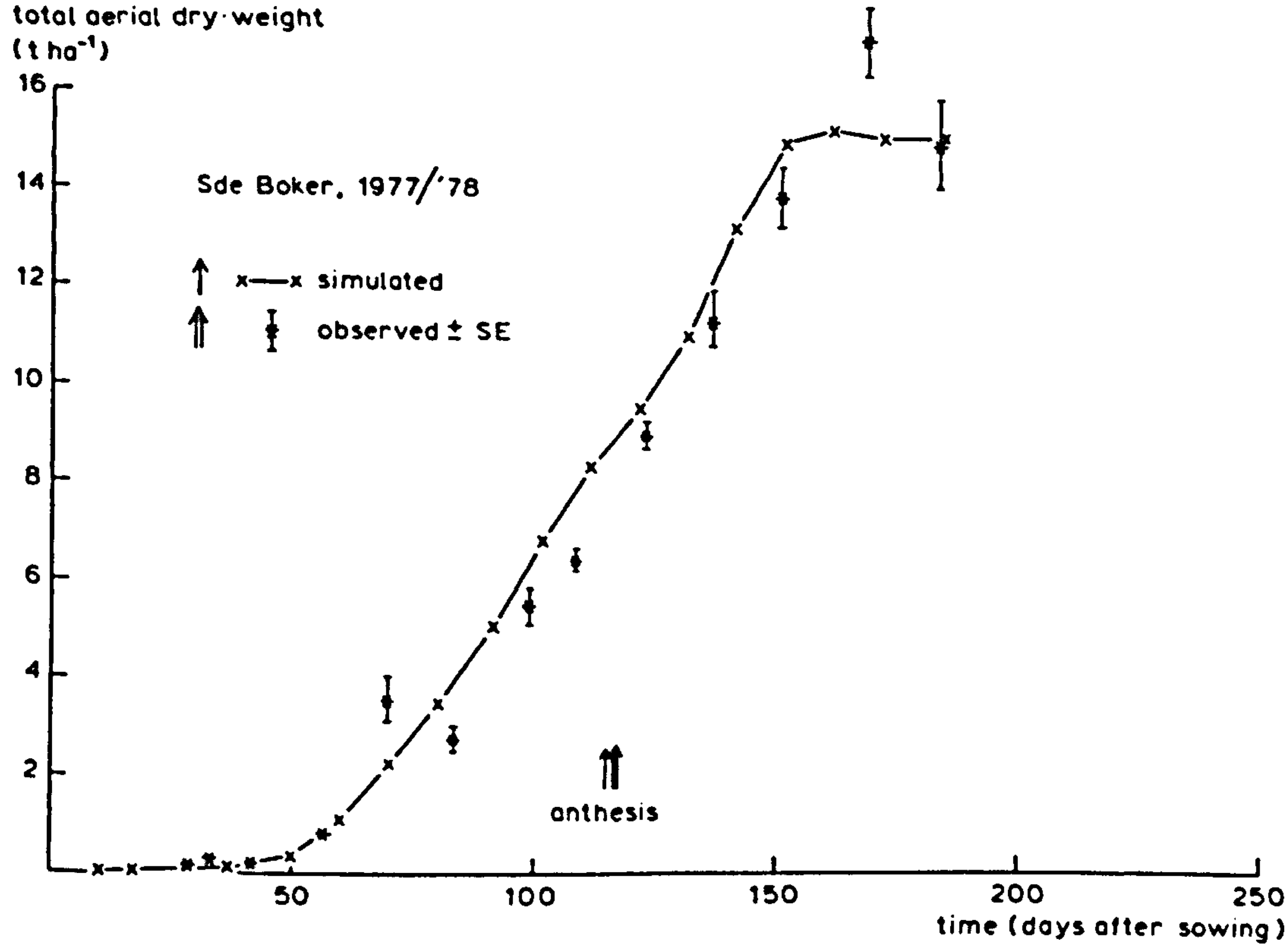

Figure 41. Comparison of measured and simulated time course of total aerial dry matter production for 'unstressed' treatment in Sde Boker, Israel, 1977/1978.

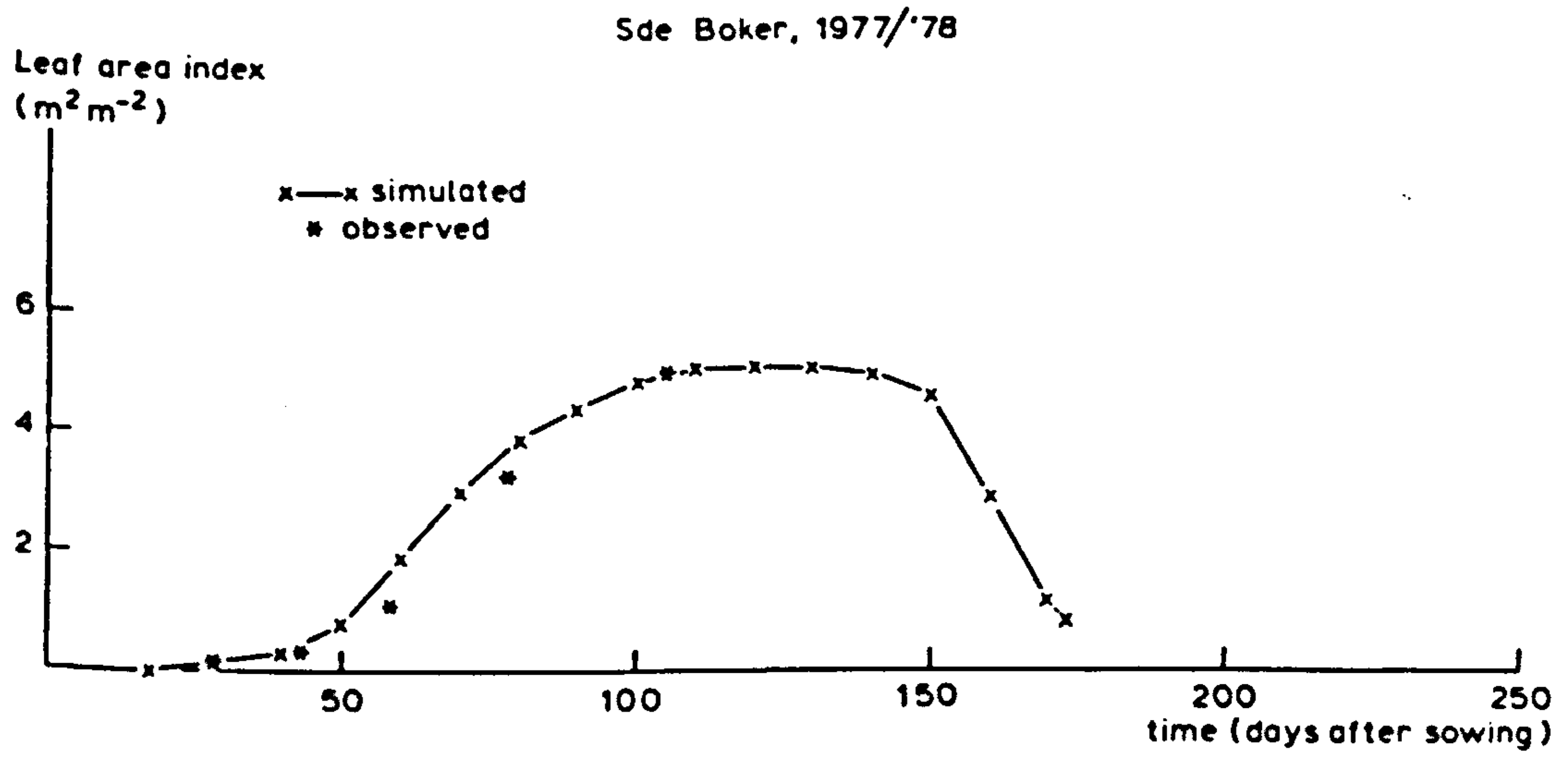

Figure 42. Comparison of measured and simulated time course of leaf area index for 'unstressed' treatment in Sde Boker, Israel, 1977/1978.

The model overestimates the effect of pre-anthesis stress (treatment 1) on dry matter production (Fig. 44). In reality, growth virually stopped, especially towards the end of the stress period between day 98 and day 109, whereas in the model growth was only moderately affected. The soil moisture store at the beginning of the stress period was overestimated in the model by about 20 to

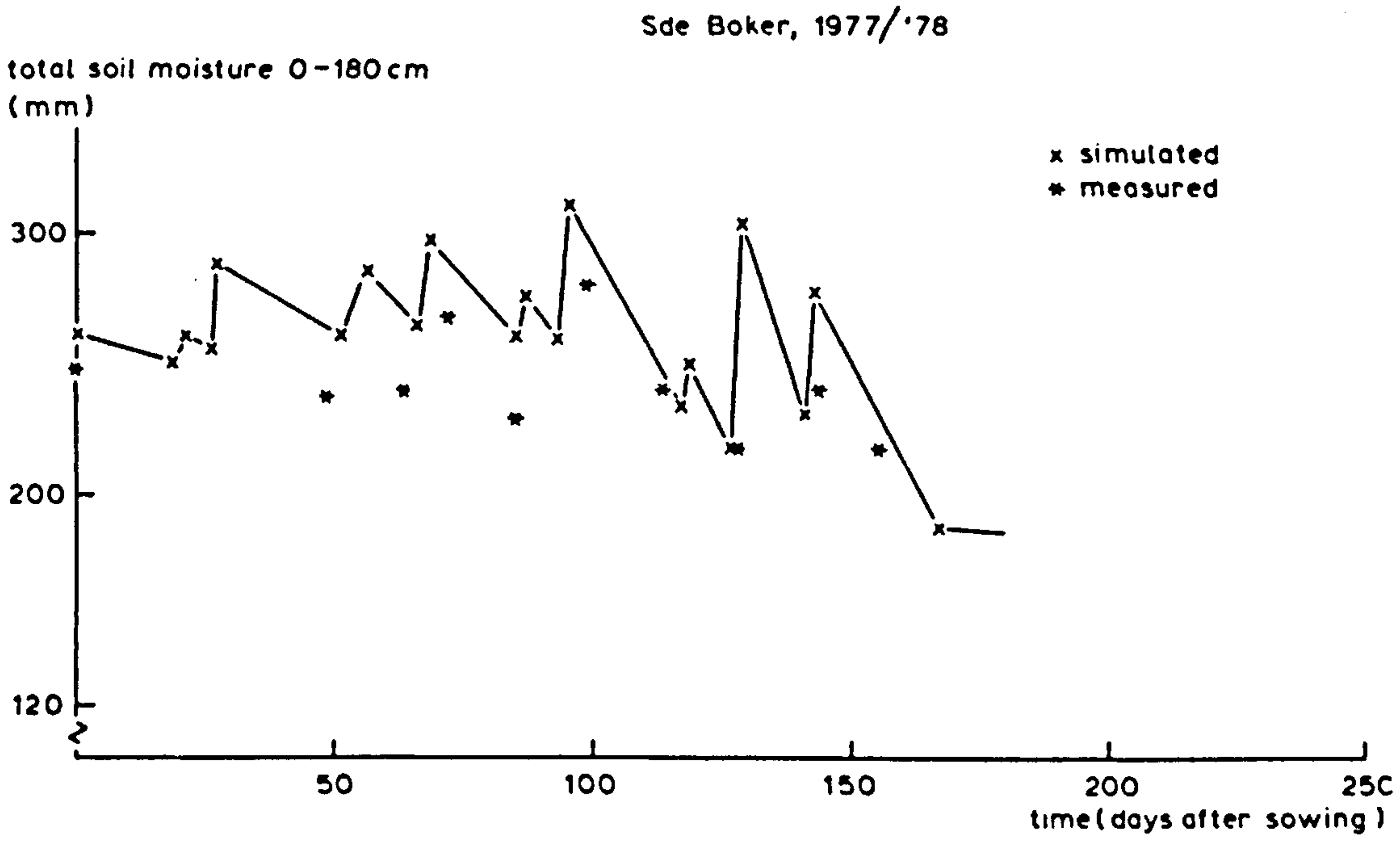

Figure 43. Comparison of measured and simulated time course of total soil moisture for 'unstressed' treatment in Sde Boker, Israel, 1977/1978.

Table 19. Comparison of measured and simulated yield components for non-stressed treatment for Sde Boker, Israel, 1977/1978

	Observed	Simulated
Ear number (ears m^{-2})	513	480
Grain number (grains ear^{-1})	32.7	31.1
Grain weight (10^{-6} kg $grain^{-1}$)	56.3	49.0
Grain yield (kg ha^{-1})	7790	7324

30 mm. After alleviation of stress, the simulated growth rates are similar to observed but slightly higher, so that the difference in accumulated dry matter is as much as 4000 kg ha^{-1} by day 140. This difference is subsequently reduced to less than 1000 kg ha^{-1} at maturity.

Yield components (Table 20) are very poorly predicted: the number of ears per unit area was underestimated by about 40%, whereas the number of grains per ear is overestimated by more than a factor two. In combination with a grain yield that is slightly overestimated, that results in a weight per grain that is about 25% lower than observed. However, it should be noted that multiplying the observed yield components gives a different grain yield from that observed. This is an indication of the magnitude of error that can be introduced when yield and yield component measurements are taken from different samples of

Table 20. Comparison of measured and simulated yield components for three stress treatments for Sde Boker, Israel, 1977/1978.

Crop characteristic	Stress treatment 1		Stress treatment 2		Stress treatment 3	
	observed	simulated	observed	simulated	observed	simulated
Grain yield (kg ha^{-1})	5590	5858	4980	4609	6580	5021
Ear number (ears m^{-2})	658	480	434	480	485	480
Grain number (grains ear^{-1})	13.0	30	27.1	31	31.4	31
Grain weight (10^{-6} kg $grain^{-1}$)	55.2	41	53.7	31	49.2	34

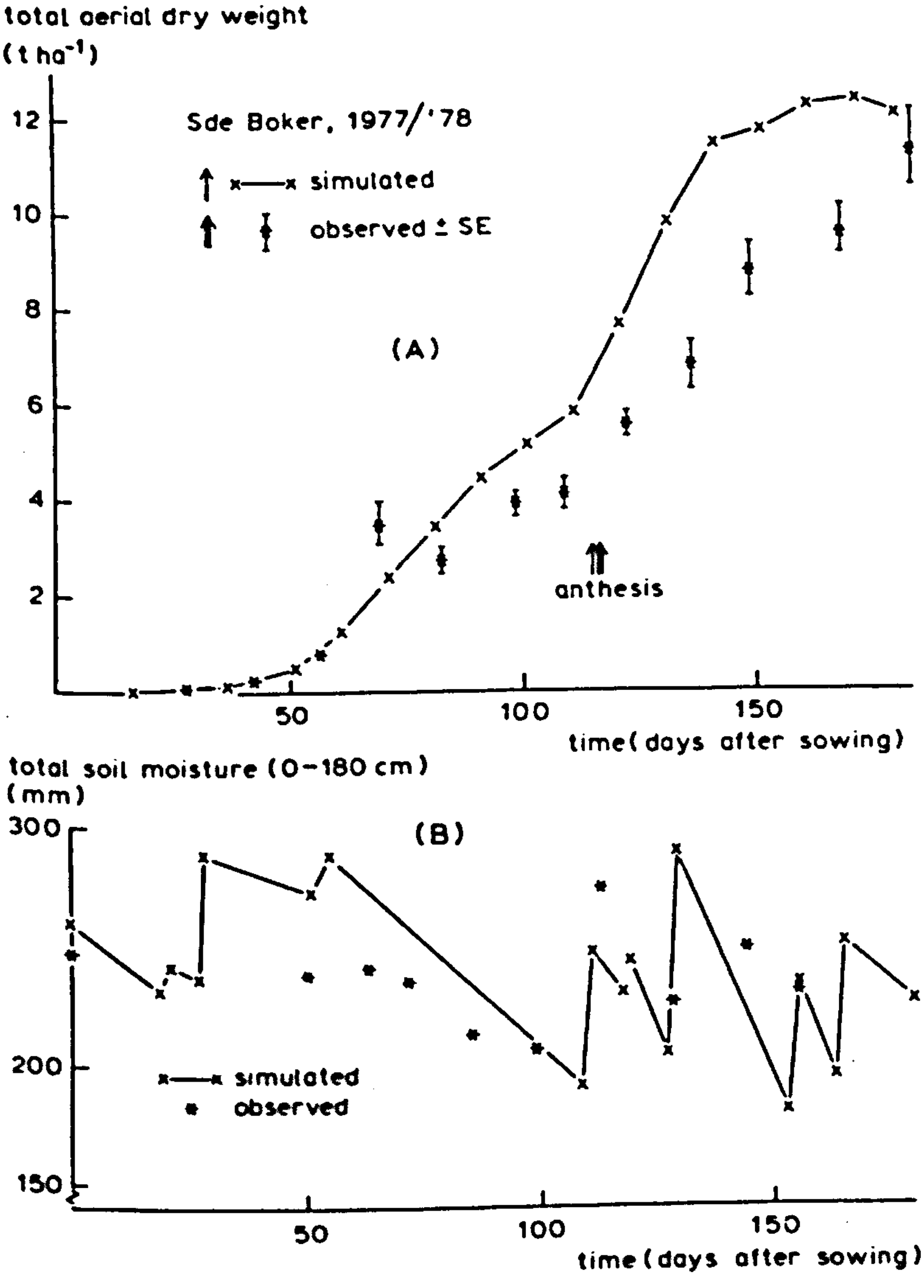

Figure 44. (A) Comparison of measured and simulated time course of total aerial dry matter production for 'stress treatment 1' in Sde Boker, Israel, 1977/1978; (B) Comparison of measured and simulated time course of total soil moisture for 'stress treatment 1' in Sde Boker, Israel, 1977/1978.

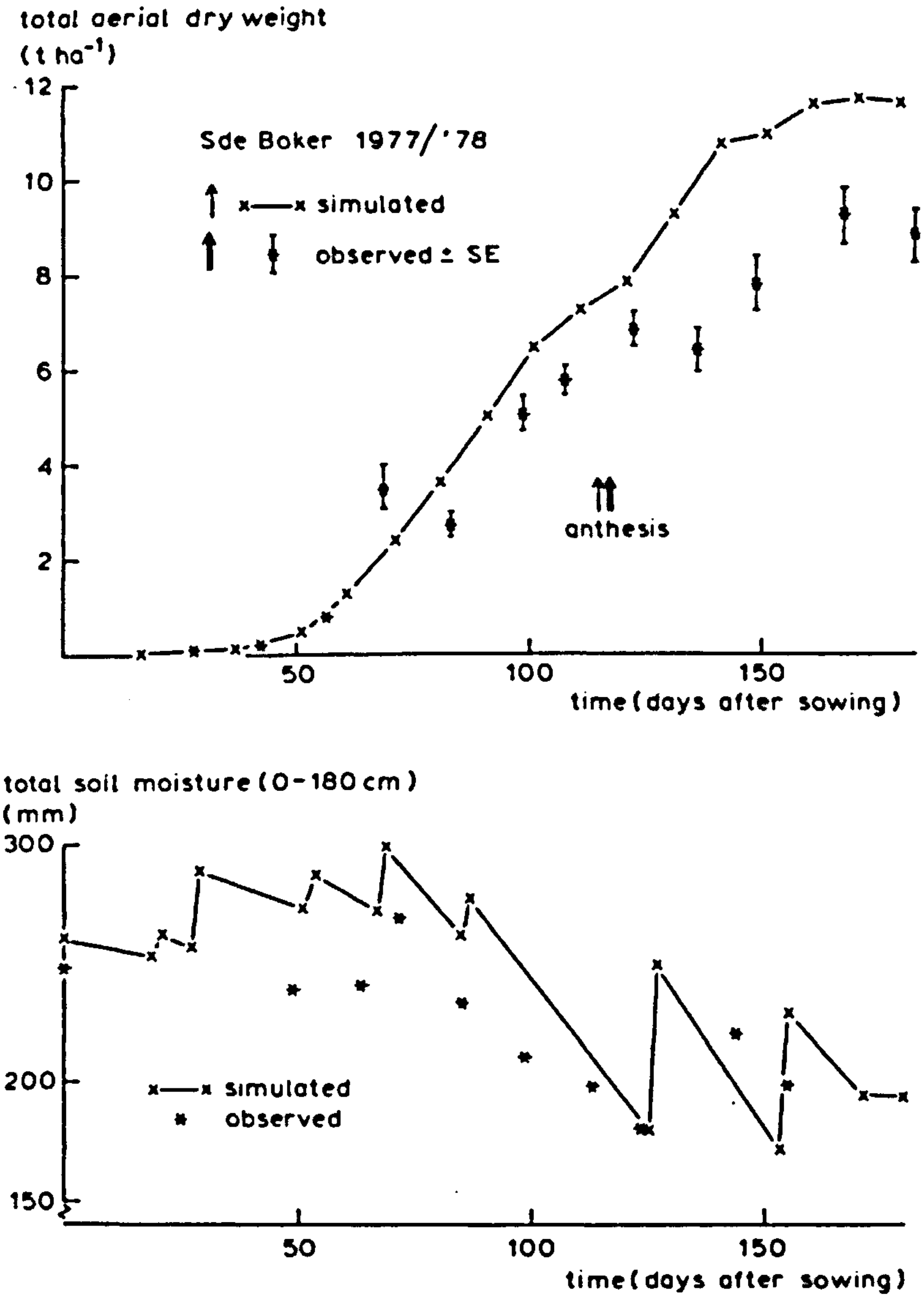

Figure 45. (A) Comparison of measured and simulated time course of total aerial dry matter production for 'stress treatment 2' in Sde Boker, Israel, 1977/1978; (B) Comparison of measured and simulated time course of total soil moisture for 'stress treatment 2' in Sde Boker, Israel, 1977/1978.

the same plot. The model deviated considerably from observed data under these conditions, despite the fact that the soil moisture balance and the reaction of the crop to water stress are among the most thoroughly tested parts of the model and have been succesfully used to describe growth of both wheat and natural vegetation under similar environmental conditions (van Keulen et al., 1981; van Keulen, 1975).

The agreement between simulated and observed results is not much better when stress is applied around anthesis (treatment 2, Fig. 45). The model predicts only a moderate check in growth rate where a severe check was observed. Consequently, total dry matter production is overestimated by more than 2000 kg ha^{-1}. On the other hand, yield components are simulated

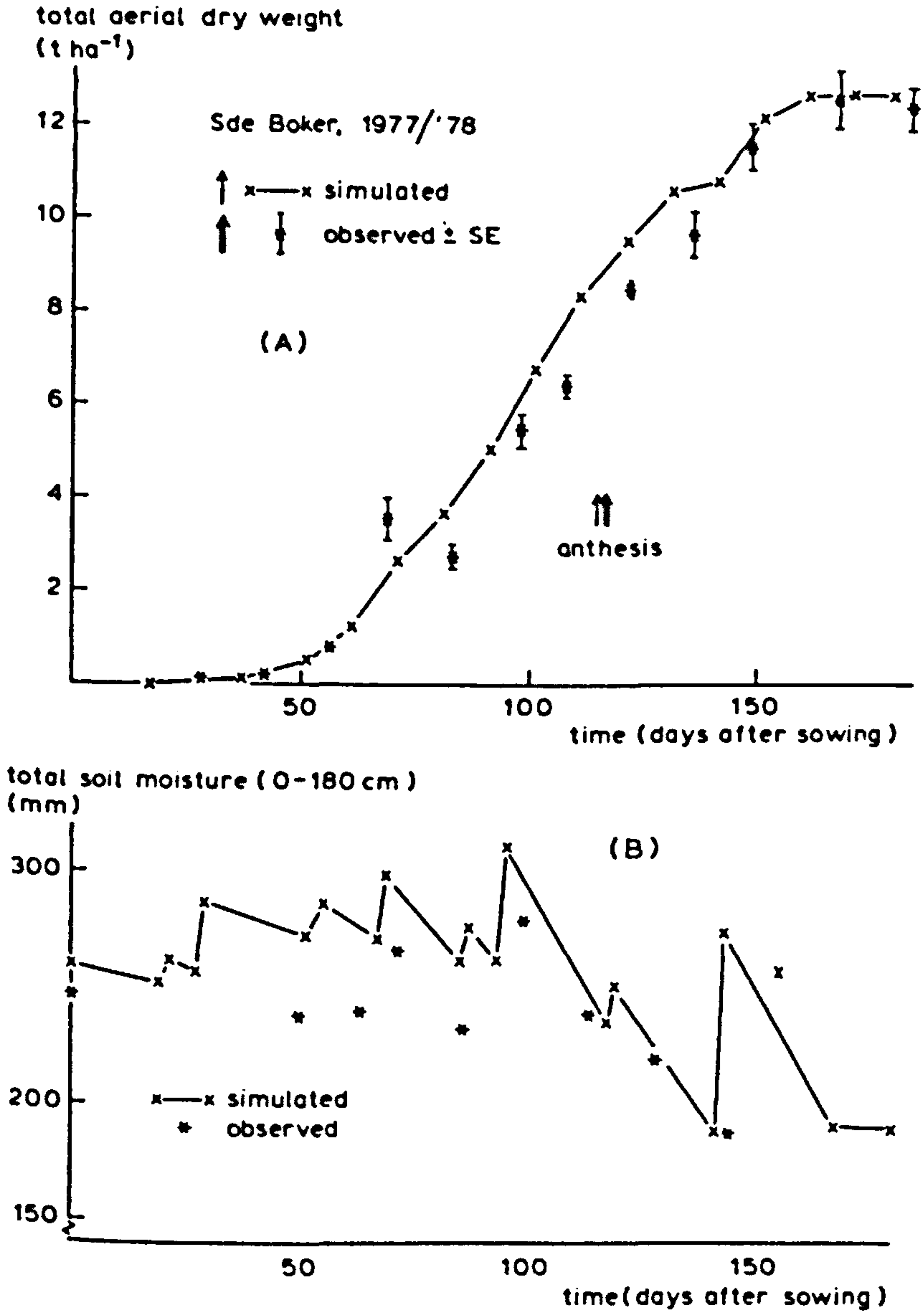

Figure 46. (A) Comparison of measured and simulated time course of total aerial dry matter production for 'stress treatment 3' in Sde Boker, Israel, 1977/1978; (B) Comparison of measured and simulated time course of total soil moisture for 'stress treatment 3' in Sde Boker, Israel, 1977/1978.

reasonably well, within 10% of the observed values (Table 20). The simulated and observed growth curves are in very close agreement over the entire growing period when stress is applied during the grain filling stage (treatment 3, Fig. 46). However, grain yield is grossly underestimated in the model.

The glaring discrepancies between the observed data and the model are partly, but not only, caused by 'noise' in the observed data. Improvement in the model to present a better account of the observed crop behaviour in this situation is definitely a challenge, but is beyond the scope of the present study.

5.1.4 Rutherglen 1971

The next experiment used for validation was carried out in 1971 at the research station of the Australian Department of Agriculture near Rutherglen (36°S, 146°E). Details on the experiment, that was specially conducted to collect a comprehensive data set for model development and validation are given by Paltridge et al. (1972) and Connor (1975). Wheat cv. Sherpa was sown at a rate of 67 kg ha^{-1} on 11 May 1971. The land was ploughed out of long term annual pasture consisting of subterranean clover, Wimmera ryegrass and barley grass. Superphosphate was applied at 225 kg ha^{-1}, together with a broad spectrum pre-emergent weedicide.

No data on soil and crop nitrogen are given. It is assumed that the nitrogen accumulated in the soil over the years by the subterranean clover and that mineralized during decomposition of the ploughed-in material is sufficient for the following wheat crop. In order to ensure adequate nitrogen for crop growth in the simulation exercise, the model was initialised with a total of 100 kg ha^{-1} of mineral nitrogen. A substantial proportion of that initial store was lost in the model due to leaching because the potential rooting depth at the site is stated to be only 0.8 m. To make up for this loss 50 kg ha^{-1} of mineral N had to be added 50 days after sowing.

The standard temperature-development rate relation (Section 3.2) predicted anthesis date about 10 days earlier than reported. To adjust the model cultivar to 'Sherpa', the cultivar-specific development rate parameter for pre-anthesis development rate was set to 0.8.

The 'standard' carbohydrate requirements for organ initiation resulted in gross overestimation of the numbers of organs formed and individual grain weight at harvest was consequently far too low. As these values are also 'cultivar' characteristics, the values were adjusted to 700 mg $tiller^{-1}$ and 225 mg ear^{-1} (Table 21).

The results of the simulation (Figs. 47 and 48, Table 21) show that the course of dry matter production closely follows the measured values. As pointed out in the introduction to this section, the variation in the field data can make a validation excercise inconclusive. Depending on the replication used, the simu-

Table 21. Comparison of measured and simulated yield components for Rutherglen, 1971

	Observed (Connor, 1975)	(Paltridge et al.,1972)	Simulated
Ear number (ears ha^{-1})	477	461	514
Grain number (grains ear^{-1})	28.1	27.7	25.3
Grain weight (mg $grain^{-1}$)	34.5	35.1	34.3
Grain yield (kg ha^{-1})	4624	4482	4499

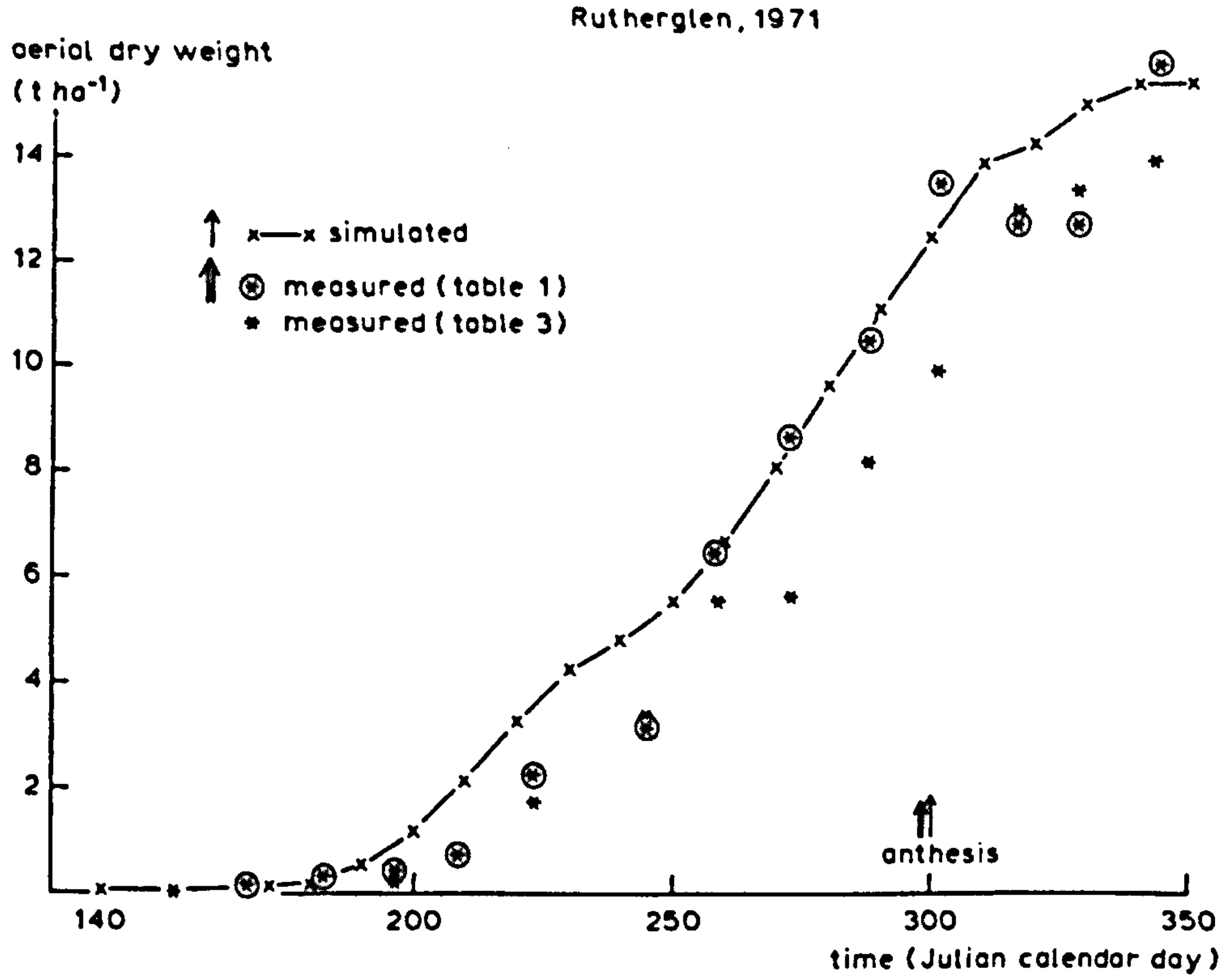

Figure 47. Comparison of measured and simulated time course of total aerial dry matter production in Rutherglen, Australia, 1971.

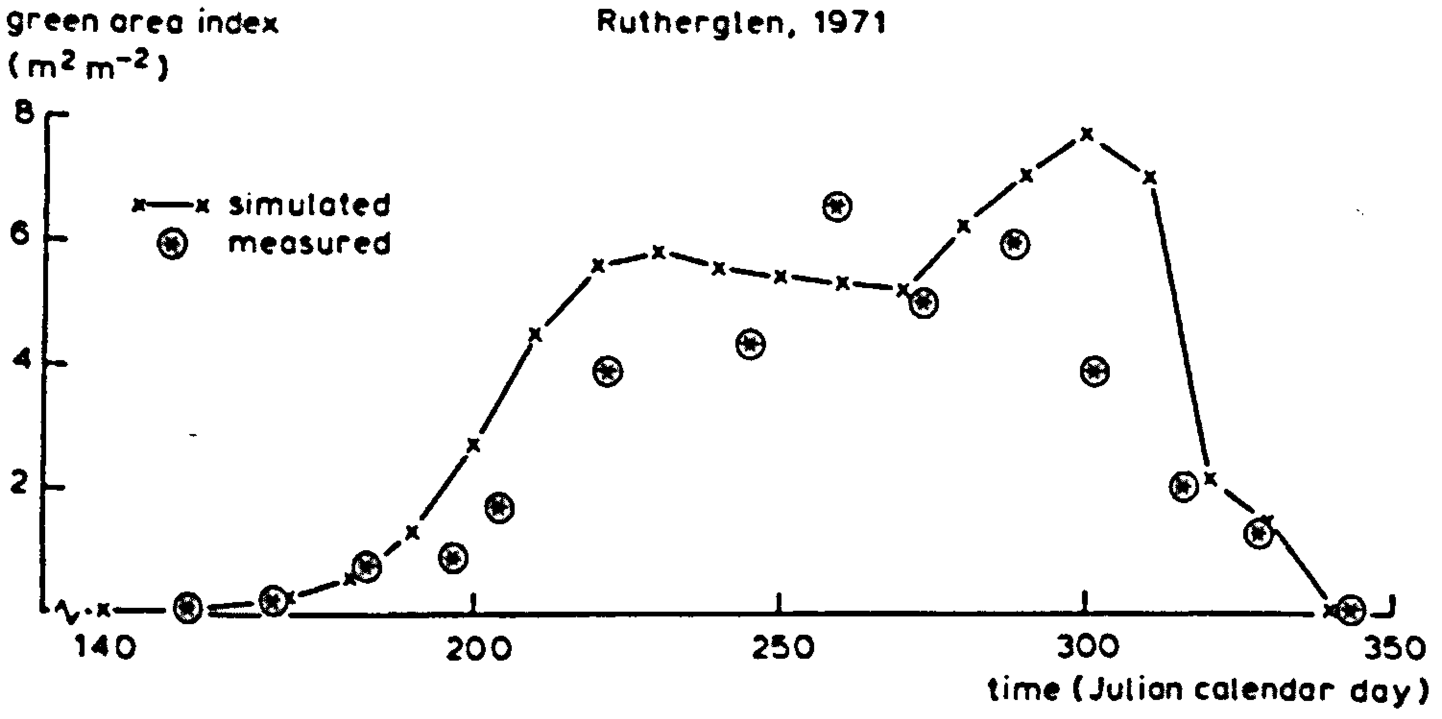

Figure 48. Comparison of measured and simulated time course of total green area index in Rutherglen, Australia, 1971.

lated values can either overestimate dry matter accumulation for most of the season, or follow the measured values closely.

The simulated time course of the green area index (total of green leaf blades, green stem area and green ear area) is roughly similar to the observed data, but generally overestimated. An interesting phenomenon occurs between day 270 and day 290. Both the simulation and the experimental data indicate that the green area decreases between day 250 and day 270 and subsequently increases till it finally drops to zero. In both situations it appears that the area of leaf blades declines after day 250, but that the contribution of stem and head area to total green area after that date more than compensates for that loss.

The yield components (Table 21) present an interesting situation. The Rutherglen data are reported by both Paltridge et al. (1972) and Connor (1975) and both sets are given in Table 21, together with the simulated results. The variation between the two authors reporting the same experiment is more or less identical to the variation between the observed and simulated results. This situation underlines a problem in field experimentation that could be alleviated in the future by using appropriate simulation models to guide field experimentation.

Despite all these problems, the present model, after suitable 'cultivar' adjustment, simulated the Rutherglen wheat crop fairly well.

5.1.5 Tel Hadya

Another experiment that yielded an extensive set of data suitable for model validation was conducted as part of the cultivar testing program of ICARDA (International Centre for Agricultural Research in the Dry Areas) at Aleppo, Syria. The trial was located at the experimental farm of the Centre at Tel Hadya (36°N, 35°E) and included three cultivars, Sonalika, Mexipak and Novi Sad (Stapper, 1984).

To describe pre-anthesis phenology according to the available data, the cultivar-specific development factor was set at 0.9 for the medium duration cultivar Mexipak. The organ size parameters were set to 700 mg per ear, 80 mg

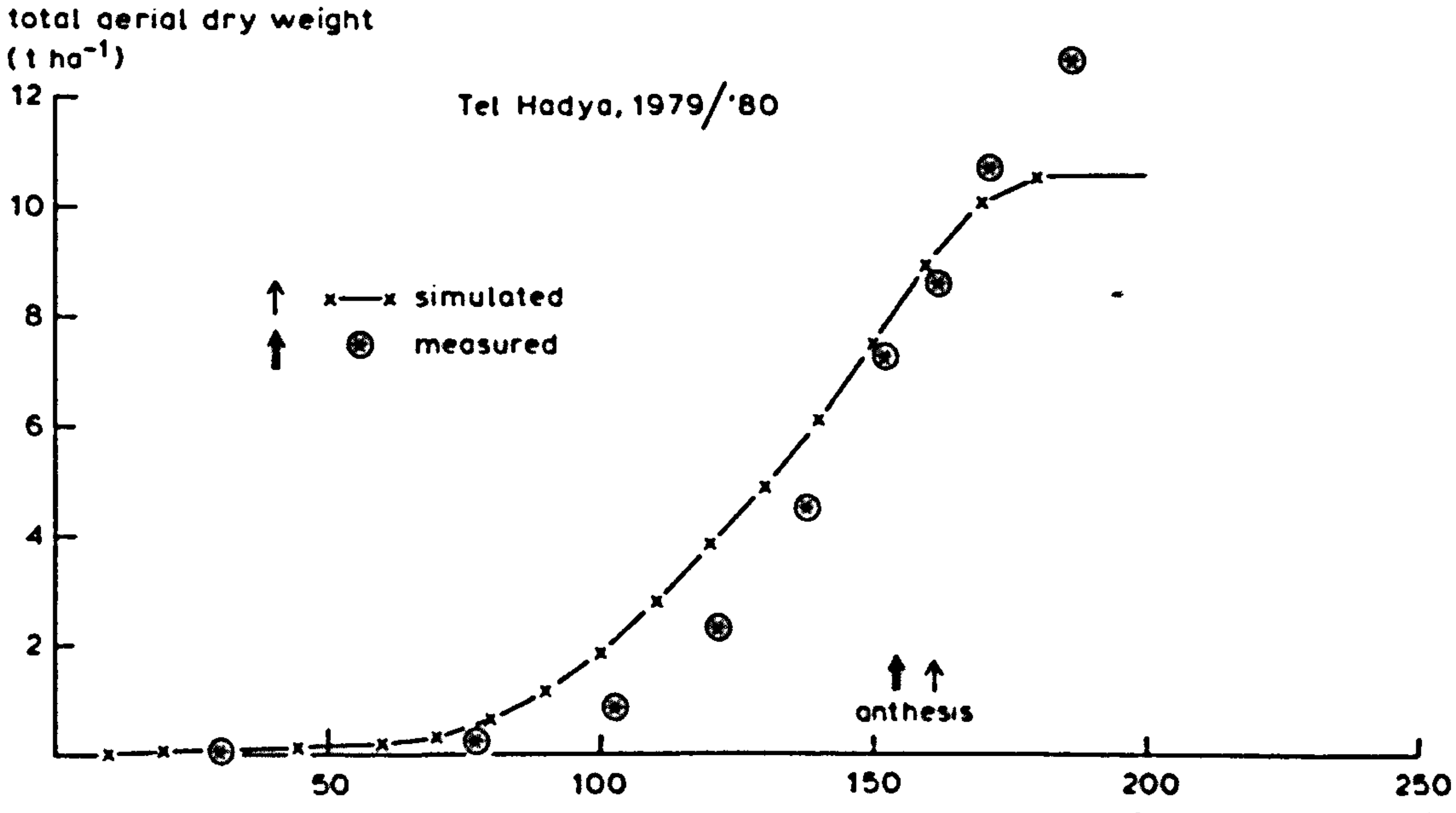

Figure 49. Comparison of measured and simulated time course of total aerial dry matter production in Tel Hadya, Syria, 1979/1980.

Table 22. Comparison of measured and simulated yield components for Tel Hadya, Syria, 1979/80

	Observed	Simulated
Ear number (ears m^{-2})	359	345
Grain number (grains ear^{-1})	42.9	48
Grain weight (10^{-6} kg $grain^{-1}$)	27.3	25
Grain yield (kg ha^{-1})	4090 (4204)	4227

per spikelet and 2.25 mg per floret. Although Stapper (unpublished data) reports that top dressing was applied in one of the treatments, information on both the quantity applied and the application date were not available. In the model runs it was assumed that 90 kg N ha^{-1} was applied at about the start of stem elongation. Data on the initial amount of mineral N in the soil were also not reported, so that estimates had to be made, based on data reported by Harmsen (1984) for the same region.

The results (Fig. 42, Table 22) show that the time course of dry matter accumulation is overestimated during the early growth stages – up to about day 150 – and underestimated towards the end of the growth cycle. The experimental data show that dry matter accumulation continues at an almost constant rate until maturity, whereas the simulated rate slows down at about the end of grain fill (day 185). The total above ground dry weight is underestimated by 2000 kg ha^{-1}. On the other hand, calculated grain yield at 4227 kg ha^{-1} (Table 22) is close to the observed value of 4090 kg ha $^{-1}$, and the yield components are also similar to the measured values. In view of the similar grain yields, the source of the discrepancy in total dry matter accumulation between day 170 and day 185, is not clear. It also seems unlikely that the additional 2000 kg ha^{-1} would have contributed so little to grain yield. This may be another case of spurious variation in the field. Total N uptake is simulated to within 10% of observed as 130 kg ha^{-1} at anthesis compared to 118 kg ha^{-1} measured; at the end of the growth cycle it is simulated as 145 kg ha^{-1} compared to 132.5 kg ha^{-1} observed. Grain N concentration is simulated at 0.020 kg kg^{-1} compared to 0.022 kg kg^{-1} measured. Phenology was simulated fairly accurately with anthesis two days earlier than observed. This can be tuned more precisely with the 'cultivar-specific' development rate parameter.

Earlier and later cultivars were simulated by setting the cultivar-specific pre-anthesis development factor at 1.05 and 0.875, respectively, leaving all other parameters unchanged (Table 23). The differences in anthesis date in the three cultivars was accurately simulated but all anthesis dates were simulated two days earlier than observed.

Total dry matter production ranked from high to low in the order: medium, late, early in both observed and simulated, with the simulated values consis-

Table 23. Comparison of measured and simulated results for three cultivars at Tel Hadya, Syria, 1979/1980.

Crop characteristic	Early cv.		Medium cv.		Late cv.	
	Observed	Simulated	Observed	Simulated	Observed	Simulated
Total dry matter (kg ha^{-1})	10180	9165	12560	11191	11760	10481
Grain yield (kg ha^{-1})	4000	4245	4090	4227	3670	3841
Anthesis date	April 12	April 10	April 24	April 22	April 27	April 25
Ear number (ears m^{-2})	318	287	359	345	355	383
Grain number (grains ear^{-1})	32	56	43	48	37	47
Grain weight (10^{-6} kg grain^{-1})	41	27	27	25	31	21

tently lower than observed for all cultivars. Simulated grain yield was very close to observed for all cultivars. The yield components compare less favourably: simulated ear number increases with increasing length of the growth cycle. In the experiment the standard cultivar had a higher ear number than the earlier one, but there was no further increase with increasing length of the growth cycle. Nevertheless, ear number was simulated to well within 10%. Simulated grain number per ear was overestimated: 56 for the early cultivar, compared to 32 observed and 47 compared to 37 in the late cultivar. Simulated grain weights were accordingly underestimated: 27 vs. 41 and 21 vs. 31 for the early and late cultivar, respectively.

From these results we can conclude that adjusting the growth duration parameter was enough to account for differences in dry matter accumulation and yield among cultivars, but that there were further cultivar-specific differences that determined the yield components. These could be simulated more accurately by adjusting the organ formation parameters to reflect the cultivar characteristics more accurately. This result can serve as a reminder that cultivar differences can rarely be characterized by single parameter.

The model performance was evaluated against a more extensive data set from the '80/'81 season. Figure 50 shows that the course of dry matter production as well as phenological development of the 'standard' cultivar in that season was predicted slightly better than in the previous season. The longer duration of dry matter production in the experiment compared to the simulation recurs in this season for reasons that can only be guessed.

Simulated grain yield was almost identical to observed yield (Table 24), and both were lower than in the '79/'80 growing season, mainly because of the lower rainfall in this season. The simulated yield components on the other hand, are considerably different from observed: ear number per unit area and grain number per ear are underestimated both by about 12 and 20%, respectively. As the grain yield is simulated accurately, the weight per grain which is calculated by dividing grain yield by grain number, is accordingly overestimated.

In the early cultivar the simulated results for both total dry matter (6362 vs. 9580 kg ha^{-1}) and grain yield (2741 vs. 3470 kg ha^{-1}) are seriously underestimated. The reason for the lower grain yield can be ascribed to the low number of ears simulated. On the other hand, the simulated values for the late cultivar are very close to the observed values (total dry matter production simulated 8622 kg ha^{-1} vs. 8600 observed, and simulated grain yield 3380 vs. 3150 observed). The yield components are equally well simulated, and only weight per grain is slightly higher than observed (Table 25).

In the '80/'81 season the three cultivars were also grown without N fertilizer application. As no data on soil N status are available, the mineral N content in the soil was initialized so as to ensure that the observed N uptake by the vegetation at the end of the growing season was simulated accurately. This, however, could be an underestimate of peak nitrogen uptake, as has been shown in previous cases.

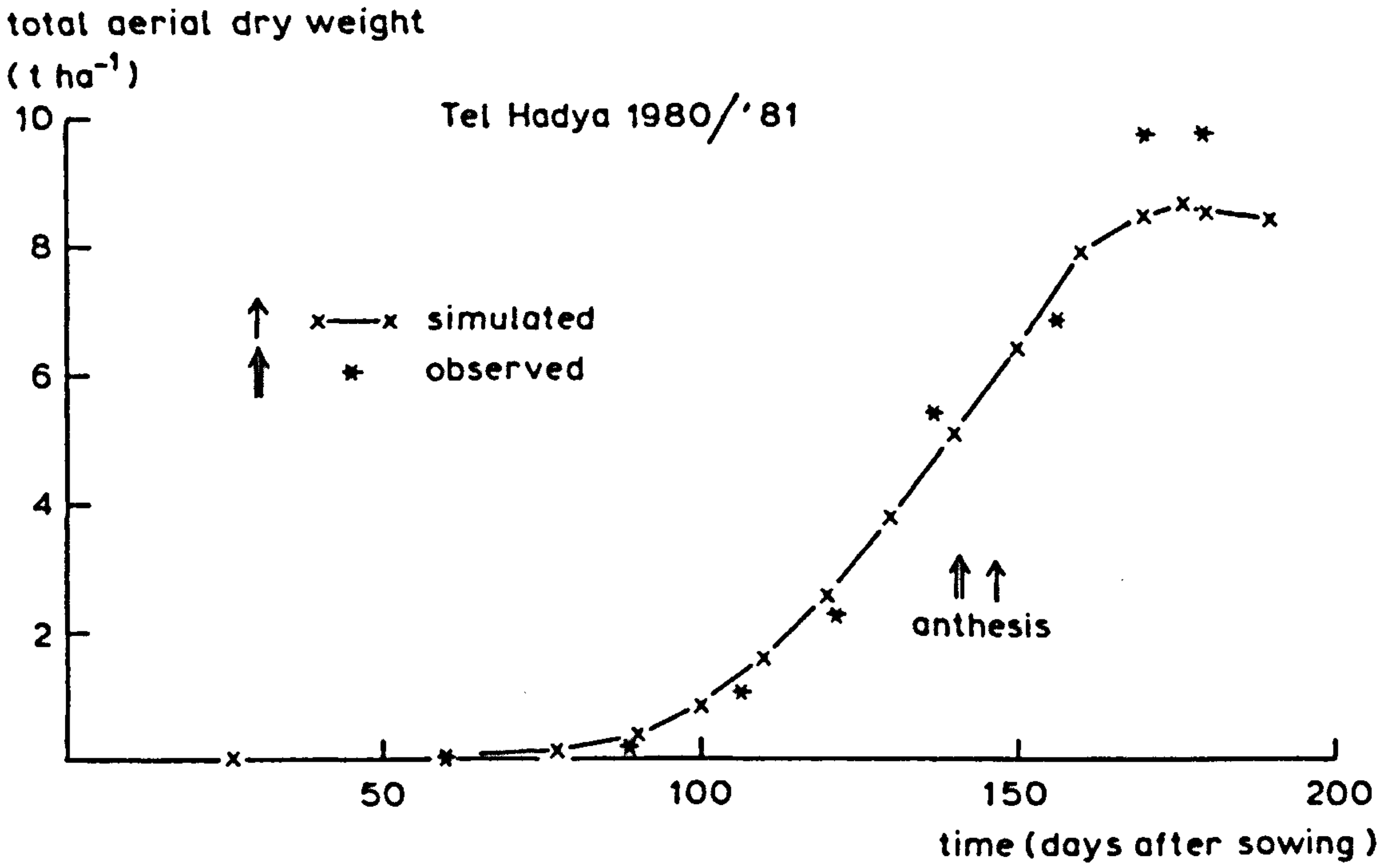

Figure 50. Comparison of measured and simulated time course of total aerial dry matter production in Tel Hadya, Syria, 1980/1981.

Table 24. Comparison of measured and simulated yield components for Tel Hadya, Syria, 1980/81, medium duration variety.

	Observed	Simulated
Ear number (ears m^{-2})	291	261
Grain number (grains ear^{-1})	41	32
Grain weight (10^{-6} kg grain^{-1})	28.7	40
Grain yield (kg ha^{-1})	3420	3352

The results (Table 26) are reasonably encouraging; for the early and 'standard' cultivars total dry matter production and grain yield are simulated within 10% of the observed values, but the late cultivar yield is overestimated in contrast to the underestimated yield in the 'high N' treatment. Ear number is consistently overestimated in the simulation for all three cultivars. Grain numbers per ear are simulated within 10% of the observed values but simulated weight per grain for the early and 'standard' cultivar is underestimated.

For all three cultivars the simulated nitrogen concentration in the grain is much lower than the observed value. As total uptake of nitrogen was set to observed uptake, translocation of N must have been much more 'efficient' in reality than in the model. This aspect of the model warrants further study, in which model formulation and experimentation should be closely associated (Greenwood, 1978).

Table 25. Comparison of measured and simulated results for three cultivars grown at Tel Hadya, Syria with nitrogen fertilizer added, 1980/1981.

Crop characteristic	Early cv.		Medium cv.		Late cv.	
	Observed	Simulated	Observed	Simulated	Observed	Simulated
Total dry matter (kg ha^{-1})	9580	6362	9790	8435	8600	8622
Grain yield (kg ha^{-1})	3470	2741	3420	3352	3150	3380
Anthesis date	April 13	April 15	April 19	April 25	April 23	April 27
Ear number (ears m^{-2})	334	240	291	261	260	260
Grain number (grains ear^{-1})	27	29	41	32	36	32
Grain weight (10^{-6} kg $grain^{-1}$)	38	39	29	40	34	41

Table 26. Comparison of measured and simulated results for three cultivars grown at Tel Hadya, Syria, 1980/81 season, with no fertilizer added.

Variable	Early cv.		Medium cv.		Late cv.	
	Observed	Simulated	Observed	Simulated	Observed	Simulated
Total dry matter (kg ha^{-1})	4800	4948	4950	4701	3970	4733
Grain yield (kg ha^{-1})	1920	2051	1920	1804	1540	1871
Ear number (ears m^{-2})	213	240	209	248	192	249
Grain number (grains ear^{-1})	25	28	30	28	27	25
Grain weight (10^{-6} kg $grain^{-1}$)	36.7	31	31.0	26	30.0	30
N-uptake (kg ha^{-1})	39.7	36	41.9	36	33.4	37
N-concentration grain (kg kg^{-1})	0.0165	0.010	0.0162	0.011	0.0167	0.011

5.1.6 Conclusions

Despite some serious deviations between simulated and observed values, the model, when properly initialized, simulated a recognizable wheat crop over a wide range of growing conditions. In particular, responses to treatment differences were generally well predicted qualitatively. These results could have been better had there been more adequate data on initial site conditions and some distinguishing physiological characteristics of the different cultivars. In view of these results, aspects of organ formation, phenology, nitrogen dynamics in the soil and in the plant should be studied more closely in different environmental contexts.

The effects of agronomic practice and plant characteristics on model behaviour can now be evaluated for a spring wheat crop growing under well-defined Mediterranean environmental conditions where cool, wet winters prevail. As the validation study has shown, the model results must be treated with caution, and where they are interesting or counter-intuitive, should be regarded as hypotheses to be tested under appropriate field conditions.

5.2 Performance tests

5.2.1 Migda 1979/1980

In this section, we will investigate the response of the model in a good year to parameter changes that represent agronomic practices and plant characteristics. The 'standard' 1979/80 Migda run for both 'high N' and 'low N' initial soil nitrogen conditions is used to test the effects of these parameter changes mainly on yield, grain size and grain nitrogen concentration as well as on total dry matter production. Where possible, the results will be evaluated in the light of experimental evidence reported in the literature. The 1979/80 season was a favourable one for wheat and so the results of this analysis do not necessarily hold for all other years. Long term effects over a range of years will be explored in Subsection 5.2.3.

A. Agronomic practices

a. Effect of sowing density (SWDF)

The standard sowing rate used in the model is about 100 kg ha^{-1}, equivalent to a seed density of about 260 m^{-2}. The plant densities tested were 1.5, 1.0, 0.5, 0.25 and 0.125 times the standard. In the 'high N' and 'low N' treatments grain yields are lower at low sowing densities, especially when these drop below 130 plants m^{-2} (Fig. 51). With 'low N', dry matter production does not increase at plant densities above 130 plants m^{-2}; with 'high N' there is a consistent increase. The number of organs formed, particularly the number of ears and the number of grains decline as a result of lower

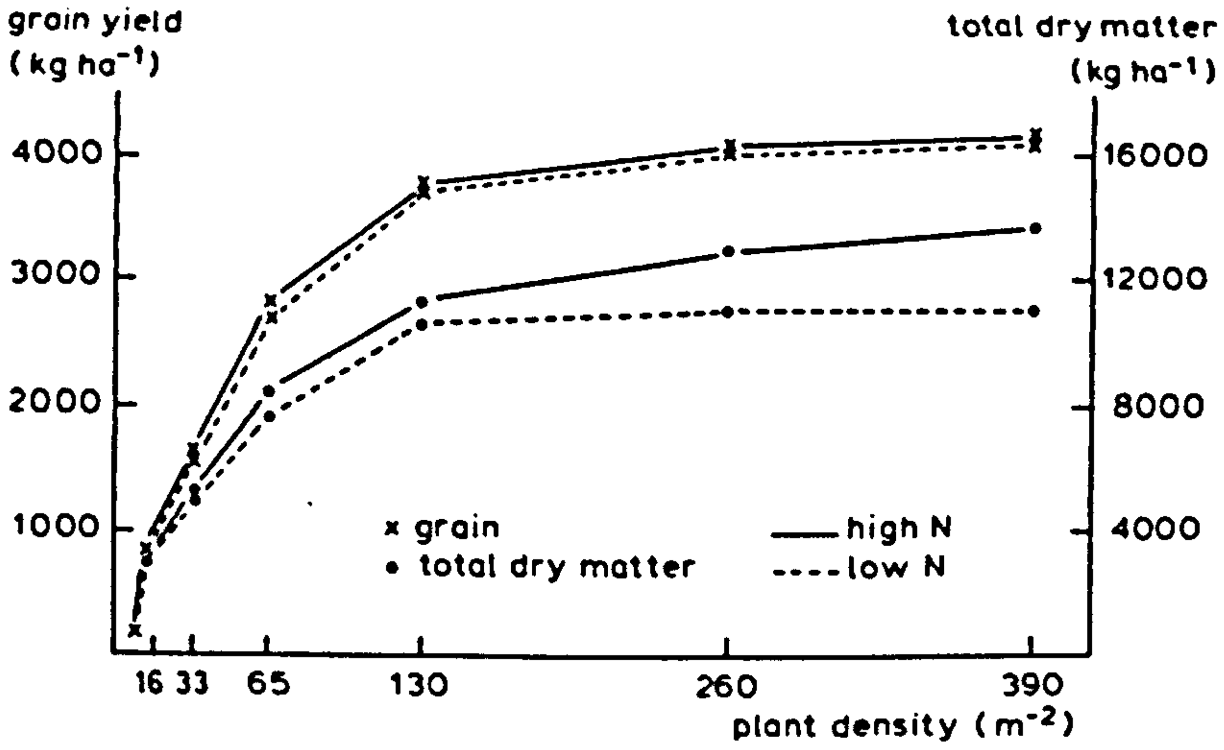

Figure 51. Simulated effect of plant density on grain yield and total dry matter production for 'high N' and 'low N' treatments in Migda, Israel, 1979/1980.

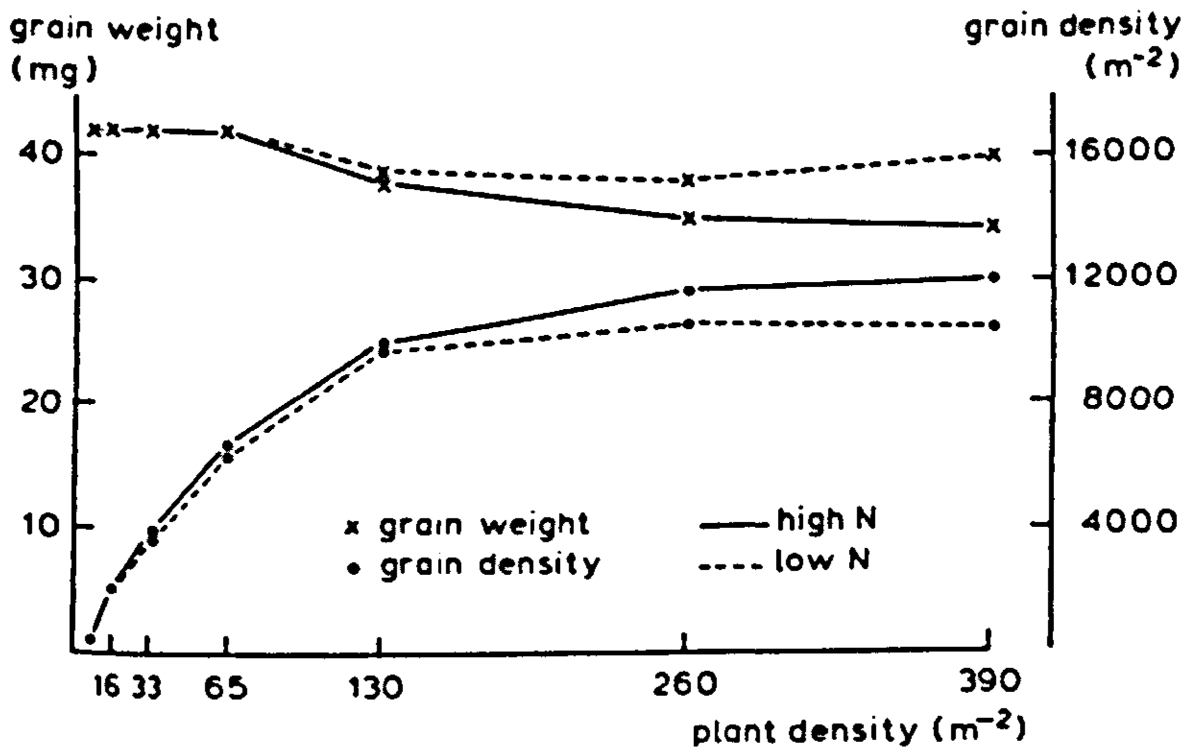

Figure 52. Simulated effect of plant density on grain density and grain weight for 'high N' and 'low N' treatments in Migda, Israel, 1979/1980.

assimilation rates per unit soil area caused by lower leaf area at the low plant densities. Compensation does take place, however, so that the number of grains does not fall proportionally to the sowing density, and individual grain weights are generally higher at lower sowing densities (Fig. 52). The effect of sowing density is thus expressed by a combination of sink and source effects. These model results are similar, at least qualitatively, to experimental results reported in the literature (Puckridge & Donald, 1967) over a comparable range of plant densities (Table 27), especially when differences in soil nitrogen availability are taken into consideration. Many of the variables are even numerically similar.

Effects of sowing density in drier years will be discussed in Subsection 5.2.3. Puckridge and Donald (1967) ask whether plant varieties differ with regard to crowding. This sort of question as well as those on interactions between cultivar characteristics, plant density and growing conditions, can be initially explored with the present model.

Table 27. Comparison of model results on sowing density with data from an experiment reported by Puckridge and Donald, 1967. (P&D).

	P & D (a)					Model					
Plant density (plants m^{-2})	1.4	7	35	*184*	*1078*	16	33	65	130	260	390
(b)				154	447						
Sowing rate (g m^{-2})	0.045	0.24	1.2	6.3	37.0	0.625	1.25	2.5	5	10	15
Grain yield (g m^{-2}) (c)	46	173	247	234	185	86	162	83	378	*408*	*415*
										404	410
Total d.m. (g m^{-2}) (c,d)	126	483	812	891	738	311	534	858	1136	*1301*	*1375*
			(891)	(923)	(852)					1115	1113
Grain wt (mg $grain^{-1}$)	34	35	33	33	33	42	42	42	38	35	34
Grain N(g kg^{-1})	27	26	25	25	25	31	28	25	*27*	*29*	*28*
									22	21	21
Grains ear^{-1}	3	38	30	21	19	38	38	38	37	30	26
Ear density (ear m^{-2}) (c)	41	130	252	323	303	54	102	176	*270*	*390*	*462*
									244	321	415
N-uptake (g m^{-2}) (c, e)	1.7	8.0	12.0	14.5	15.5	5.4	9.1	14.3	20.4	25.3	26.4
									13.1	13.0	13.0

(a) Range of densities in P & D comparable to model densities
(b) P & D high initial plant densities and final plant densities.
(c) Model high N/low N values.
(d) P & D final and (peak) dry matter production
(e) P & D peak N uptake

b. Effect of sowing date (SOWD)

In arid and semi-arid regions, where rains are erratic and unpredictable, sowing is often delayed until an effective rain event has made the soil sufficiently wet to minimize the risk of germination failure. This practice can result in logistic problems and a late start of growth. In the present paragraph, model behaviour is examined as a consequence of different sowing dates ranging from day 60 (end of November) when the first effective rains were recorded till day 105 (mid January).

For both the 'high N' and 'low N' treatments, grain yield and total dry matter production decreased with later sowing dates. Grain yield in the 'high N' treatments suffered the severest reduction (Fig. 53). This effect is due to the shorter total growing period at later sowing dates, that results from the higher temperatures later in the season. Anthesis for sowing on day 105 is only 17 days later than for sowing on day 75. Grain filling is restricted and small grains are produced at later sowing: 20 mg grain^{-1} for the crop sown on day 105, compared to 35 mg grain^{-1} for the crop sown at day 60 in the 'high N' situation. In the 'low N' treatment the effect of late sowing is similar to that for the 'high N', but not quite as severe, so that at the later sowing date, grain yields are *higher* in the 'low N' situation (Fig. 53). Grain weights are 38, 39, 29 and 42 mg grain^{-1} for sowing on day 60, 75, 90 and 105, respectively. This irregularity is due to complex interactions between temperature, assimilation and organ formation. Extreme cases of such variation can be seen in the field in dry years when small differences in soil moisture and nitrogen availability due to micro-topography cause very uneven, patchy growth.

In conclusion, lower total dry matter and lower grain yields are to be expect-

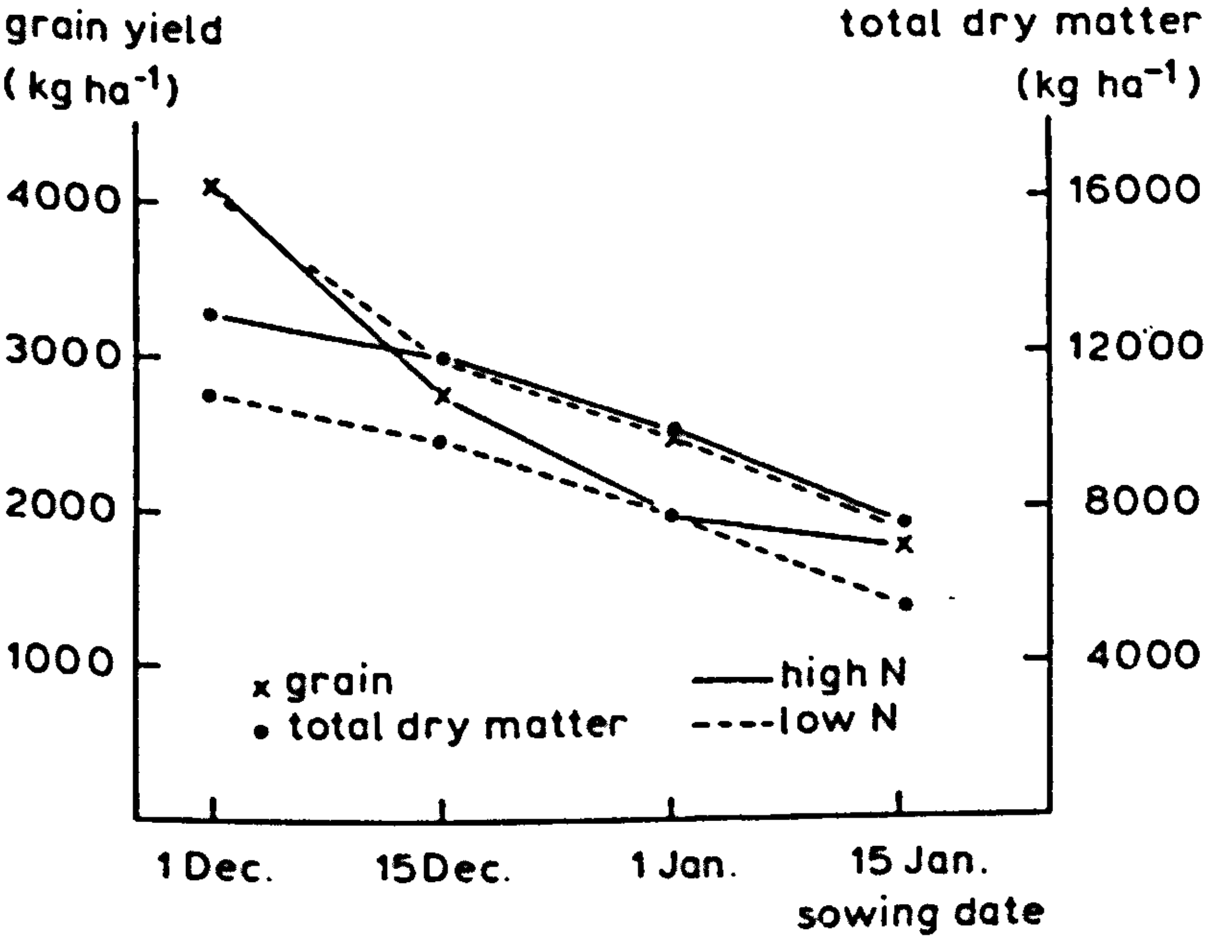

Figure 53. Simulated effect of sowing date on grain yield and total dry matter production for 'high N' and 'low N' treatments in Migda, Israel, 1979/1980.

ed when sowing is postponed in a year like the 1979/80 growing season where effective rains occurred relatively early. The main effect appears to be associated with the higher development rate, and consequently shorter duration of the growing periods in the case of late sowings. The lower yields predicted as a result of higher temperatures during the growing period, expecially during the post-anthesis period, are supported by many studies (cf. Monteith, 1981b; Spiertz, 1977).

c. Fertilizer application (NGIFT)

It has been suggested that the availability of plant nutrients in the soil, mainly N and P is the main factor constraining agricultural production in the Mediterranean region (Benjamin et al., 1986; van Keulen, 1975), and in comparable regions elsewhere (Penning de Vries & van Keulen, 1982). This is generally true of total dry matter yields but not always of small grain production under dryland conditions (Amir et al., 1982; 1981; Syme, 1972). To test the influence of nutrient supply on wheat yields, the model was run with fertilizer application rates of 0, 30, 60, 90 and 120 kg N ha^{-1}, applied as a basic dressing on day 0, which represents the 1st October. The effects of fertilizer application also depend on the nitrogen supply from natural sources (organic matter, rain, fixation by symbiotic and free-living micro-organisms). In the 'standard' situation, 100 kg ha^{-1} of mineral nitrogen are available in the soil at the onset of the rainy season, so that even in the non-fertilized, 'low N' situation, 127 kg ha^{-1} of N are taken up by the end of the growing season. We will discuss the effects of fertilizer application only in the case of 'low N', because N supply in the 'high N' case is already very high and additional N supply has no effect on plant performance.

The response to increasing amounts of fertilizer N was very small, increasing the grain yield from 4043 kg ha^{-1} at zero application to 4073 kg ha^{-1} at an application rate of 30 kg ha^{-1}, followed by a decline to 3968 kg ha^{-1} as the application rate increased to 120 kg ha^{-1}. The increase in total dry matter production over the same range was from 11 148 to 12 846 kg ha^{-1}. The harvest index declined from 0.36 to 0.31 with increasing N application, a phenomenon that is well-documented (Donald & Hamblin, 1976). Such effects of N-fertilizer applications are not unusual under dryland Mediterranean conditions, where additional N often increases vegetative growth more than grain growth.

It is interesting to note that the efficiency of nitrogen uptake from applied fertilizer, 'the recovery fraction' (van Keulen & van Heemst, 1982; van Keulen, 1977), has a constant value of about 0.42 over the full range of nitrogen applications. The nitrogen harvest index (nitrogen recovered in grain as a fraction of total N-uptake) dropped from 0.65 to 0.46 as N-application increased from 0 to 120 kg N ha^{-1}. The nitrogen use efficiency (kg grain increment per kg of N applied) went down from 1.0 at the lowest application rate to -0.625 at the highest application rate. With grain at US$ 0.18 kg^{-1} and nitrogen at US$

0.60 kg^{-1} of N on the farm at current prices (Israel, 1986), the threshold value for economically attractive application would be well above 3.3.

In conclusion if more than 100 kg ha^{-1} mineral N is present in the soil at the onset of the growing season, only minor effects of N-fertilizer application can be expected. Under 1979/80 climatic and initial soil conditions, N application is not economically justified at the above quoted prices. N-fertilizer loss in the model was high because it was 'applied' in the top 2 cm of soil. This layer can lose N from ammoniacal fertilizer by volatilization. If this is prevented (by 'applying' nitrate-N, simulated by setting the model parameter NH4FP = 0), then the recovery fraction increases from 0.42 to 1.0 (Gasser & Iordanu, 1967).

d. Topdressing of nitrogen (NAPDAY)

Nitrogen can be applied as a topdressing in the course of the growing season rather than as a basic dressing. The advantage of such practice would be that the fertilizer is only given if the moisture conditions are favourable. Moreover, at that moment the demand of the crop is higher, leading to higher uptake rates, a shorter residence time of the nutrient in the soil and lower losses of the element (van Keulen & van Heemst, 1982; van Keulen, 1977). We used the model to test the effect of topdressing nitrogen at a rate of 60 kg ha^{-1}, given at different application dates: day 30 (October 30), 75 (December 14), 105 (January 13) and 135 (February 12). As in the previous section, we will discuss the effect of topdressing in the 'low N' situation only.

The uptake efficiency of the fertilizer is again 0.42 when given on day 30, (equivalent to a basic dressing) but is very high, around 1.0, when given as topdressing late in the season. The effect on crop performance is greatest for the earlier application date (4115 kg ha^{-1} of grain when topdressed vs. 4048 kg ha^{-1} when applied on the soil surface at the beginning of October). This result leads to a nitrogen use efficiency of around 1.2 kg of grain per kg nitrogen applied. However, even in this case there is no economic justification for N fertilizer application under the specific study conditions.

It can be concluded that topdressing of N-fertilizer is an efficient method of application. Alternatively, the nitrogen fertilizer, when given in ammoniacal form should be disked in or applied below the surface layer. The advantages of this method are well documented (Terman, 1980).

B. Plant characteristics

a. Effect of development rate in the pre-anthesis phase (CULTP)

Earlier or later flowering cultivars are suited to different environments. The effect of flowering date as a plant characteristic can be tested with the model by varying the development rate of the crop. In the following analysis, 0.9, 1.0, 1.1 and 1.2 times the development rate of the 'standard' cultivar were compared. The slower rates represent later and the faster, earlier cultivars. The

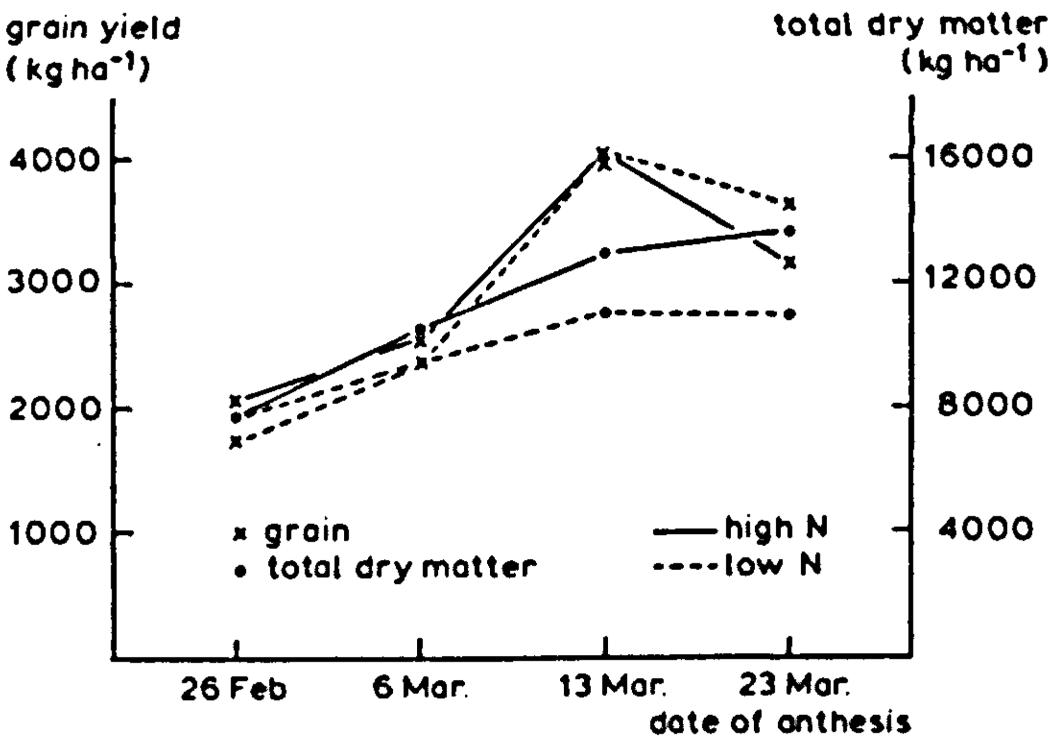

Figure 54. Simulated effect of development rate in pre-anthesis phase on total dry matter production and grain yield for 'high N' and 'low N' treatments in Migda, Israel, 1979/1980.

effects on grain yield are similar for both the 'high N' and the 'low N' treatment: development rates slower or faster than the 'standard rate' lead to lower grain yields (Fig. 54). In the early flowering type, yield is reduced because of lower grain numbers; in the late flowering type by both low grain number and by poor grain fill, which results in grain weights of 27-28 mg grain^{-1} compared to 40 mg in the early type. With respect to total dry matter yield, the effects of flowering date are slightly different in the 'high N' and 'low N' situations. Whereas total dry matter production increases steadily with later flowering in the 'high N' situation, there is only a moderate increase at 'low N' from early to standard flowering. At the latest flowering date, there is even a slight decrease that could be related to more rapid senescence at 'low N'.

The strong interaction between the rate of development of the crop on the one hand and both the organ formation and the nitrogen-dependent leaf longevity on the other hand is reflected in the model results. Faster development leads to a shorter growing season and less vegetative dry matter, incomplete light interception and lower carbohydrate availability for organ formation. At the same time, however, the rate of organ formation increases but the duration of each organ formation phase shortens. Intuitive prediction of the cultivar effect under such highly variable climatic conditions is therefore hazardous. The model shows some promise in being able to reproduce some of these complex responses of the crop and may be useful in evaluating long term implications of differences in development rate (Section 5.3).

b. Effect of development in the post-anthesis phase (CULTM)

Wheat cultivars differ with respect to their temperature requirements from anthesis to maturity but the differences between them seem to be small. This is also the case with rice cultivars (van Keulen, 1976b). The model can be used to evaluate the effect of such differences on grain yield. Four 'cultivars' were defined, with post-anthesis development rates of 0.9, 1.0, 1.1 and 1.2 times the rate of the 'standard' cultivar at similar temperatures.

The effect of slower post-anthesis development rate is different for the 'high N' and 'low N' treatments. There is a very small reduction in grain yield in the 'low N' treatment when the period between anthesis and the end of grain filling is longer than the 'standard' and an equally small increase in the 'high N' treatment. As soil moisture and reserve carbohydrates are depleted in both the 'high N' and 'low N' treatments towards the end of grain filling, the shorter ripening period would result in slightly lower maintenance requirements. That could account for the small difference in grain yield between CULTM 0.9 and 1.0 in the 'high N' treatment. A ripening duration shorter than the 'standard' (CULTM=1.1) has a small effect on crop performance. A further shortening of the grain filling period (CULTM = 1.2, which is probably unrealistic in view of the limited variability encountered in wheat cultivars) leads to only a small difference in the 'high N' situation, but to an almost 10% reduction in the 'low N' treatment, possibly because of incomplete utilization of reserve carbohydrates.

The effect produced by the model is somewhat unexpected as generally longer maturation periods are associated with higher grain yields (cf. Monteith, 1981b; Spiertz and Ellen, 1978; Warrington et al., 1977). It must, however, be noted that we are testing dryland conditions where moisture stress during the late grain-filling period is a dominant limiting factor.

c. *Effect of depth extension rate of the root system (DGRRT).*

The importance of root development and root distribution in determining adaptation of wheat to arid conditions has been discussed by Passioura (1972). In the present model we can test the effect of differences in the potential rate of root depth extension (DGRRT). Higher root extension rates increase the depth of the rooting zone and the amount of moisture available for the vegetation, whenever any moisture is present at depth, either from the previous season (fallow) or from current rainfall. But, as the root integrates water uptake over time and over the entire depth of the rooted profile, lower 'average' soil moisture potentials may be sensed by the root system. As a result, uptake can be slower and transpiration may be reduced, causing stress that may be partially compensated by greater moisture availability at a later stage of crop development. Another phenomenon that can affect moisture availability is the fact that root activity is considered constant over the entire rooted depth. Greater rooting depth then results in slower uptake of moisture from the upper soil layers with the consequence that slightly more water is available for loss by soil surface evaporation. These processes are reflected in the present model.

The values used for root depth extension rate in this sensitivity test were 0.9, 1.2 (the standard), 1.5 and 1.75 cm d^{-1}. It appears that the effect of more rapid root extension in the 'high N' treatment is very small for this growing sea-

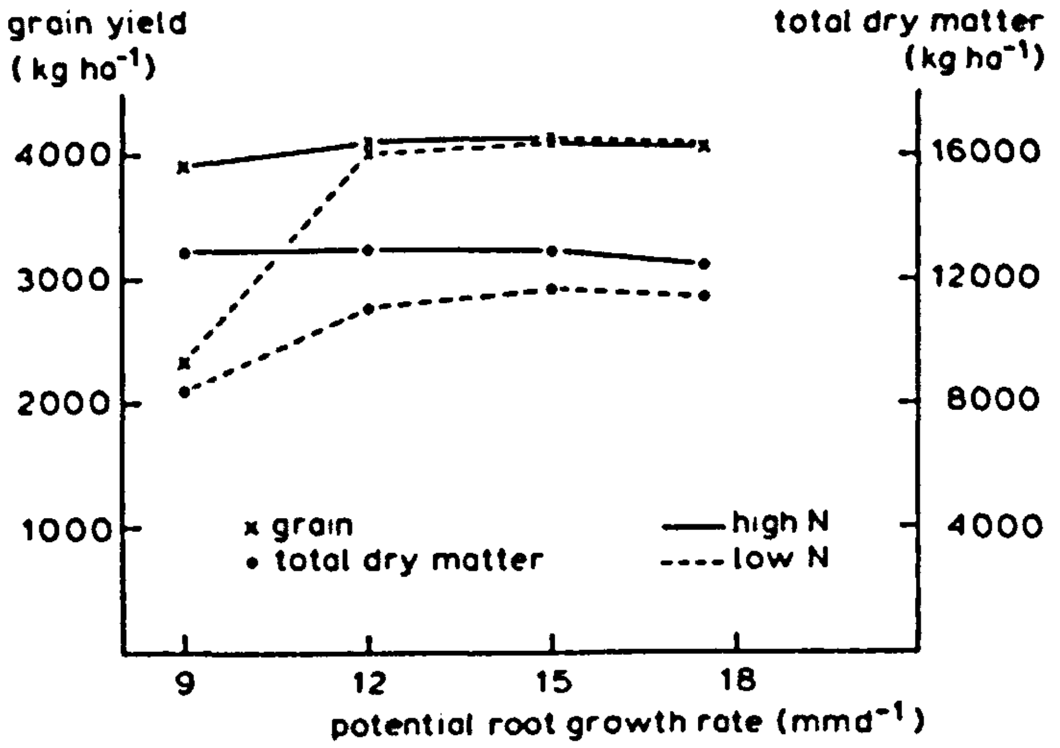

Figure 55. Simulated effect of potential root extension rate on total dry matter production and grain yield for 'high N' and 'low N' treatments in Migda, Israel, 1979/1980.

son. On the whole there appears to be a very small negative effect on grain yield at higher root extension rates, indicating that early depletion of soil moisture may have caused later stress (Fig. 55). In the 'low N' treatment, on the other hand, both grain yield and total above ground dry matter production increase very significantly as extension rate increases from 0.9 to 1.2 cm d^{-1}. This is a result of the effect of root growth on the time course of nitrogen availability. At still higher extension rates, the effect on crop performance is negligible.

In this growing season, with its particular initial distribution of water and nitrogen in the soil profile, root extension rates have different implications for the 'high' and 'low N' situations. It would appear that faster root extension need not *a priori* be an advantage even under dryland conditions. This may be the case for other seasons as well (Section 5.3).

d. Effect of potential growth rate of individual grains (PGRIGF)

Grain size, up to a genetically controlled limit, is determined by the growth rate of individual grains and the duration of grain fill. In some cases, where grain number is small for whatever reason, growth capacity of grains may limit yield. This would be a case of sink limitation. In the model the potential growth rate of the grains is introduced as a function of crop temperature, derived from various sources (Section 3.3). In the present test, the rates obtained from this function were multiplied by values between 0.9 and 1.2 in order to simulate different potential grain growth rates.

The simulation results show that grain yields increase modestly with higher potential grain growth rates for both the 'high' and 'low N' treatments (Fig. 56). In the 'high N' situation, grain yield increases from 4047 to 4154 kg ha^{-1}, and in the 'low N' situation from 3942 to 4147 kg ha^{-1} over the full range. Grain weight increases from 35-37 to 36-39 mg over the same range.

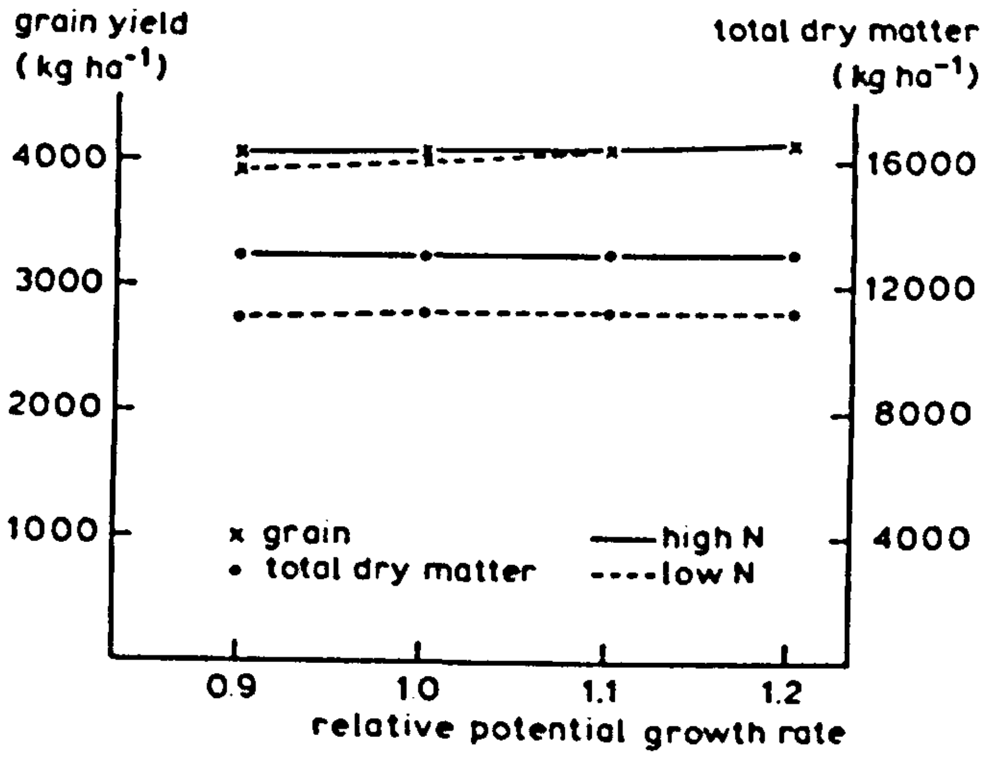

Figure 56. Simulated effect of relative potential grain growth rate on total dry matter production and grain yield for 'high N' and 'low N' treatments in Migda, Israel, 1979/1980.

At first sight these effects suggest that grain yield is limited by sink capacity in both situations. That is, however, not strictly true because in the present case higher potential grain growth rates result in faster translocation of reserves to the grain. As less time is required for reserve translocation, less of the carbohydrates accumulated before the onset of grain fill are available for maintenance respiration. Consequently, where the grain filling period could be usefully prolonged (i.e. lower temperatures and good, late-season soil moisture conditions), higher potential grain growth rates could be a disadvantage as more rapid reserve depletion could accelerate leaf senescence.

The nitrogen concentration in the grain hardly changes with the higher grain yields that are associated with the higher potential grain growth rates. As nitrogen uptake does not change significantly either, the total amount of nitrogen translocated to the grain increases concurrently with grain growth rates. This phenomenon may explain the fact that despite the generally observed negative correlation between grain yield and grain nitrogen concentration, deviations do exist that result in higher yields of both nitrogen and grain (Kramer, 1979). In such a case, both the harvest index (HI) and the nitrogen harvest index (NHI) are higher. At 'low N', HI increases very slightly from 0.357 to 0.368 as grain growth rate increases; NHI increases from 0.637 to 0.638.

e. *Effect of nitrogen turnover rate in vegetative material (RRTORT).*

The relative turnover rate of nitrogen in the vegetative material represents the fraction of the protein nitrogen in the vegetation that is catabolyzed each day into a labile pool suitable for translocation to the grains. The standard value is set at 0.25 and our sensitivity test includes values between 0.15 and 0.30. The lowest value is derived from Peoples et al. (1980) and Dalling et al. (1976).

Grain nitrogen concentration in both the 'high' and 'low N' treatments is

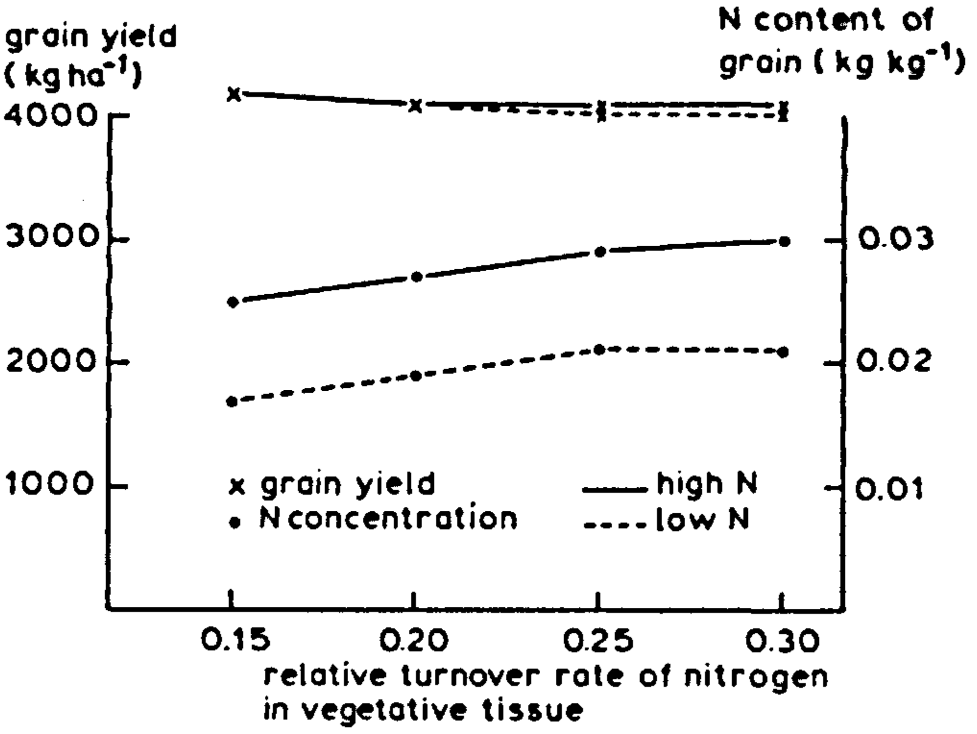

Figure 57. Simulated effect of relative turnover rate of nitrogen in vegetative tissue on grain yield and nitrogen content of grain for 'high N' and 'low N' treatments in Migda, Israel, 1979/1980.

sensitive to changes in nitrogen turnover and increases with RRTORT (Fig. 57). Grain yields are far less sensitive. As a result, both NHI and N uptake increase slightly as a result of the higher N demand that is caused by more rapid depletion of N from leaves and other vegetative tissues. Nitrogen harvest index increases from 0.41 to 0.48 in the 'high N' crop and from 0.55 to 0.65 in the 'low N' crop.

The effect of nitrogen turnover rate on dry matter production and grain yield is negligible when nitrogen availability is high and moisture stress sets in only towards the end of grain fill, but the effect on nitrogen uptake and nitrogen harvest index is quite considerable. As a result of this process, grain protein concentration is increased without loss in grain yield (Johnson et al., 1968).

f. Leaf longevity (AVLTLF)

Green area duration is largely dependent on leaf longevity and can influence the productive capacity of the plant, unless other factors limit crop production (Watson, 1947a; 1947b). To evaluate the effect of leaf longevity in the 'standard' growing conditions, three values were tested: 50 (standard value), 60 and 70 days. These longevity values represent benchmark life-spans at 15°C. In the model, leaf senescence is directly influenced by accumulated temperature (Subsection 3.6.2).

Increasing leaf longevity by 10 days increased grain yield by a mere 6 kg ha^{-1} in the 'high N' crop and by 85 kg ha^{-1} in the 'low N' crop, with all of the yield differences being reflected in heavier grains. Whereas nitrogen concentration in the grain went up in the 'high N' crop from 0.029 to 0.030 kg kg^{-1}, it was hardly affected in the 'low N' crop. Effects on straw yields were negligible in both cases. Increasing leaf longevity by another 10 days, had virtually no effect on crop performance. N uptake was also unaffected, so that the higher yields obtained with a moderate increase in leaf longevity, resulted in more efficient utilization of the N that was taken up. As a result the nitrogen concentration in the vegetative material was reduced from 0.015 to 0.014 kg kg^{-1} in the 'high N' crop and from 0.007 to 0.006 kg kg^{-1} in the 'low N' crop.

Even though leaf longevity has been shown to influence crop performance, it is not clear that leaf longevity *per se* is a controlling factor in senescence or whether it is related to the nitrogen turnover and sink/source relationships within the plant (Wiegand & Cuellar, 1981). This must be determined by experiment. The model, however, does clarify some of the implications of leaf longevity for crop performance (Austin, 1982; Kramer, 1979b).

g. Canopy temperature (CTEMPF)

Differences in transpiration rates of the canopy that are caused by differences in LAI and in the N-status of the plants can influence canopy temperature (Seligman et al., 1983). These temperature differences influence development rate, maintenance respiration and other processes, so that their effect on crop performance can vary under different growing conditions. We have used the model to estimate the effect of the magnitude of the canopy temperature response on crop performance in the 'high' and 'low N' situations. The temperature response can be related to T/T_0 by setting CTEMPF to values greater than zero. We have run the model with values of CTEMPF set to 0, 3 and 5.

The canopy temperature effect delays anthesis in the 'high N' crop by 1-2 days and hastens it by up to 1 day in the 'low N' crop. There is, indeed, evidence that crops suffering from N stress tend to flower and ripen sooner than crops well supplied with N (Seligman et al., 1983; van Dobben, 1960; Khalil, 1956). Concurrently with this phenomenon there is a reduction in grain yield in the 'low N' crop of 264 kg ha^{-1} with CTEMPF=5 compared to an increase of 72 kg ha^{-1} in the 'high N' crop. The yield reduction is caused mainly by fewer grains that are set at the higher temperatures (Rawson & Bagga, 1977; Hsia et al., 1963).

h. Effect of moisture stress on leaf area (MAXARR)

During the vegetative phase of crop growth, moisture stress often causes leaf rolling (Begg & Turner, 1976; Fischer, 1973). As a result leaf area is effectively reduced. The cost is less radiation for photosynthesis, but the benefit is less transpiration when moisture availability is a limiting factor. In the model, the effect of leaf rolling can be simulated by varying the value of MAXARR, which is the relative amount of effective leaf reduction as a consequence of moisture stress, monitored basically by T/T_0. The following values of MAXARR were tested: 0.7, 0.85 and 1.0.

The 1979/80 season was particularly unsuitable for testing moisture stress, because moisture was seldom limiting during the vegetative phase. As a consequence, crop performance was singularly insensitive to differences in MAX-

ARR and the largest effects were no more than 0.5%.

i. Assimilate requirements for organ formation

Organ formation in the model is based on the hypothesis that the rate of organ formation is related to the rate of carbohydrate flow available for organ formation and the carbohydrate requirement for the formation of a competent organ. This requirement can be seen as a genetic characteristic that determines whether a cultivar tends to tiller profusely and whether it tends to produce more or less ears with more or less spikelets and florets. In this paragraph, we will study the possible effects on crop morphology and performance of variations in assimilate requirements for organ formation.

The following range of values will be examined:
Tillers – 175 to 1050 mg tiller^{-1}
Ears – 500 to 1500 mg ear^{-1}
Florets – 11.25 to 67.5 mg floret^{-1}

In both the 'high N' and 'low N' crop, grain yield and dry matter production were remarkably insensitive to changes in carbohydrate requirements for organ formation, despite large differences in ear and grain number. There was no sink limitation under the standard run conditions and higher grain weight compensated for lower grain number in most cases. The only outstanding exception occurred when the requirement for floret formation was set at 67.5 mg floret^{-1}. This requirement reduced grain number per ear from 30-33 to 20-23. As grain size was hardly affected, yield was reduced from 4084 to 3348 kg ha^{-1} and from 4043 to 3101 kg ha^{-1} in the 'high N' and 'low N' situation, respectively.

The lesson that can be drawn from this exercise is that under relatively favourable dryland conditions, grain number is generally high enough to prevent serious sink limitations, even though there may be considerable variation in grain weight among cultivars with different carbohydrate requirements for organ formation. Under optimum conditions and also under severe stress conditions, the carbohydrate requirement may well be an important determinant of yield. These possibilities will be explored in Subsections 5.2.2 and 5.2.3.

5.2.2 Potential yield

The model was developed to simulate wheat growth under conditions where water and nitrogen may be limiting. It should, with minimum adjustment, be able to simulate the limiting condition where water and nitrogen are available in abundance. The following series of tests was designed to determine what crop parameters ('cultivars') or agronomic practices are associated with 'potential yields' of spring wheat under Mediterranean weather conditions given adequate water and nitrogen supply. These parameter sensitivities were tested over a series of four years using actual climatic data from the Migda/Gilat site in the Northern Negev of Israel (Tadmor et al., 1974) for the years

Table 28. Parameter values for 'potential yield' sensitivity analysis.

Parameter		Units	Potential yield standard
CULTP	– development rate factor, pre-anthesis phase	unitless	0.9 (later)
CULTM	– development rate factor, post-anthesis phase	unitless	0.9 (later)
AVLTLF	– leaf longevity	d (at 15 °C)	70
CHFTB	– assimilate requirement, tiller formation	mg tiller^{-1}	700
CHFEB	– assimilate requirement, ear formation	mg ear^{-1}	800
CHFSB	– assimilate requirement, spikelet formation	mg spikelet^{-1}	45
CHFFB	– assimilate requirement, floret formation	mg floret^{-1}	17.4
TRP	– moisture stress switch	unitless	-1 (no stress)
NGIFT	– N-fertilizer application	kg ha^{-1}	150
NAPDAY	– day of N-fertilizer application	d	95 (= 3 Jan.)
IAS1	– mineral N in 0-2 cm soil layer	kg ha^{-1}	5
IAS2	– mineral N in 2-5 cm soil layer	kg ha^{-1}	10
IAS3	– mineral N in 5-10 cm soil layer	kg ha^{-1}	22.5
IAS4	– mineral N in 10-20 cm soil layer	kg ha^{-1}	12.5
IAS5	– mineral N in 20-30 cm soil layer	kg ha^{-1}	12.5
IAS6	– mineral N in 30-60 cm soil layer	kg ha^{-1}	37.5
IAS7	– mineral N in 60-90 cm soil layer	kg ha^{-1}	0
SOWD	– sowing date	d	45 (14 Nov.)
SWDF	– sowing density factor	unitless	1.5
TLNI	– initial plant density	plants m^{-2}	390

1975/76 to 1978/79. The 'standard' parameter values for this set of runs are given in Table 28. They define a later flowering crop than the one used for the '79/'80 runs.

A. Agronomic practices

a. Plant density (SWDF)

The standard 'potential yield' data set was run at a range of plant densities from 3.3 to 390 plants m^{-2}. Up to the highest density tested grain yield increased with plant density (Fig. 58). The largest numerical differences were between the 1975/76 and 1977/78 growing seasons, especially with regard to grain yield and grain number at the lower plant densities. Even though there was much compensation in grain numbers, it was not enough to allow the crop to attain high yields, because during the earlier phases of growth assimilation was severely restricted by low leaf area indices at the low plant densities. Ear num-

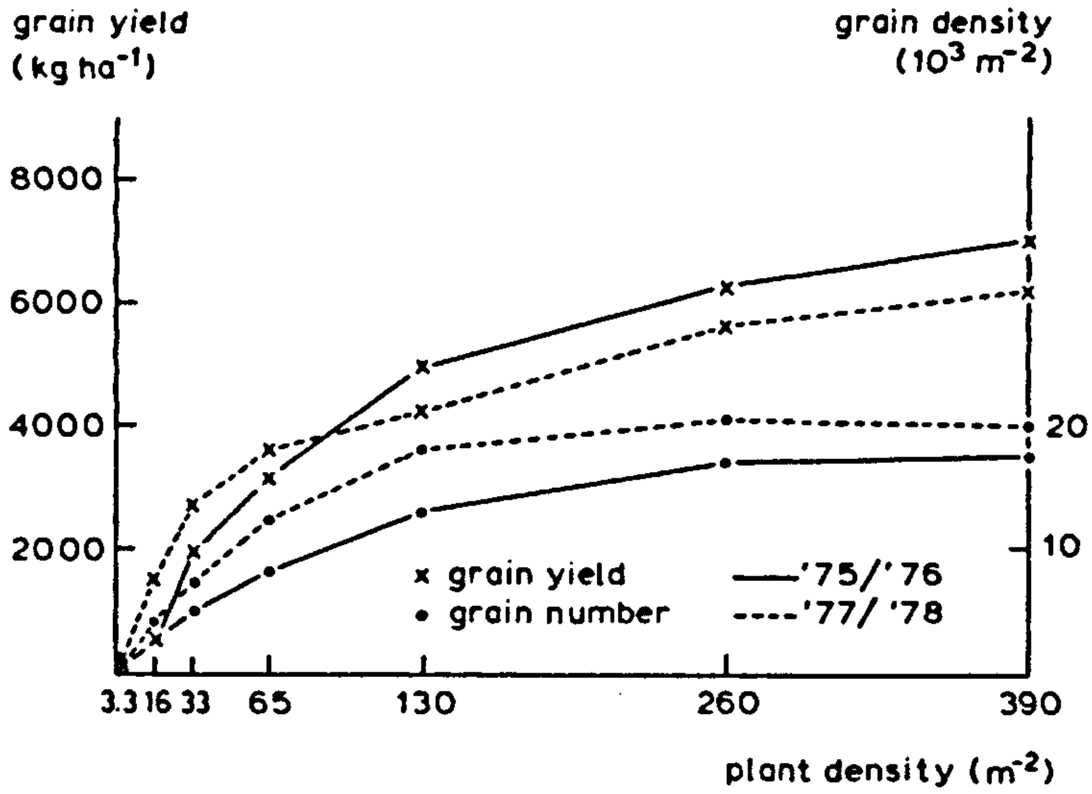

Figure 58. Simulated effect of plant density on grain yield and grain density for two growing seasons in Migda, Israel, under optimum moisture and nutrient conditions.

bers increased from 1.1 – 1.3 ears per plant at the high densities to 3.0 – 3.8 ears per plant at the low densities. More profuse tillering might have improved performance in some years, but in most, production would have been assimilate limited. In 1977/78 at the lowest density of 3.3 plants m^{-2}, when yield was about 200 kg ha^{-1}, grain weight was only 20 mg and even at a density of 33 plants m^{-2}, when yield was well over 2500 kg ha^{-1}, grain weight was only 37 mg.

The grain yields attained at the highest plant density varied between 6234 kg ha^{-1} in 1977/78 and 7018 kg ha^{-1} in 1975/76. These differences stem not only from variations in radiation but also from other climatic influences, mainly temperature, as well as from different morphological responses to the variable time course of radiation and temperature. Moisture and nitrogen availability, as was pointed out above, was not limiting in these runs.

In conclusion, it appears that under optimum growing conditions, high plant densities are necessary to obtain high yields, a result that accords with practice. It should be noted that the model can simulate excellent yields with only small parameter changes necessary to define a more productive 'cultivar'. These are, however, not record yields under favourable conditions. Plant characteristics necessary to attain record yields will be discussed later in this subsection.

b. Sowing date (SOWD)

Response of the crop to differences in sowing date between 14 November and 13 January for the two years 1975/76 and 1977/78 was very similar when measured as total dry matter (Fig. 59). There was a small increase as sowing was delayed from 14 November to 29 November and then a gradual decrease in dry matter yields from 16 000 kg ha^{-1} to just below 13 000 kg ha^{-1} as sow-

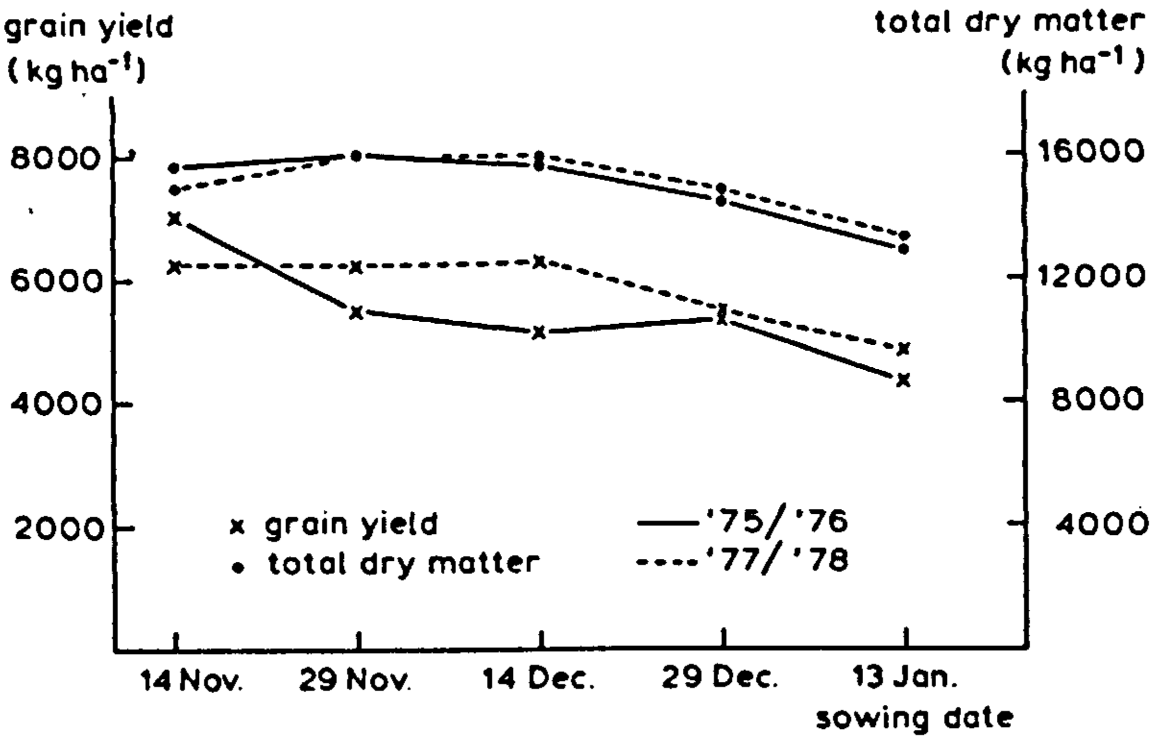

Figure 59. Simulated effect of sowing date on total dry matter production and grain yield for two growing seasons in Migda, Israel, under optimum moisture and nutrient conditions.

ing was delayed to 13 January. The response of grain yield was different in these two years. As a rule, yield was lower the later the sowing date but there were exceptions. In 1975/76 yield was lower as sowing date advanced from 14 November to 29 November, after which it was relatively insensitive to sowing date, although a clear drop occurred when sowing was delayed to the middle of January. In 1977/78 on the other hand, yield was hardly affected by sowing date between 14 November and 14 December, and only at later sowing dates did grain yield decrease significantly.

These differences are also a result of different radiation and temperature regimes in the two seasons. They indicate that grain yield is more sensitive than total dry matter yield to variations from year to year even when water and nutrients are not limiting. This conclusion is supported by experimental evidence (Amir et al., 1982).

c. *Topdressing (NGIFT)*

The initial store of mineral N in the soil was set to 100 kg ha^{-1} in the top 60 cm soil layer (Table 28). The effect of different amounts of additional N fertilizer given as topdressing on day 95 (= 3 January) was tested in a 'standard potential yield' crop. Grain yield responded significantly over the four years to a topdressing of 30 kg ha^{-1}, increasing from under 6000 kg ha^{-1} to over 6500 kg ha^{-1} (Fig. 60). Higher applications of N had a small and variable effect in the different years, even though N-uptake by the crop increased almost linearly with increased fertilizer application, from around 105 kg ha^{-1} with no N application to around 250 kg ha^{-1} with a topdressing of 180 kg ha^{-1}. Consequently, N-concentration in the grain also went up from 0.011 kg kg^{-1} with no N fertilizer to 0.022-0.026 kg kg^{-1} at the highest application rate.

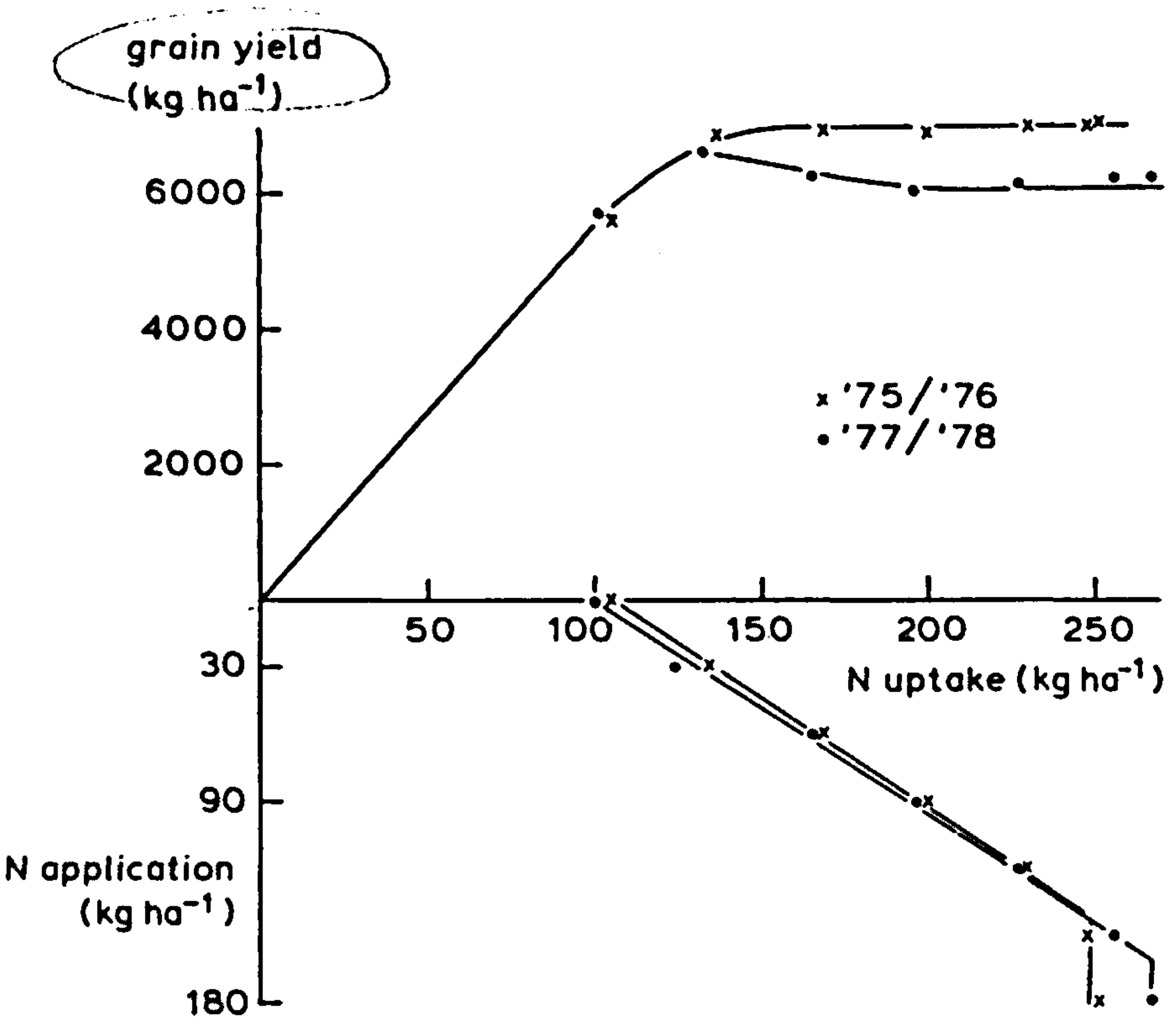

Figure 60. Simulated relation between nitrogen uptake and grain yield, and between nitrogen dressing and nitrogen uptake for two growing seasons in Migda, Israel, under optimum moisture conditions.

d. Time of fertilizer application (NAPDAY)

Four N fertilizer application dates were tested: 30 October, 14 December, 3 January and 13 January, coinciding with a preplanting application, application during early tillering, during late tillering and just after terminal spikelet formation. In all cases 150 kg ha^{-1} of nitrogen was added to the top soil layer in the form of ammonium.

Nitrogen recovery by the vegetation is almost complete for the first three application dates, but is around 0.8 for the last application date. The effect of delay in application of fertilizer is identical in all four years, although the intensity is not the same. The optimum application date appears to be at the beginning of January, earlier and later applications both resulting in lower grain yields and lower total dry matter yields (Table 29), although the effect on total dry matter is very small.

The effect on grain yield is a combination of grain number and grain weight. Delayed application results in lower ear numbers, and lower grain numbers. Higher grain weight more than compensates for lower grain numbers up to the early January application, but not afterwards. In three out of four years the late application of N results in higher nitrogen concentrations in the grain, despite the lower total uptake. This has some experimental confirmation (Langer & Liew, 1973).

Table 29. Response of a spring wheat crop to time of fertilizer application (NAPDAY).

Variable	NAPDAY	1975/76	1976/77	1977/78	1978/79
Grain yield (t ha^{-1})	30	6.8	6.6	5.7	6.5
	75	6.8	6.6	5.6	6.6
	95	7.0	6.9	6.2	6.9
	105	5.6	6.4	5.8	5.6
Total shoot weight (t ha^{-1})	30	16.1	15.6	15.2	15.2
	75	15.8	15.5	15.0	15.1
	95	15.8	15.5	15.0	15.0
	105	14.4	14.3	14.7	13.5
Grain weight (mg)	30	37	30	25	35
	75	37	30	26	35
	95	40	32	31	40
	105	47	43	45	45
Grain number (10^3 grains m^{-2})	30	18.2	22.3	22.0	18.8
	75	18.1	21.9	22.4	18.6
	95	17.4	21.3	20.0	17.5
	105	11.9	15.0	12.6	12.3
Grain N conc. (kg kg^{-1})	30	0.022	0.022	0.027	0.023
	75	0.023	0.022	0.027	0.023
	95	0.022	0.022	0.026	0.022
	105	0.026	0.023	0.026	0.025

B. Plant characteristics

a. Pre-anthesis development rate (CULTP)

Four values for CULTP were tested: 0.8, 0.9, 1.0 and 1.1. As a rule, later cultivars are necessary to attain potential yields under optimum growing conditions. This is also reflected in the model where later anthesis, up to about day 150 (end of February) generally results in higher grain yield. The desirable degree of lateness, however, varies between years (Fig. 61). Most of the four years tested are like 1975/76 where the standard cultivars reaching anthesis on 25 February, attains the highest grain yields and later cultivars are less suitable. The higher grain yields associated with later anthesis date are generally accompanied by higher grain numbers (Fig. 62). Again, 1977/78 is an exception in that it is generally less sensitive to anthesis date and in that the highest yields are obtained with the cultivar having the latest anthesis date (7 March). In this season, grain weight and grain N concentration are particularly insensitive to

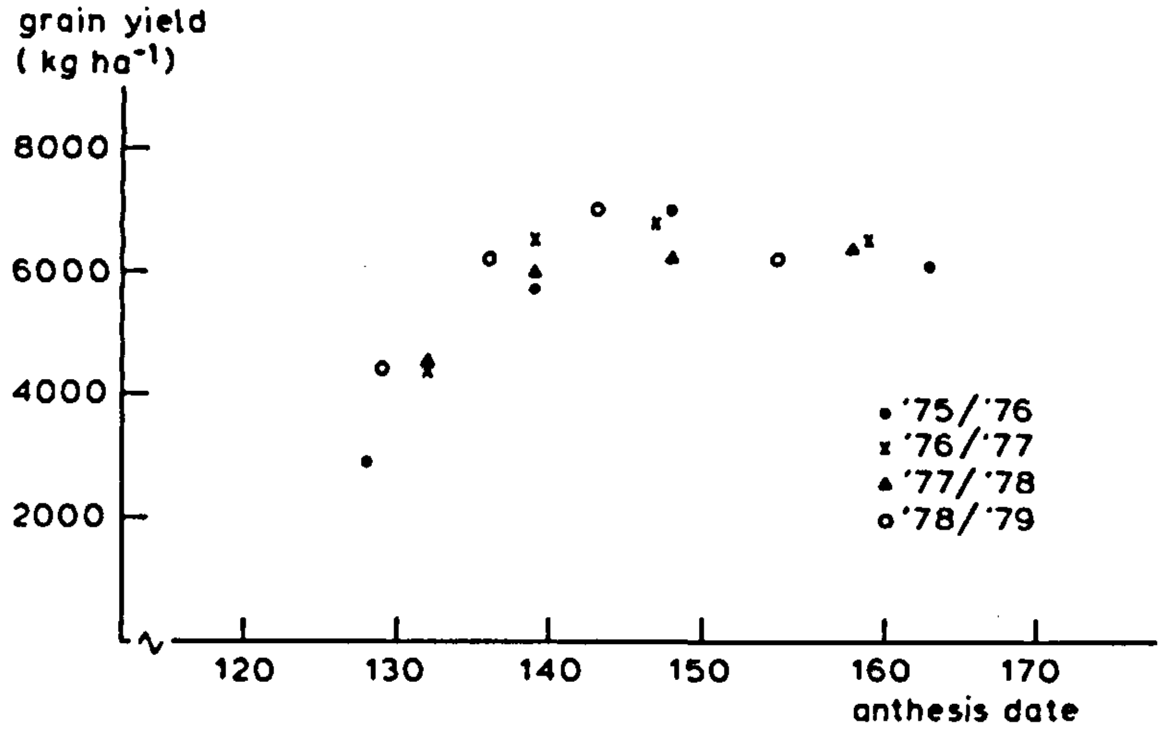

Figure 61. Simulated effect of pre-anthesis development rate, reflected in anthesis date, on grain yield in four growing seasons in Migda, Israel, under optimum moisture and nutrient conditions.

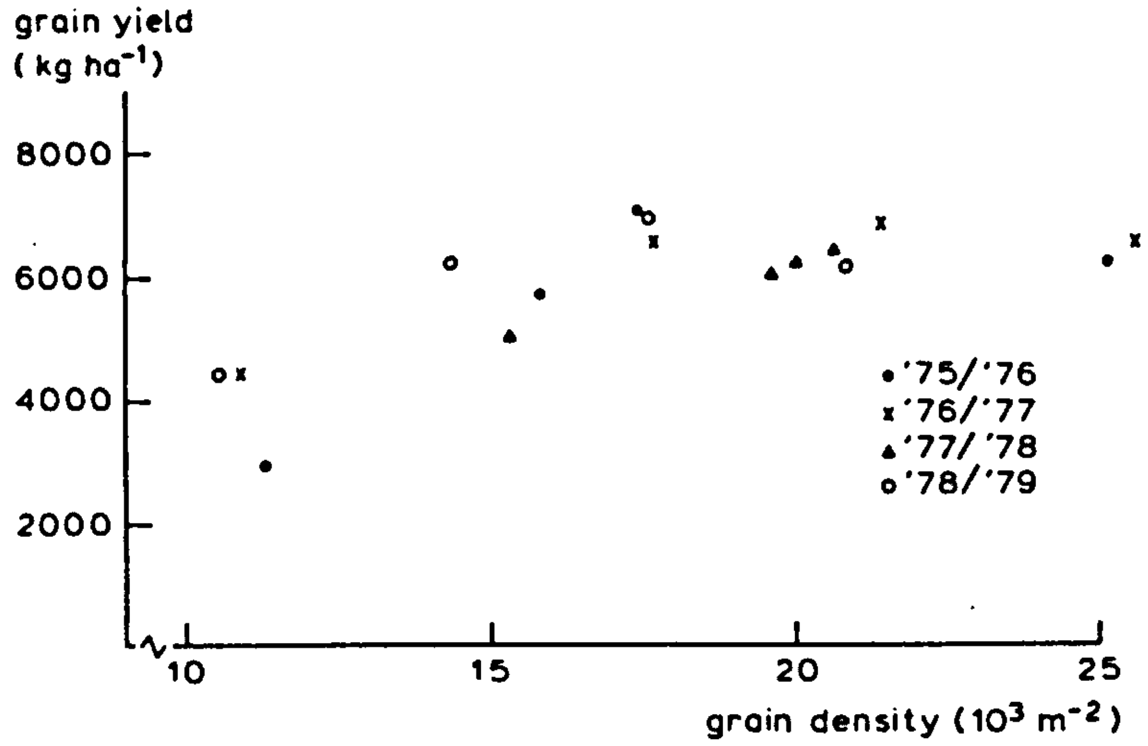

Figure 62. Simulated relation between grain density and grain yield in four growing seasons in Migda, Israel, under optimum moisture and nutrient conditions.

anthesis date, whereas in 1975/76 both these characteristics responded strongly to changes in development rate during the pre-anthesis phase: grain weight varied from 24 to 40 mg grain^{-1} and N concentration in the grain from 0.026 to 0.017 kg kg^{-1}.

We can conclude that appropriate date of anthesis is, as a rule, an important factor in attaining potential yields, but that in some years it may not be very obvious. However, as we will see below, there are other plant characteristics that can over-ride anthesis date in importance.

b. Development rate between anthesis and maturity (CULTM)

Variation in the rate of development between anthesis and maturity over the range of 0.8 and 1.2 times the 'standard' rate has only a small effect on total dry matter production, but stronger effects on grain yield. Increasing the development rate, i.e. shortening the period between anthesis and the end of grain fill, and at the same time the period for grain set, generally leads to lower grain yields. Compared to the 'standard potential yield' cultivar, a longer grain filling duration can increase yield between 1 and 3%. When the duration of the period between anthesis and maturity is shorter both grain density and grain weight are lower. The intensity of the interaction varies with environmental conditions: in '75/'76 grain yield is reduced by 35%, and in '77/'78 by only 7% as the length of the anthesis – to – maturity period is decreased (i.e. CULTM is increased from 1.0 to 1.2).

c. Rate of depth extension of the root system (DGRRT)

Differences in potential daily rate of root extension (DGRRT) have an anomalous effect on simulated crop performance. As a rule, grain yields tend to be lower as root growth becomes faster. The effect is particularly marked as DGRRT increases from 1.2 to 1.5 cm d^{-1}. Nitrogen uptake increases as does grain N concentration, but to a very small degree. It is not immediately obvious why the model should respond the way it does. It may stem from differences in the rate of N uptake that can influence a number of processes, mainly photosynthesis (through its effect on F_{mn}, Eqn. 39), respiration (Eqn. 45), leaf area development (Eqn. 91) and assimilate partitioning (Eqn. 49). In this series of runs on 'potential yield', water availability is not limiting. Nitrogen, however, even though given in abundance (100 kg ha^{-1} mineral N initially in the soil and another 150 kg applied on day 95, i.e. 3rd January), is available in different concentrations in the soil profile (Table 27). Nevertheless, it is surprising to find a consistent reduction in grain yield as the rate of root growth increases and as nitrogen uptake is increased. Whether this is simply the result of incorrectly balanced conceptualization of the nitrogen economy in the model, or whether such responses also occur in reality, would have to be resolved by experiment.

d. Potential growth rate of the grain (PGRIGF)

Despite expectations to the contrary, the potential growth rate of the grain had a relatively small and variable effect on crop performance in the context of the standard 'potential yield' run. The reason is probably that grain number (17 000 – 23 000 grains m^{-2}) was large enough to prevent any sink limitation. Indeed, grain size was less than maximum and varied between 31 and 39 mg $grain^{-1}$ between years.

In some years, however, the effect is present: in '75/'76 increasing the potential growth rate of the grain leads to increased grain yields over the full range of values tested: grain weight increases from 39 to 41 mg $grain^{-1}$. In '77/'78 the reverse is the case: grain yield decreases (slightly) with increasing potential grain growth rate. The two other years are intermediate in that grain yield first increases with a small increase in potential growth rate and decreases with higher rates. These variable results originate from the fact that two mechanisms are involved and they work in opposite directions: higher potential growth rate of the grains leads to more rapid utilization of reserve carbohydrates by the grain, so that less of that store is utilized for maintenance respiration; on the other hand, more rapid utilization leads to earlier exhaustion of the reserve store and consequently to accelerated senescence of the green tissue. The net result of both processes depends on the particular environmental conditions in any given year.

e. Turnover rate of protein in the vegetative tissue (RRTORT)

The relative turnover rate of protein determines the amount of nitrogen available for translocation from the vegetative structures to the grain (Eqn. 70). The more rapid the turnover, the greater the amount of protein N that undergoes decomposition into simpler forms that can be translocated to the grain. Nitrogen depletion of the leaves can initiate senescence, so that the turnover rate of proteins should have an effect on leaf longevity, assimilation rate and N concentration in the grain.

The 'potential yield' model was run with a range of values for RRTORT from 0.075 to 0.30. Increasing RRTORT consistently decreased grain yield (by producing smaller grains) and increased N concentration in the grain (Fig. 63). In any particular year, the relationship between RRTORT and grain yield or N concentration in the grain was almost linear. The specific seasonal conditions affect this relationship and when grain yield is plotted against N concentration in the grain, an inverse relationship is obtained, but with considerable scatter around the regression line (Fig. 64). This variation is well documented (cf. Kramer, 1979b; Bhatia & Rabson, 1976; Malloch & Newton, 1934) and is sometimes suggested as a basis for selection for protein-rich grains

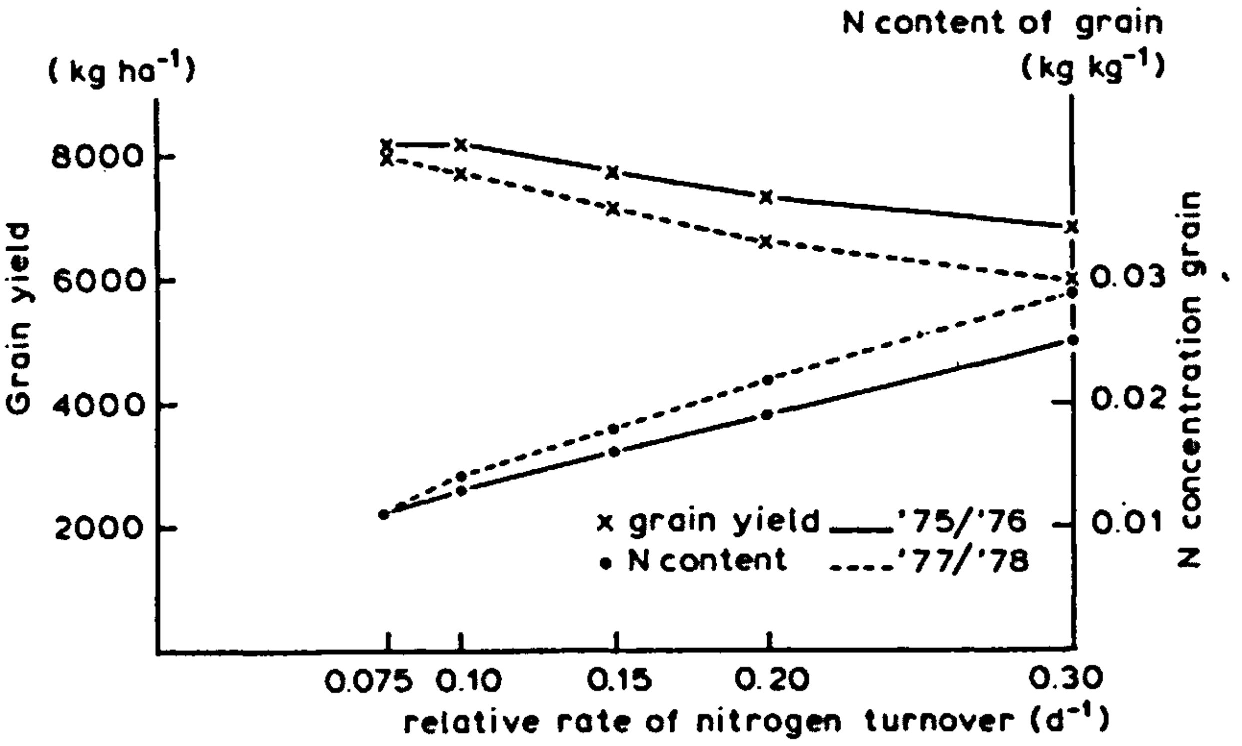

Figure 63. Simulated effect of relative turnover rate of nitrogen in vegetative tissue on grain yield and nitrogen content of grain in two growing seasons in Migda, Israel, under optimum moisture and nutrient conditions.

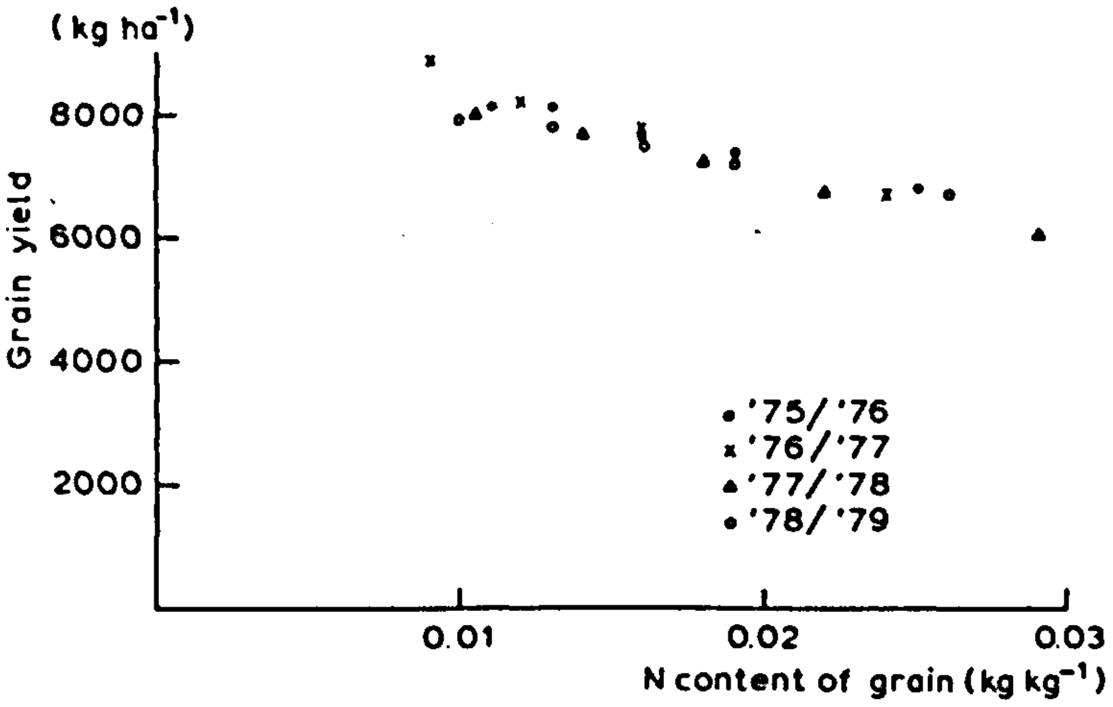

Figure 64. Simulated relation between grain yield and nitrogen content of grain in four growing seasons in Migda, Israel, under optimum moisture and nutrient conditions.

(Kramer, 1979a; Mesdag, 1979). The model results suggest that these effects are not necessarily genetic but can also occur as a result of relatively small differences in growing conditions, even when water and nitrogen are abundantly available.

On the other hand, if protein turnover rate could be manipulated genetically or otherwise, it could be important in developing high-yielding varieties, at a cost however, of lower N concentration in the grain. Alternatively, high protein varieties could be developed but at a cost of grain yield. What the value of the trade-off would be is dependent on the relative values of the yield and the protein increment. There remains the question of whether the values of the physical trade-off between yield and protein content can be reliably derived from the model. That too, will have to be decided by experiment.

f. Leaf longevity (AVLTLF)

Leaf area duration should be related to yield, especially under favourable growing conditions. Extending leaf longevity beyond the end of the grain filling period, however, serves no purpose and may result in greater maintenance costs and problems during mechanical harvesting. We have evaluated the effect of leaf longevity by varying the parameter AVLTLF from 50 to 80. The 'standard potential yield' value is 70. All these values refer to potential leaf longevity at 15 °C (Subsection 3.6.2).

The effect of different AVLTLF values is variable: in '75/'76 reducing its value below the 'standard', results in a barely perceptible decrease in grain yields, as does increasing its value. In '76/'77 there is a considerable decrease in grain yield at lower values of AVLTLF but hardly any effect of increasing AVLTLF. In '77/'78 there is virtually no effect of AVLTLF over the full range of values tested, while for '78/'79 there is a small increase in grain yield when AVLTLF is reduced by 10 days, but a decrease with further reduction, similar to the effect of increasing values. On the other hand, grain N concentration increases with increasing leaf longevity (Fig. 65). This is an effect opposite to that of lower RRTORT (previous paragraph) even though in both cases, leaf longevity is increased. The reason is that in the one case (lower RRTORT) leaf longevity is increased by reducing N translocation to the grain, whereas in the other (longer AVLTLF) no such restriction is imposed and leaf longevity as an intrinsic characteristic of the plant is not necessarily related to N translocation to the grain. Possibly, cultivars that have high yields and relatively high N concentrations in the grain have long-living leaves and relatively high RRTORT. As a result, N uptake should also be higher, so that this character will only be expressed when N is abundantly available, as it is in these test runs. If these two characteristics are separately controlled genetically, then it may be possible to combine them in order to develop a high yielding, high protein cultivar.

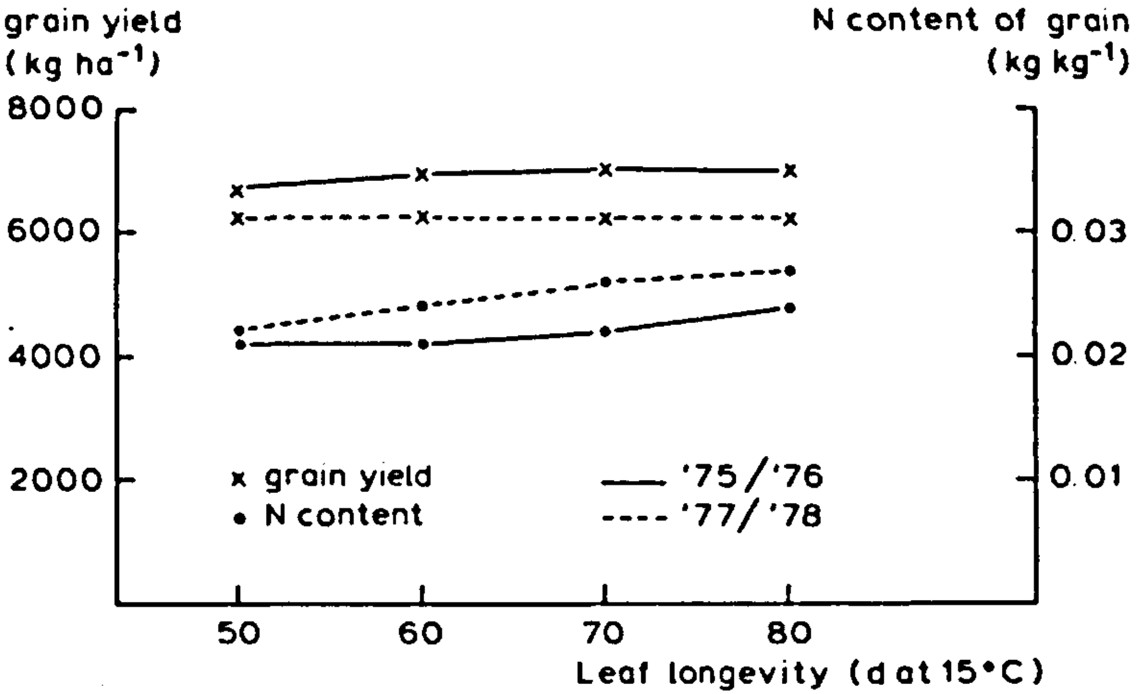

Figure 65. Simulated effect of leaf longevity on grain yield and nitrogen content of grain in two growing seasons in Migda, Israel, under optimum moisture and nutrient conditions.

g. *Canopy temperature (CTEMPF)*

Some information on the effect of transpirational cooling on canopy temperature indicates that it can make a perceptible difference to the rate of development (Seligman et al., 1983). Such effects can be mimicked in the model by setting CTEMPF to values greater than zero. The value of CTEMPF reflects the intensity of evaporative cooling but without a detailed process model can only be set arbitrarily. We will examine the effect of varying CTEMPF from 0 to 5 °C. Activating CTEMPF results in a cooler canopy that matures later. Anthesis is postponed from day 143-148 to around day 153 as CTEMPF increases from 0 to 3 °C. This may to be an exaggeration because differences in development rate of the crop due to canopy temperature differences do not generally separate anthesis dates by more than 5 to 7 days. So, probably, a realistic value for CTEMPF would be about 2.

Reduction in canopy temperatures tends to increase grain yield under favourable growing conditions. Slower development which causes later anthesis results in higher grain yields (Fig. 61). This phenomenon is partly connected with higher grain numbers (Fig. 62), but also with more total assimilation. This is reflected in a relatively constant harvest index of around 0.44 (with extreme values of 0.41 and 0.46) and a total shoot weight that increases with grain yield.

Lower temperatures are associated with higher wheat yields (van Keulen & de Milliano, 1984; Monteith, 1981b). However, later anthesis or slower development are not in themselves necessary for higher yields. The context, it would seem, is all-important in evaluating crop manipulation, whether by agrotechnical means or genetic manipulation. If this is self-evident, then generality in crop science is indeed an elusive quality.

h. Organ formation

Under dryland conditions, organ numbers seldom limit grain yield. As a rule, organ numbers tend to reflect growing conditions (Fischer, 1979). Under optimum growing conditions, organ number, and finally grain number may determine yield, because of the determinate size of the wheat grain, which seldom exceeds 50 mg in weight. In the model, organ number is defined for tillers, ears, spikelets, florets and grains. The number of organs in any particular case is determined by the number of precursor organs, by assimilatory intensity during organ formation and by the assimilate requirement for formation of a competent organ. Morphological differences between cultivars can be simulated by varying the assimilate demand for different organs (Section 3.6). In the following sensitivity test we have varied the requirement separately for tillers, ears and florets: for tillers from 175 to 1050 mg per tiller, for ears from 200 to 1600 mg per ear, and for florets from 4.375 to 35 mg per floret.

Whereas tiller number decreases with greater assimilate requirement, the effect on crop yield is very small, generally less than 2.5 percent. Ear numbers show a slight tendency to increase as tiller number decreases. This appears to be associated with a lower loss of leaf area from excess tillers that do not form ears and slowly die. This result is difficult to check with experimental data because tiller numbers in plant density experiments have a much wider range of tillers per unit area and consequently ear number is more strongly influenced by tiller number. But even in such experiments ear number is very similar over a narrower range of tiller densities (Darwinkel, 1978).

As assimilate requirement for ear formation increases from 200 to 1600 mg per ear (as a cultivar characteristic) ear number decreases. Grain yield and total dry matter production are hardly affected and grain number and grain size are also fairly constant, even as ear number goes down from more than 600 ears m^{-2} to less than 400 ears m^{-2}. Only the number of grains in the ear increases from 27-32 to 44-55.

The effect of changes in floret assimilate requirement is, as expected, to decrease the number of florets as the requirement increases from 4.375 to 35 mg

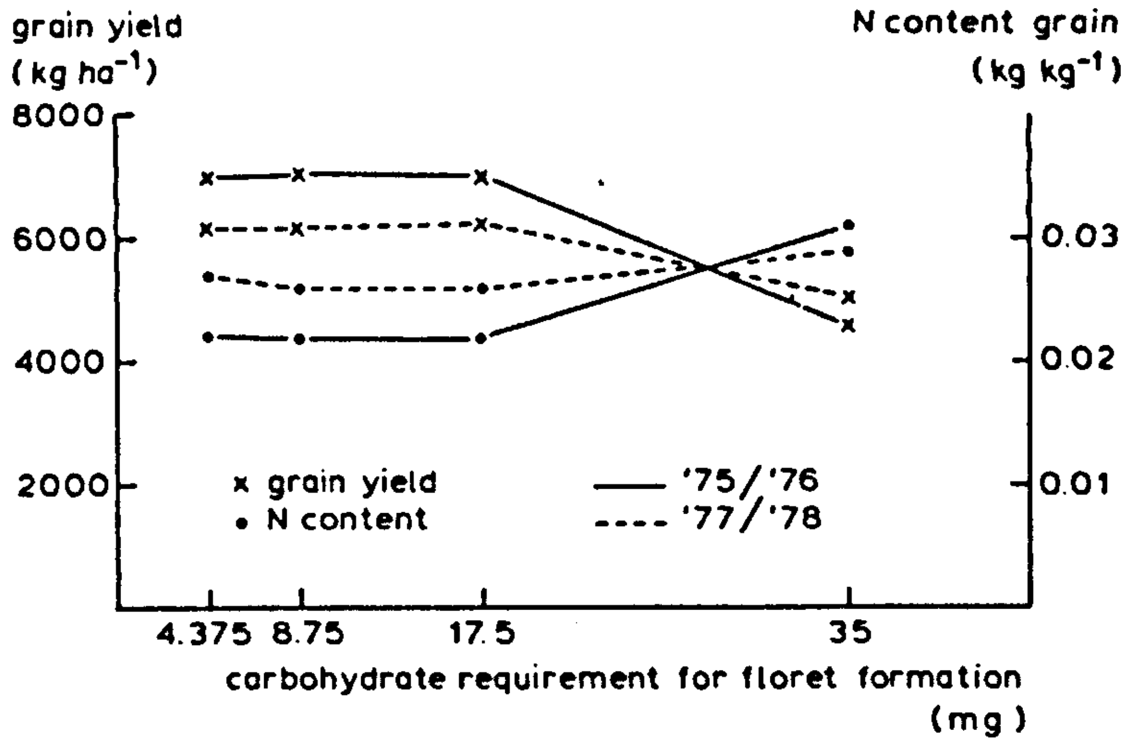

Figure 66. Simulated effect of various carbohydrate requirement values for floret formation on grain yield and nitrogen content of grain in two growing seasons in Migda, Israel, under optimum moisture and nutrient conditions.

per floret. Consequently, grain number is also reduced, from 22 000 – 29 000 grains m^{-2} at the low requirement to 9 000 – 10 000 grains m^{-2} at the high requirement. At the optimum conditions defined in these tests, grain weight seldom exceeds 45 mg per grain and so grain yields of more than 6 000 kg ha^{-1} require at least 15 000 grains m^{-2}. In such cases grain density determines grain yield (Fig. 66). There are differences from year to year, and in 1977/78 grain yield and N concentration in the grain were less sensitive than in 1975/76 to floret numbers as the carbohydrate requirement for floret formation approached 35 mg per floret.

In general, this pattern of response to grain number is well-known in wheat plants. Darwinkel (1978, Fig. 9) shows that grain number increases with plant density to an asymptote of about 16 000 grains m^{-2} up to which point it is a major determinant of grain yield. In the model the last phase of grain number determination, the grain formation stage, is critical. In the earlier stages, where tillers or ear numbers are involved, there is enough time left for compensatory growth of grain forming organs. These results suggest that in the context of high yielding crops, it would be more important to ensure ample floret formation than to ensure large numbers of tillers or ears. An excess number of grains in the model would result in small grains, even under optimum conditions. In practice, the decrease is less severe because, when assimilate supply limits grain fill, less grains tend to fill and mature. In the model, reduction of grain number after the onset of grain fill is not treated and so all grains are equal,- even those that should have been aborted after the beginning of grain fill.

i. Conclusions

If acceptable performance under certain boundary conditions is a necessary, if not sufficient, criterion of model validity, then the present model has performed reasonably well under 'potential yield' conditions. In order to simulate a high yielding crop only a small number of parameter changes are necessary, most of them related to water and nitrogen availability and 'cultivar-specific characteristics'. Under suitable conditions when water and nitrogen are not limiting, yields of more than 8000 kg ha^{-1} (cf. Fig. 63) can be simulated for the climatic conditions of the northern Negev. These are somewhat higher than the highest yields obtained under experimental conditions in the region and appear to be close to the limit attainable. The model suggests that crop performance under optimum conditions is relatively sensitive to plant characteristics related to leaf protein turnover and leaf longevity, but not sensitive to faster root growth. These are suggestions which may be worth testing under different regional climatic conditions.

5.2.3 Long term crop responses

a. Background and revalidation

The model can be used to assess the effects of agrotechnical practices and plant characteristics on crop performance over a period long enough to characterise the climatic variability of a site. Such an exercise was conducted for the Migda site (van Keulen, 1975; Tadmor et al., 1974), for which 21-years of climate data are available. The 'standard run' data set (Table 17) was used and the sensitivity to a set of 10 parameters was investigated. Data on wheat yields are available for six years during which wheat was grown continuously with no rotation or fallow. These data can be used as a revalidation set for the model.

Over the six years for which appropriate data are available, simulated yields are generally underestimated in the poor years and overestimated in the good years (Table 30). Because the model does not take into account diseases, pests or special soil properties that can reduce yield, one would expect the simulated results to overestimate the measured yields as a rule. The underestimation in the poor years is more difficult to explain. It could be related to the effect of soil heterogeneity on crop yields when the response to improved growing conditions is sigmoid. Then, soil heterogeneity on a micro-scale would lead to lower observed yields under good growing conditions, and higher observed yields under poor growing conditions in dry years (Fig. 67; de Wit & van Keulen, 1987; Noy-Meir, 1981). As substantial soil heterogeneity on a micro-scale exists at Migda, even though the soil is fairly homogeneous on a macro-scale, this phenomenon may be sufficient to explain the simulated results. If not, there are also other factors that could have caused the discrepancy, especially in the drier years.

In 1978/79, postponing sowing date from the end of November to the end of December more than doubled the simulated yields. In the field, a similar result could occur even with the early sowing as a result of a second flush of tillering after a long, dry mid-season spell, followed by later rains. The grain yield from the later tillers could add significantly to that of the earlier drought-stricken tillers. This phenomenon is not accounted for in the present model. In 1976/77 simulated yields are similar to recorded only when 120 kg N ha^{-1} is applied. It could be that at the beginning of the recorded series, the N status of the field was much better than in later years, and better than the standard values used in the test runs. The underestimate in 1981/82 was not materially changed by different values for the agrotechnical and plant characteristic parameters that were examined, and so the reason for the deviation could well be site heterogeneity (Fig. 67). Simulated grain numbers were very low in 1981/82 and seemed to be limiting yield in the simulated results. In other years, simulated grain numbers were similar to those commonly observed. Despite these deviations, there is a good correlation between observed and simulated yields ($r^2=0.944$ without corrected values for 1976/77 and 1978/79; 0.975 with the corrected values) and the mean yields for the six years are very similar (Table 30). Even though the simulated results are never precise replicates of the field performance, they are sufficiently close to be of interest in examining long term crop response.

The results of the 21 year run for the 'standard' parameter set are given in Table 31. The average rainfall for this period is about 9 mm higher than the long term average. The mean yields are very close to the average yields for the

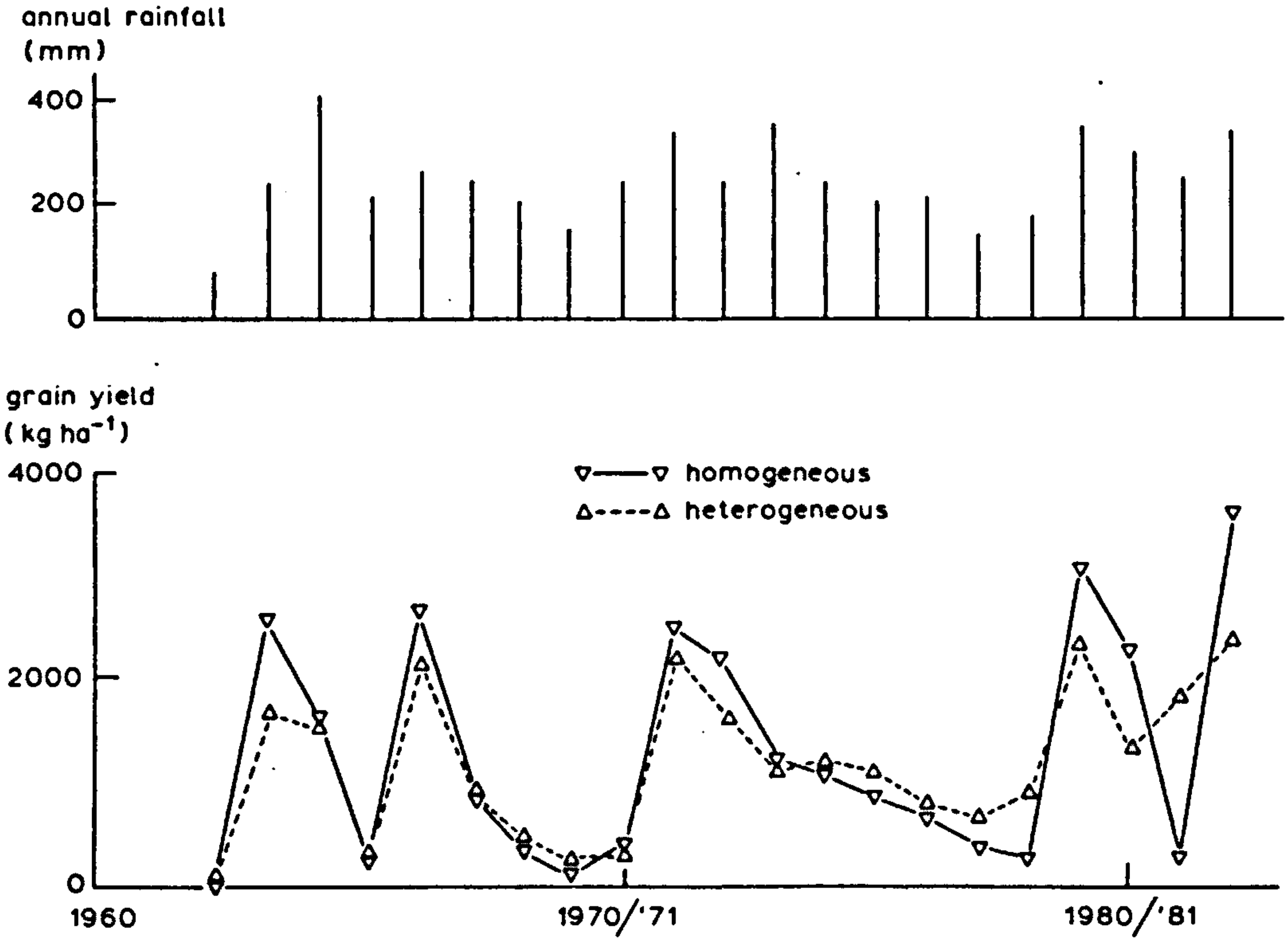

Figure 67. Simulated grain yield for a 21-year period in Migda, Israel, with homogeneous distribution of rainfall infiltration and heterogeneous distribution where half the area loses 30% of the rainfall as runoff to the other half. Annual rainfall is represented in the upper part of the figure.

Table 30. Comparison of simulated grain yields and measured yields on continuous wheat fields at the Migda Experimental Farm.

Year	Simulated[1]		Observed[4]
		kg ha^{-1}	
1976/77	744	(1078)[2]	1120
1977/78	483		370
1978/79	316	(786)[3]	920
1979/80	3646		3080
1980/81	2571		2090
1981/82	317		700
mean	1346		1380

1) Corrected to 89% dry matter content
2) Fertilizer application, 120 kg N ha^{-1}, compared to no extra fertilizer
3) Sowing date Dec. 30th, compared to standard Nov. 30th
4) Source: Benjamin et al., 1982

region (yields are given here as dry matter; for comparison with recorded grain yields, the data should be corrected to 89% dry matter by dividing by 0.89). The mean shoot weight is almost identical to a 10-year mean dry matter yield of ungrazed native vegetation given adequate N-fertilizer (Benjamin et al., 1982). The variation of both grain yield and total shoot weight is very large, and considerably greater than the variation in total annual precipitation (van Keulen, 1975; Lomas, 1972). That is the result of the strong effect of rainfall distribution on water use efficiency, which has a mean and SD of 4.6 ± 3.14 kg grain per mm of annual precipitation.

The other characteristics are more difficult to evaluate on a long term basis but the values for individual grain weight, N concentration in the grains, grain and ear density, are values commonly encountered in the region. Total N uptake at 85 ± 26 kg ha^{-1} would represent a crop that is given 30 to 60 kg N ha^{-1} yr^{-1} and compares with 30-80 kg N ha^{-1} that has been recorded in other experiments in a somewhat drier part of the region (Amir et al., 1982).

In conclusion, the model simulates a recognizable wheat crop with characteristics similar to those recorded in the region. It does not replicate each situation precisely, sometimes because of shortcomings in the model structure, but probably more often because of environmental heterogeneity and inaccuracies in the site-specific input data, both with respect to weather and soil. Effects of previous crop or fallow are not treated explicitly in the model except through

Table 31. Annual precipitation and crop performance between 1962 and 1983 simulated with th standard parameter set.

Year	Rainfall mm	Grain yield* t ha^{-1}	Shoot weight* t ha^{-1}	Grain weight* mg grain^{-1}	Grain N-conc g kg^{-1}	Grain density grains m^{-2}	Ear density ears m^{-2}	N-uptake kg ha^{-1}	Anthesis date
'62/63	78	0.00	0.08	–	–	–	–	–	–
'63/64	354	2.55	8.02	42	24	5950	350	106	10 Mar
'64/65	414	1.61	6.91	39	36	4035	269	94	5 Mar
'65/66	219	0.43	1.96	40	22	1040	260	45	19 Apr
'66/67	282	2.66	8.77	38	20	6750	375	105	28 Mar
'67/68	260	0.89	4.14	20	18	4420	260	97	7 Mar
'68/69	212	0.29	2.93	6	23	4940	260	92	2 Mar
'69/70	165	0.23	1.21	32	10	780	260	32	26 Feb
'70/71	263	0.41	2.84	9	29	4680	260	84	4 Mar
'71/72	349	2.46	8.77	42	26	5909	311	104	12 Mar
'72/73	245	2.32	7.57	40	22	5688	316	102	8 Mar
'73/74	371	1.16	4.66	37	10	3120	260	93	8 Mar
'74/75	251	1.11	5.05	41	25	2600	260	96	7 Mar
'75/76	204	0.93	2.68	28	12	3380	260	65	10 Mar
'76/77	212	0.66	3.54	14	31	4743	279	97	3 Apr
'77/78	159	0.43	2.62	9	17	4785	319	89	17 Mar
'78/79	200	0.28	2.36	5	10	4978	262	55	5 Mar
'79/80	368	3.25	10.21	42	19	7800	390	105	13 Mar
'80/81	302	2.29	7.19	40	27	5760	288	101	15 Mar
'81/82	257	0.28	1.15	42	30	780	260	27	7 Apr
'82/83	366	3.73	10.46	41	17	9114	434	109	15 Mar
mean	263	1.33	4.91	30	21	4563	296	85	14 Mar
S.D.	85	1.13	3.18	14	8	2194	52	26	13 days

* all in dry matter

initial soil moisture and nitrogen parameters that are entered to reflect some of the particular site conditions in any one year. The model simulates a healthy crop growing in a good, homogeneous soil, adequately supplied with all other nutrients, except N, which can be manipulated. With these limitations the analysis of long term effects of agrotechnical practice and plant characteristics can be undertaken with some confidence but tempered with caution.

A. Agrotechnical practices

a. Sowing density (SWDF)

The sensitivity of grain yield to sowing density is low for densities above half

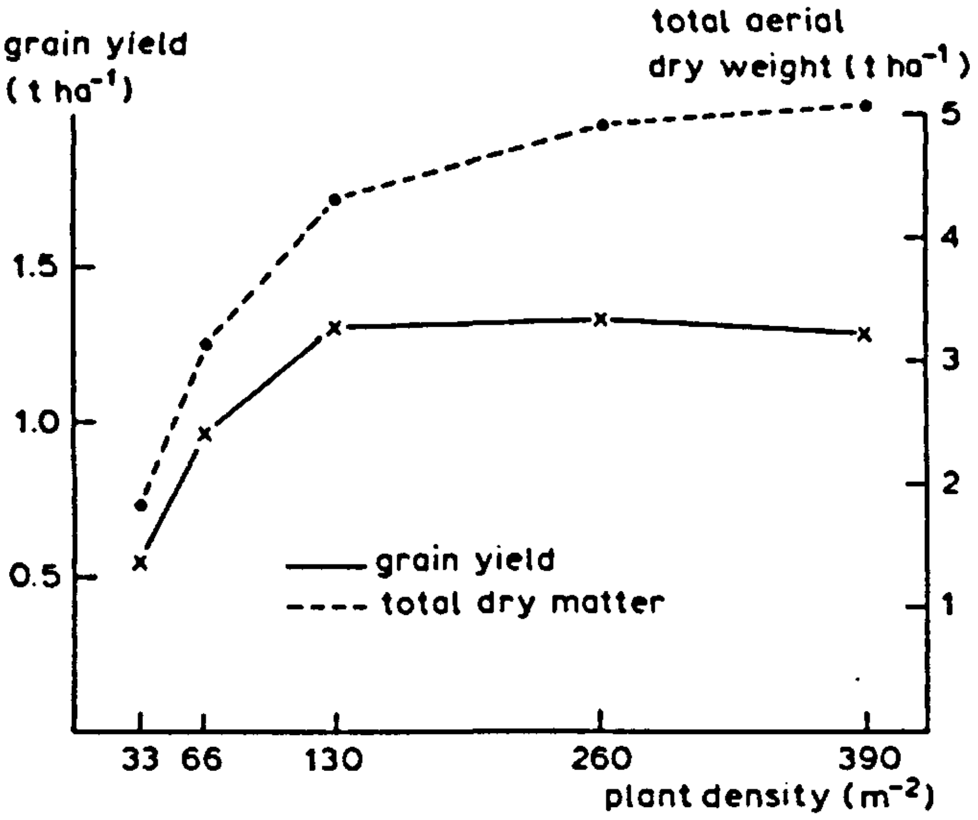

Figure 68. Simulated effect of sowing density on average total dry matter production and average grain yield for a 21-year period in Migda, Israel.

Table 32. Plant density and the simulated mean 21-year yield components (Migda climatic data).

Plant density plants m^{-2}	Grain weight mg $grain^{-1}$	Grain number grains m^{-2}	Ear number ears $plant^{-1}$
390	28.8	4388	1.04
260	29.3	4188	1.13
130	32.4	3488	1.41
65	38.0	2185	1.64
33	40.1	1161	1.65

the standard rate of 260 plants m^{-2} (Fig. 68). Below 130 plants m^{-2}, yield drops off drastically, largely due to lower tiller and grain densities (Table 32). As there are many dry years, tillering is restricted by the low carbohydrate flow caused by water stress. In better years, ear number per plant at the lowest density is sometimes more than 3 and grain density more than 3 500 grains m^{-2}. Shoot weight increases with plant density, strongly till 130 plants m^{-2} and more modestly at higher plant densities. Grain N concentration increases from 0.019-0.02 kg kg^{-1} at the high densities to 0.023-0.024 kg kg^{-1} at the low ones.

The variation between years is very large, but some crop parameters are more variable than others (Table 33). Grain yield has the highest variability which is hardly affected by plant density. Total shoot weight is less variable, but the variability decreases with increasing plant density. Individual grain weight, is again less variable and decreases drastically as plant density decreases. Where-

Table 33. Plant density and its effect on the coefficient of variation of various crop parameters.

Plant density plants m^{-2}	Grain yield	Shoot weight	Grain weight	Grain number	Ear density	Grain N-conc.
			coefficient of variation			
390	.81	.60	.53	.47	.08	.50
260	.85	.65	.49	.45	.18	.44
130	.87	.72	.37	.47	.34	.41
65	.85	.76	.16	.46	.45	.33
33	.82	.79	.09	.45	.47	.37

as variability of grain number per ear is low and insensitive to plant density, variability of ear density is sensitive and increases steeply as plant density decreases. Grain N concentration is less variable at lower plant densities. These results reflect the conservative nature of the plant whereby many plant characteristics tend to be less variable than the total dry matter or grain yield of the crop. The two extreme cases of relative stability are at both extremes of plant density: variation in individual grain weight is small at low plant densities and variation in ear density is very low at high plant densities.

The simulated results indicate that sowing density in this region could be reduced to half the standard rate without affecting grain yields. Higher sowing densities are often used in the belief that higher plant densities improve weed control. On the other hand, Bedouin farmers in the region practice relatively low sowing densities. Where weeds are not a serious problem, this would appear to be appropriate for these growing conditions.

b. Sowing date (SOWD)

Highest mean grain and total dry matter yields for the 21 year period are obtained when the sowing date is postponed till the end of November (Fig. 69). This is somewhat later than standard practice in the region where sowing is generally completed by mid-November. Variability in crop yields is very high at the earlier sowing dates and decreases as sowing is postponed. The coefficient of variation (CV) for grain yield falls from 0.95 to 0.72 for sowing dates from 30 October to 28 December. The variation in shoot weight follows a similar pattern, CV dropping from 0.79 to 0.57. Mean individual grain weight, which varies from 28 to 31 mg grain^{-1}, becomes more variable as sowing date is postponed, with the CV increasing from 0.43 – 0.44 to 0.55 – 0.58. Mean grain N concentration increases from 0.0183 to 0.0247 kg kg^{-1} and CV falls from 0.54 to 0.34 with later sowing dates.

Variation in yield and crop characteristics decreases with later sowing dates. For sowings after November 30, however, this increased stability is won at the

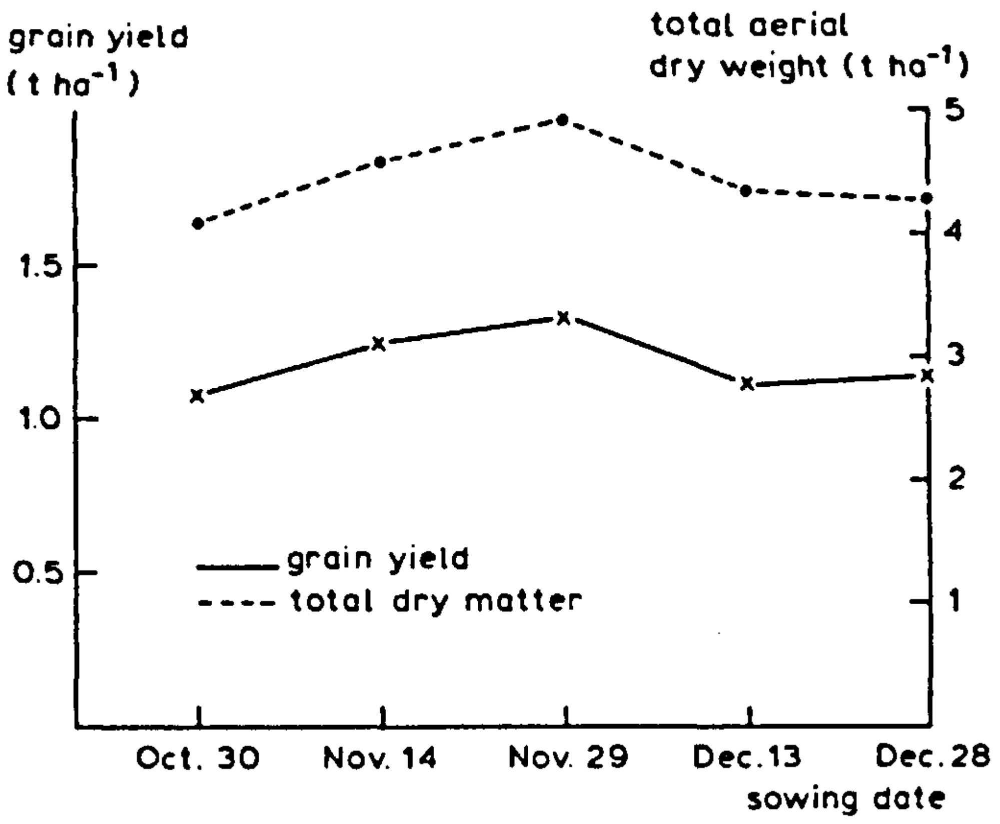

Figure 69. Simulated effect of sowing date on average total dry matter production and average grain yield for a 21-year period in Migda, Israel.

cost of grain yield.

This study examined the effects of constant sowing dates. The model could also be used to examine the effects of variable sowing dates that are determined according to the soil moisture status. Opportunistic sowing is indeed practiced, – mainly by Bedouin farmers. This and other sowing strategies need to be investigated on a long term basis, as variation from year to year is so large that short term observations can be misleading.

c. *Nitrogen fertilization (NGIFT)*

In all the runs of the 21-year series, the initial mineral N status in the soil assumes that 100 kg N ha^{-1} is available at the start of the growing period and is distributed in the top 60 cm of the soil as follows:

0 – 2 cm – 5.0 kg ha^{-1}, 2 – 5 cm – 10.0 kg ha^{-1},
5 – 10 cm – 22.5 kg ha^{-1}, 10 – 20 cm – 12.5 kg ha^{-1},
20 – 30 cm – 12.5 kg ha^{-1}, 30 – 60 cm – 37.5 kg ha^{-1}.

This is an N level that would be appropriate for a crop to which 30 – 60 kg N ha^{-1} were added regularly, or for a field that was bare fallowed in the preceding year. The simulated response of the crop to further additions of N fertilizer over 21-years was, as a consequence, small on most crop characteristics, and limited to the lowest level applied (Table 34). Only N uptake increased significantly at higher N applications.

These results are similar to those obtained under experimental conditions at a nearby site where, however, annual rainfall was on the average 10 to 20 mm less. There too, N response was limited to low levels of application, and higher levels in dry years even reduced yields (Amir et al., 1982). Reduced grain yields

Table 34. N-fertilizer application and simulated crop responses averaged over 21 growing seasons.

Fertilizer application, kg N ha^{-1}	0	30	60
Grain yield*, (t ha^{-1})	1.33	1.44	1.47
Shoot weight*, (t ha^{-1})	4.91	5.25	5.36
Grain weight*, (mg grain^{-1})	29.33	28.9	28.5
N-conc in grain, (g kg^{-1})	20.2	20.6	21.3
N-uptake, (kg ha^{-1})	81	94	103
Ear density, (ears m^{-2})	295	300	300

* all in dry matter

Table 35. Simulated grain yield response to nitrogen fertilizer application over 21 years (t ha^{-1}).

N-fert. applic. rate, kg ha^{-1}	0	30	60	90	120
Year					
1962/63	0.0	0.0	0.0	0.0	0.0
1963/64	2.6	2.6	2.6	2.6	2.6
1964/65	1.6	2.0	2.2	2.2	2.2
1965/66	0.4	0.4	0.4	0.4	0.3
1966/67	2.7	2.5	2.5	2.5	2.5
1967/68	0.9	0.9	0.9	0.9	0.9
1968/69	0.3	0.3	0.3	0.4	0.4
1969/70	0.2	0.3	0.2	0.2	0.2
1970/71	0.4	0.4	0.4	0.4	0.4
1971/72	2.5	3.2	3.6	3.6	3.7
1972/73	2.3	2.4	2.5	2.5	2.5
1973/74	1.2	1.1	1.0	1.0	0.9
1974/75	1.1	1.1	1.0	1.0	0.9
1975/76	0.9	0.9	0.9	0.9	0.9
1976/77	0.7	0.7	0.7	0.9	1.0
1977/78	0.4	0.4	0.4	0.4	0.4
1978/79	0.3	0.3	0.3	0.3	0.3
1979/80	3.2	3.9	3.9	3.8	3.8
1980/81	2.3	2.7	2.8	2.8	2.8
1981/82	0.3	0.3	0.3	0.3	0.3
1982/83	3.7	3.9	4.1	4.1	4.2
mean	1.33	1.44	1.47	1.48	1.48
S.D.	1.13	1.30	1.34	1.33	1.35

due to nitrogen application were simulated in 4 – 5 years, no significant responses in 9 years and a modest increase in yields in 8 of the 21 years (Table 35).

The implication of this analysis is that if 100 kg ha^{-1} of mineral N is available in the soil at the beginning of the growing season, there is no economic justification for adding fertilizer N. The small effect gained by applying an additional 30 kg N ha^{-1} has a marginal efficiency of about 4 kg grain kg^{-1} N applied.

Examination of a range of fertilizer application dates indicated that in the years when the crop did respond to N fertilizer, it was not sensitive to application date till mid-January. If that is so, then application of more fertilizer N (above the base 100 kg N ha^{-1} available at the onset of the growing season) could be postponed till January and be given only if justified by crop development and ambient weather conditions in a particular season.

B. Plant characteristics

a. Crop development rate (CULTP, CULTM)

Different intrinsic plant development rates can be simulated in the model by adjusting the development response to temperature. In this way it is possible to evaluate the response of earlier or later 'cultivars' to a set of environmental conditions. The response to variations in development rate is examined when it is varied both before and after anthesis. In both cases, development rate was accelerated or slowed down by 10% of the standard rate.

The mean 21-year response to later or earlier cultivars was very similar for both pre- and post-anthesis variations. Slower development (i.e. 'late cultivars') gave grain yields that were 5 -6 % higher than the standard. Faster development ('earlier cultivars') gave grain yields 8 – 10% less than the standard. Whereas slower post-anthesis development fairly consistently increased yields, differences in pre-anthesis development were much more variable. Slower pre-anthesis development sometimes increased, sometimes decreased yields. The overall increase derives mainly from a dramatic effect of slower development in 1973/74, when the later cultivar was far superior to the standard (Table 36). This occurred as a result of poor growing conditions early in the season which limited ear formation, and better conditions later in the season. Earlier anthesis was severely penalised in this season, even though total annual rainfall was 371 mm. With rain distribution heavily slanted to the later part of the season, it is possible that in the earlier cultivar, a second flush of tillering and ear formation could have reduced the difference between cultivars. As stated earlier, this aspect of crop response is not covered in the present model and may be a reason for underestimates of yield where a second tillering flush is possible. Consequently, the small difference in cultivar response may be more apparent than real in the case of the pre-anthesis differences. The higher yield response obtained with slower post-anthesis development rate appears to be

Table 36. Simulated effect of pre-anthesis development rate on crop response in 1973/74.

Crop characteristic	Early cv.	Standard	Late cv.
Grain yield* (t ha^{-1})	0.67	1.16	2.86
Shoot weight* (t ha^{-1})	3.17	4.66	8.05
Grain weight* (mg $grain^{-1}$)	42	37	42
N-conc in grain (g kg^{-1})	17	10	23
Grains per ear	6	12	26
Ear density (ears m^{-2})	260	260	260
N-uptake (kg ha^{-1})	62	93	104
Anthesis date	26 Feb	8 Mar	14 Mar
Transpiration/rainfall ratio	0.22	0.26	0.57

* all in dry matter

more reliable, because it is more consistent over the 21 years and not dependent on the second tillering flush. There are apparently only small differences in post-anthesis development rates among cultivars, but the present analysis indicates that wherever such intrinsic variation does exist, it could possibly be usefully exploited for arid zone wheat breeding. An interesting point in this regard is the fact that most Bedouin land-race cultivars in Israel are late flowering types (A. Blum, ARO, pers. commun.).

b. Rate of depth extension of the root system (DGRRT)

The rate of depth extension of the root system can be varied in the model. The standard potential root depth extension rate of 1.2 cm d^{-1} was determined in the laboratory on various annual species (Tadmor et al., 1968) and it may not necessarily be appropriate for wheat. A series of potential growth rates from 0.9 to 1.75 cm d^{-1} were tested in the model. The results indicate that in the long run, there is an advantage to faster root development under dryland conditions (Table 37). The effect is discernible especially between the 0.9 and 1.5 cm d^{-1} growth rates, with negligible effects of faster rates (except on N-uptake, which is slightly increased). The effect of faster root growth on simulated plant characters is diffuse in that it affects them all, but to a small degree. The greater part of the effect appears to be mediated through a more efficient transpiration/rainfall ratio and somewhat higher grain numbers. These results are different to those obtained under optimum growing conditions (Subsection 5.2.2) and illustrate again the importance of enviromental effects on the expression of intrinsic plant characters (Passioura, 1977).

c. Potential growth rate of the grain (PGRIGF)

The rate of grain fill is strongly affected by the potential growth rate of the

Table 37. Mean 21-year simulated crop response to differences in root growth rate.

Pot. root gr. rate, mm d^{-1}	9.0	12.0	15.0	17.5
Grain yield* (t ha^{-1})	1.26	1.40	1.50	1.52
Shoot weight* (t ha^{-1})	4.83	5.15	5.31	5.32
Grain weight* (mg $grain^{-1}$)	30.3	30.3	31.4	31.4
N-conc in grain (g kg^{-1})	22.4	21.2	20.7	19.9
Grain density (grains m^{-2})	4204	4419	4542	4530
Transpiration/rainfall ratio	0.48	0.50	0.52	0.52

* all in dry matter

individual grain, expecially in the early stages when the carbohydrate reserve level is high. In the 21-year results grain yield is directly related to the potential growth rate of the grain, the mean 21-year yield increasing more or less regularly from 1292 to 1562 kg ha^{-1} as the growth rate of the individual grain increases from 0.9 to 1.2 times the standard rate. This is an unexpected result under semi-arid conditions where grain yields are always lower than the potential of the crop. It appears, however, that precisely under such conditions rapid grain fill is an advantage when drought at the end of the season stops plant growth before full maturity. The main reason for this result could be that less time is needed to exploit the carbohydrate reserves in the plant so that less is lost to maintenance respiration or unused because of premature death of plants due to water stress. The effect of potential grain growth rate is particularly marked in years with relatively high yields. In the bad drought years, the effect is negligible.

d. Rate of nitrogen turnover in the vegetative tissue (RRTORT)

Whereas under optimum growing conditions the rate of nitrogen turnover in the vegetative tissue and hence the transfer to the grain has a marked effect on plant performance, under arid conditions it has virtually no effect in the long term on any plant characteristic except nitrogen concentration of the grain which increases from a mean 0.0164 kg kg^{-1} to 0.0227 kg kg^{-1} as the relative turnover rate is increased from 0.15 to 0.30. The effect of the rate of N-transfer on leaf senescence is here cancelled out by the effect of drought on grain fill. As a consequence, there is no consistent relationship between N-concentration in the grain and yield. This contrasts with the case where wheat is grown under optimum conditions (Section 5.2).

e. Leaf longevity (AVLTLF)

As with the rate of nitrogen transfer from vegetative tissue to grain, so increasing leaf longevity beyond the 'standard' had no effect on crop performance. Here too, drought effects appear to dominate leaf senescence to such an extent that intrinsic leaf longevity beyond the standard can very seldom be realized.

f. Canopy temperature (CTEMPF)

The effect of evaporative cooling on canopy temperature can be tested by varying a parameter that translates transpiration deficit into temperature effects on a descriptive basis. These canopy temperatures are then used to calculate development rate and other canopy-temperature dependent variables. The 'cooling effect' was varied and depending on the transpiration deficit could change canopy temperatures by up to 0, 3 or 5 °C.

The effect of these variations was small and not consistent over the range of temperature effects tested. The largest effect on the mean grain yield was only 5% for the 3° C maximum potential effect compared to no temperature effect at all. Mean ear density increased monotonically from 300 to 327 ears m^{-2} as the temperature effect increased; an effect that accounted for most of the yield difference.

The temperature effect has so many ramifications in the model (and in reality!) that there is not much to be gained by comparing long term averages. Closer investigation of this aspect will have to be conducted elsewhere.

g. Possibilities for higher grain yields

Is it possible to derive from this analysis a program for improving wheat yields in the region? In other words, can agrotechnical practice and cultivar adaptation be modified, so as to improve yields in the long run? In an attempt to examine the implications of the model in this respect, a set of parameters was defined that reflects those practices and plant characteristics which, from the previous analysis, appear to be favourable for yield improvement in the region. These parameter values and the standard set are given in Table 38. The grain yields attained with this 'optimum' set are presented in Figure 70.

The outstanding feature of these results is that the selected practices and plant characteristics do nothing to improve yields in unfavourable years. On the other hand, yields in favourable years are considerably improved and, as a result, the mean 21-year grain yield is 1735 ± 1473 kg ha^{-1}, compared to 1331 ± 1131 kg ha^{-1} in the standard run. Variability is indeed increased, but mean yields for the region are enhanced by more than 30%. An approach to the dry years could be to cut costs as much as possible by using a flexible approach to applying expensive inputs. Thus, sowing date could be postponed till a threshold soil moisture level has been attained, and N fertilizer could be given as a topdressing only in better years. There are dangers in postponing agrotechnical practices, too. The determination of long term costs and benefits of different flexible approaches is greatly facilitated by the use of a model such as the one presented here. The realization of potential benefits of different plant characteristics may, or may not be feasible biologically. That is a point

Table 38. Parameters used in the 'standard' and in the 'optimum' runs of the simulation model.

Parameter	standard value	optimum value
sowing density, plants m^{-2}	260	260
sowing date	28 Nov.	28 Nov.
N-fertilizer, kg ha^{-1}	–	30
pre-anthesis phenology	standard	later
post-anthesis phenology	standard	later
potential root extension rate, mm d^{-1}	12	15
potential growth rate of grain	standard	20% higher
maximum temperature response	0 °C	3 °C
other parameters	standard	standard

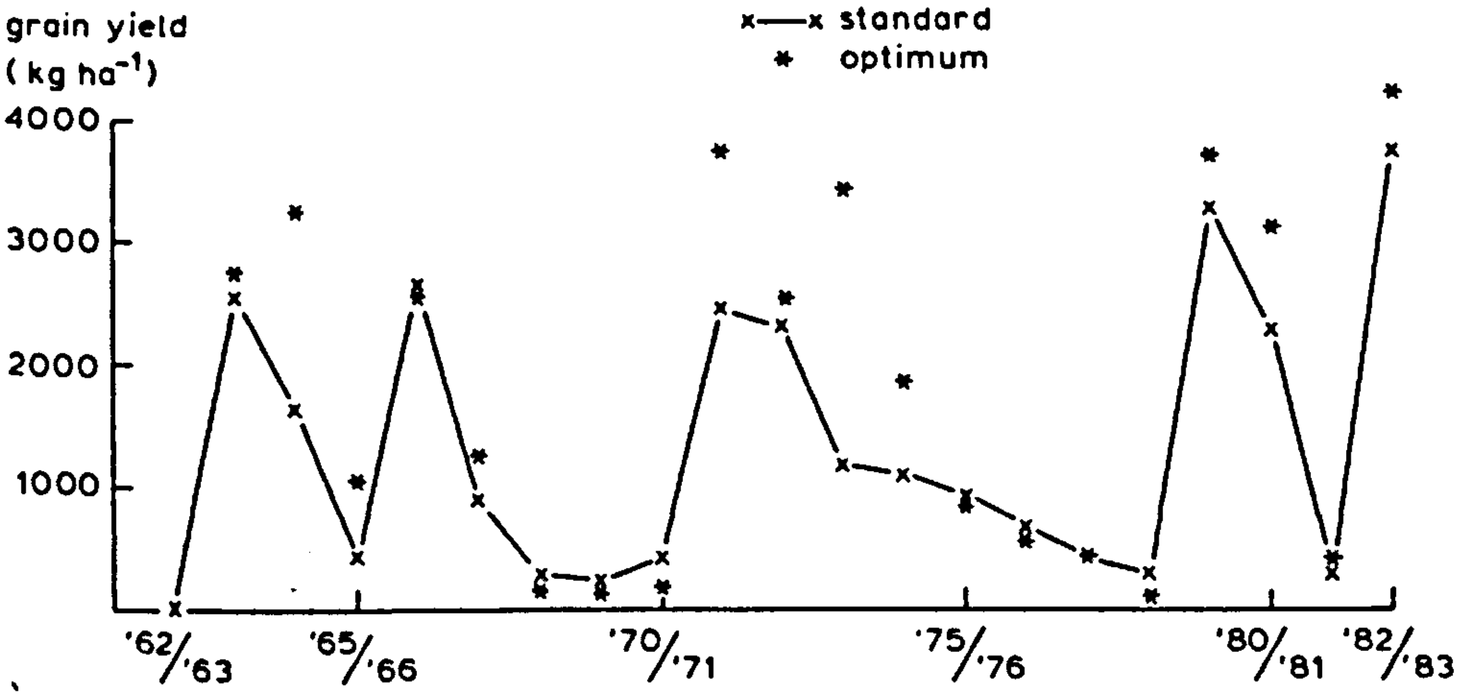

Figure 70. Simulated grain yields for a 21-year period in Migda, Israel, for both the 'standard' parameter set (Table 17) and the 'optimum' combination of plant characteristics and agronomic practice.

to be considered by plant breeders and plant physiologists (Evans & Dunstone, 1970). In order to work out a programme for improvement, each parameter should be tested individually and in various combinations so that the most effective measures could receive priority.

These model results should not be regarded as hard recommendations but rather as indicators of potentially promising approaches that should be looked at more carefully from the point of view of both research and extension.

5.3 Epilogue

The model that is the subject of this study has been developed over a period of more than 12 years; not continuously, and with long periods of dormancy so that considerably less than half that period was actively spent on the model.

Even that was a considerable effort that involved thousands of runs and many hours of computer time. With the results in front of us, we can try to ennumerate, if not evaluate, the achievements and shortcomings of this exercise.

The objectives of the simulation were originally to analyse water and nitrogen effects on wheat growth in a semi-arid environment so as to establish the theoretical yield potential of such regions when both nitrogen and water can limit growth. Because of the extreme climatic variation in such regions, long term evaluation of agrotechnical practice is not a simple or straightforward task. A reliable crop simulator appeared to be the answer to the needs not only of intellectual curiosity and of research planning, but also of rural development planners, extension officers and possibly even farm managers. Expectations were never so pretentious as to assume that the model would replace field experience and experimentation, but also not so modest that they did not hope it would serve as a useful tool to guide both research and practice. How reliable is the model as it stands today for these purposes? Or, in other words, can one derive useful conclusions with the model more efficiently than without it?

The numerous evaluation studies that were described in earlier sections of this chapter illustrated that the model can reproduce the qualitative effects of agronomic treatments and plant characters on crop performance but that the quantitative reproduction is only approximate. In some cases the deviations between simulated and observed are greater than the standard errors of the observed data. Not always was it possible to pinpoint the reasons for the discrepancies. In many cases, it seemed that the variation in observed data reflected environmental variation on both micro and meso scale that would be extremely difficult to resolve even with sophisticated monitoring. Relatively simple heterogeneity related to water distribution on a site, could produce deviations of more than 100% in some years. Such heterogeneity is rarely recorded and even then would cover only a part of the overall physical, chemical and biological heterogeneity in the environment of what are regarded as 'uniform' stands. Consequently, the field data that should reflect the 'reality' that is the basis for model evaluation, is itself inconclusive in many cases. So much so, that the evaluation of model reliability becomes a matter of subjective judgement.

Nevertheless, despite such difficulties, model behaviour often seems to improve the understanding of the reality that it tries to describe. The following examples are taken from results presented earlier in this chapter.

1. The conditions under which site heterogeneity can be important are easily demonstrated with the model, and as a rule seem to indicate that the response of wheat yields to better growing conditions is indeed sigmoid.

2. The relation between yield enhancement and yield stability can be explored in different contexts. It appears that yield stability in itself is not a desirable

goal when it is achieved by lower yields in good years and very little change in yields in bad years.

3. Long term effects of agronomic practice can be analysed over a number of years large enough to provide the perspective necessary for understanding the reasons for successful or unsuccessful techniques. The analysis of sowing date is a case in point.

4. The response of crop performance to different plant characteristics can be evaluated for different environmental situations. The importance of some mechanisms, like nitrogen turnover rates in the leaf, can be the key to better yields under good growing conditions yet have negligible effects in a semi-arid situation. Others are less obvious. Thus, possible improvement of yield levels with later ripening varieties under dry conditions seems counter-intuitive. Yet it appears that this is so not only in the model but that traditional land races used by the local Bedouin are also later maturing.

Whereas the model can meet modest expectations in these categories, there are others where its shortcomings make its use hazardous. These would include the following:

1. Yield prediction for a specific field or region where initialization and meteorological data as well as site specification are inadequate. This model, like any conceivable crop model, requires accurate initialization and reliable values for the main meteorological driving variables. As these are available for only few sites, this difficulty will probably remain unsolved indefinitely.

2. Model conclusions with regard to the morphological response of the crop must remain tentative because the mechanisms that determine these responses are described only approximately; not only in the model, but also in the literature.

3. Even though the model deals specifically with nitrogen in the soil and plant, the results are less than satisfactory. This is especially so for the soil nitrogen section where the description of tranformations related to the growth of the microbial biomass are little more than guesses.

4. As the model is by its nature a highly simplified description of a complex system, it can only simulate certain of the responses even within its 'bounds of jurisdiction'. Consequently, 'catastrophe situations', where serious deviations develop are not uncommon and very little can be done to improve model performance without serious consequences in other unrelated situations.

These shortcomings are common to all crop models; so much so that serious scientists have suggested calling a moratorium on crop models until the basis for understanding the systems being modelled is considerably widened. The fact that the model can reproduce so much of crop behaviour with so little parameter adjustment would indicate that despite all the complexity, there is a fundamental conservatism in these systems, that operates via many negative feedbacks and that keeps the systems 'on course'. It makes it possible to study these systems and to manipulate them with not entirely unpredictable results.

Finally, the model, with all its attributes and imperfections, is no more than a station that will eventually be passed as corrections, improvements, clarifications and simplifications lead to better, more reliable and more managable crop models. If the present study has illustrated some of the possibilities of crop simulation and identified some directions where improvement should be sought, it will have fulfilled its purpose to a large degree.

6 List of symbols used in equations

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
a_e	green area index of the ears	99	$m^2\ m^{-2}$	
a_{ea}	maximum green area per ear	101	m^2	ARPEAR
a_f	factor accounting for effect of age on ear yellowing	101	unitless	AGEF
a_s	green area index of stems and sheaths	99	$m^2\ m^{-2}$	STAREA
A_{sx}	maximum total green area of stem tissue	100	m^2	MXSTAR
A	rate of organ attrition at high crop density	76	$no\ d^{-1}$	
	for: tillers			DRNT
A'	relative rate of increase in dead tillers	84	d^{-1}	-
A_e'	rate of tiller attrition dependent on leaf area	85	$no\ ha^{-1}\ d^{-1}$	-
b_l	reduction factor accounting for the effect of partial shading on soil evaporation	105	unitless	-
b_s	reduction factor accounting for the effect of soil drying on soil evaporation	105	unitless	-
B	initial organ density	76	$no\ ha^{-1}$	
	for: tillers			TLNI
c	constant used in calculation of leaf boundary layer resistance	11	$(s\ m^{-1})^{0.5}$	C
c_a	current concentration of non-structural carbohydrates in the vegetation	43	$kg\ kg^{-1}$	RESL
c_{al}	threshold concentration of reserves in the vegetation for assimilation reduction	43	$kg\ kg^{-1}$	TLRGA
c_{lt}	residual non-remobilizable concentration of non-structural carbohydrates	50	$kg\ kg^{-1}$	RESLL
c_n	C/N ratio of fresh organic material per compartment	122	$kg\ kg^{-1}$	CNR(I)

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
c_{ni}	rate of change in amount of mineral nitrogen per compartment	143	kg ha^{-1} d^{-1}	DASLT(I)
c_{nx}	C/N ratio of microbial biomass	129	kg kg^{-1}	CNRMIC
c_r	residual concentration of non-structural carbohydrates in the vegetation for translocation to the grain	60	kg kg^{-1}	RESLR
C	ceiling number of an organ for:	77	no ha^{-1}	-
	tillers			TLNM
	ears			MXNE
	spikelets			MXNSP
	florets			MXNFFL
C_a	actual conductivity of the root system for moisture uptake	117	mm d^{-1}	ACOND
C_{di}	carbon available from decomposition of fresh organic material per compartment	130	kg ha^{-1} d^{-1}	CADEC(I)
C_{gi}	carbon requirement for growth of microbial biomass per compartment	130	kg ha^{-1} d^{-1}	CFBMG(I)
C_{lv}	actual stomatal conductance	16	s m^{-1}	SC
C_{lx}	maximum stomatal conductance	17	s m^{-1}	SCM
C_p	potential conductivity of the root system for moisture uptake	116	mm d^{-1}	PCOND
d_{ci}	rate of decomposition of fresh organic material per compartment	120	kg ha^{-1} d^{-1}	DECR(I)
d_{co}	relative rate of decomposition of fresh organic material under optimum conditions per compartment	120	d^{-1}	RDECR(I)
d_e	effective daylength	23	h	EDAYL
d_i	thickness of compartment	109	mm	THCKN(I)
d_l	rate of increase in leaf area	86	m^2 ha^{-1} d^{-1}	-
d_o	zero plane displacement	13	m	D
d_r	rate of drainage beyond potential rooting zone	104	mm d^{-1}	RDRAIN
d_{rc}	relative rate of decomposition of cellulose/hemicellulose under optimum conditions	121	d^{-1}	RDCELL

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
d_{rl}	relative rate of decomposition of lignin under optimum conditions	121	d^{-1}	RDLIGN
d_{rp}	relative rate of decomposition of proteins under optimum conditions	121	d^{-1}	RDCAPR
d_{rt}	relative transpiration deficit of the vegetation	19	unitless	RTRDEF
d_s	relative rate of decomposition of stable organic material per compartment under optimum conditions	123	d^{-1}	DMINR
d_{si}	current rate of decomposition of stable organic material per compartment	123	$kg\ ha^{-1}.d^{-1}$	RHMIN(I)
d_t	total nitrogen demand of the canopy	65	$kg\ ha^{-1}\ d^{-1}$	TNDEM
d_x	nitrogen demand of an organ for:	63	$kg\ ha^{-1}\ d^{-1}$	-
	roots			NDRT
	leaves			NDEM
	stems			NDEMST
e	current fraction of labile nitrogen exported from vegetative tissue	70	unitless	-
e_a	actual vapour pressure of the atmosphere	3	mbar	VPA
e_{at}	'effective' actual vapour pressure in daytime	10	mbar	VPAM
e_f	reduction factor for calculation of effective root length per compartment	112	unitless	EDPTF(I)
e_s	saturated vapour pressure of the atmosphere	3	mbar	SVP
e_{st}	'effective' saturated vapour pressure in daytime	8	mbar	SVPAM
E	potential transpiration rate of the vegetation	2	$kg\ m^{-2}\ s^{-1}$	APTRAN ($mm\ d^{-1}$)
E_a	actual rate of evaporation from the soil surface	105	$mm\ d^{-1}$	EVTOT
E_i	rate of moisture withdrawal from a compartment for evaporation	108	$mm\ d^{-1}$	ER(I)
E_n	number of ears	101	$no\ ha^{-1}$	EARN

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
E_p	potential rate of evaporation from the soil surface	105	mm d^{-1}	EVAP
E_r	extension rate of the root system	111	mm d^{-1}	RGRRL
E_{rm}	maximum extension rate of the root system	111	mm d^{-1}	DGRRT
f	realized fraction of maximum CO_2-assimilation	23	unitless	P
f'	intermediate variable for calculation of gross canopy CO_2 assimilation	30	unitless	P
f''	intermediate variable for calculation of gross canopy CO_2 assimilation	34	unitless	P
f_c	weight to relative area conversion factor used in calculation of N uptake	66	kg ha^{-1}	CF
f_{ga}	factor accounting for the effect of temperature on maximum gross assimilation rate	40	unitless	-
f_i	fraction of daily total global radiation intercepted by the vegetation	37	unitless	FINT
f_{mn}	factor accounting for influence of nitrogen concentration on maintenance respiration	44	unitless	-
f_{mt}	factor accounting for influence of temperature on maintenance respiration	44	unitless	TEF
f_o	fraction of the day that the sky is overcast	6	unitless	FOV
f_r	factor accounting for the influence of reserve level on gross CO_2 assimilation	42	unitless	REDFRL
f_{sm}	reduction factor for root water uptake as a function of available water per compartment	112	unitless	WRED(I)
f_{so}	reduction factor for root water uptake due to osmotic potential in the soil compartment	112	unitless	-

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
f_{st}	reduction factor for root conductivity due to soil temperature	117	unitless	TEC
f_t	current relative rate of nitrogen turnover in the vegetative tissue	70	d^{-1}	RTORT
f_w	fraction of water in leaf blades that can be removed	88	$kg\ kg^{-1}$	FWDB
f_{ws}	reduction factor for shoot growth due to water or nitrogen shortage	111	unitless	RFSTRS
f_x	basic relative turnover rate of nitrogen in vegetative plant parts	71	d^{-1}	RRTORT
F	rate of organ formation for:	76	no $ha^{-1}\ d^{-1}$	-
	tillers			GRNT
	ears			REARF
	spikelets			RSPLF
	florets			RFFF
	grains			RGRN
F_l	rate of organ formation as determined by carbohydrate availability	77	no $ha^{-1}\ d^{-1}$	-
F_m	maximum rate of CO_2 assimilation of a single leaf	23	$kg\ ha^{-1}\ h^{-1}$	AMAX
F_{mn}	maximum rate of CO_2 assimilation of a single leaf as influenced by N concentration	39	$kg\ ha^{-1}\ h^{-1}$	AMAXN
g	number of grains set	59	no ha^{-1}	GRN
g_a	green area index of the vegetation (including stem area and ear area)	23	$m^2\ m^{-2}$	GRAI
g_{sl}	sunlit green area of the vegetation	30	$m^2\ m^{-2}$	SLLAE
h	carbohydrate flow to above ground vegetative organs	79	$kg\ ha^{-1} d^{-1}$	FCHTV
h_c	height of the crop	100	m	CROPHT
h_i	intermediate variable used to calculate turbulent resistance	12	unitless	LNREF
h_r	reference height at which windspeed is measured	13	m	REFHT
H	rate reduction factor for organ formation due to water or nutrient stress	78	unitless	
j	number of day in julian calendar	25	unitless	DAYY

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
k	extinction coefficient for total radiation	5	unitless	EXC
k'	extinction coefficient for calculation of moisture withdrawal by soil evaporation	110	unitless	PROP
k_k	von Karman's constant	12	unitless	KARMAN
k_s	proportionality factor for the calculation of the effect of shading on soil evaporation	106	unitless	-
l_i	depth of the centre of a compartment below soil surface	110	mm	-
l_{ri}	root length in a soil compartment	112	mm	RTL(I)
L_{re}	total effective root length	113	mm	ERLT
m	factor accounting for the effect of moisture stress on turnover of nitrogen in vegetative material	71	unitless	EFFWS
m_b	factor accounting for the influence of size of microbial population on decomposition of fresh organic material	120	unitless	-
m_{bi}	nitrogen requirement or nitrogen 'surplus' in the microbial biomass per compartment	126	kg ha^{-1} d^{-1}	DBN(I)
m_c	reduction factor accounting for the effect of C/N ratio on decomposition of fresh organic material per compartment	120	unitless	CNRF(I)
m_i	proportionality factor for distribution of soil evaporation over compartments	108	unitless	-
m_{ni}	net rate of change of nitrogen in microbial biomass per compartment	126	kg ha^{-1} d^{-1}	DBIOMN(I)
m_r	relative maintenance respiration of live microbial biomass	126	d^{-1}	RRMIC
m_s	reduction factor accounting for the effect of soil moisture on decomposition of organic material per compartment	120	unitless	MF(I)
m_t	reduction factor accounting for the effect of soil temperature on decomposition of organic material	120	unitless	TF

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
m'_{ni}	value of net rate of change of microbial biomass at ($t - \Delta t$)	132	kg ha^{-1} d^{-1}	PDBIOM(I)
m_w	conversion factor from CO_2 to reduced sugars	20	kg kg^{-1}	CCO2TS
M_i	current amount of microbial biomass per compartment	127	kg ha^{-1}	BIOMN(I)
M_{xi}	potential amount of microbial biomass per compartment	127	kg ha^{-1}	BIOMX(I)
M_{xci}	potential amount of microbial biomass per compartment as determined by carbon availability	128	kg ha^{-1}	BIOMXC(I)
M_{xni}	potential amount of microbial biomass per compartment as determined by nitrogen availability	128	kg ha^{-1}	BIOMXN(I)
M_{xri}	potential amount of microbial biomass per compartment as determined by microbial growth rate	128	kg ha^{-1}	-
n	total number of compartments considered in the soil profile	17	unitless	N
n_a	'relative' nitrogen concentration in leaf blade tissue	68	unitless	RFNS
n'_a	'relative' nitrogen concentration in leaf blades used in nitrogen-induced leaf death	92	unitless	FNC
n_{al}	current concentration of nitrogen in leaf blades	17	kg kg^{-1}	FRNV
n_{am}	nitrogen concentration in plant tissue where maintenance requirement is equal to the standard value	45	kg kg^{-1}	FNMIN
n_{ax}	current concentration of nitrogen in plant organ for:	45	kg kg^{-1}	-
n_{al}	leaf blades			FRNV
n_{as}	stem			FRNST
n_{ar}	roots			FRNR
n_{ag}	grains	62		FRNG
n_{di}	nitrogen supply by diffusion per compartment	137	kg ha^{-1} d^{-1}	RNUDB(I)
n_{fi}	nitrogen concentration in fresh organic material per compartment	124	kg kg^{-1}	FNOM(I)

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
n_i	concentration of nitrogen in the soil solution per compartment	135	kg mm^{-1} ha^{-1}	CONC(I)
n_m	minimum concentration of nitrogen in plant organ for:			
n_{ml}	leaf blades	67	kg kg^{-1}	BN
n_{mr}	roots	74	kg kg^{-1}	RN
n_{ms}	stem	74	kg kg^{-1}	LN
n_{mn}	minimum nitrogen concentration in leaf blades for unrestricted transpiration	17	kg kg^{-1}	FNMN
n_{mx}	nitrogen concentration in mature tissue of an organ	64	kg kg^{-1}	-
n_{rd}	requirement for nitrogen uptake by diffusion	136	kg ha^{-1} d^{-1}	RNUDF
n_{si}	concentration of nitrogen in stable organic material	125	kg kg^{-1}	NCH
n_t	total rate of nitrogen uptake by the vegetation	138	kg ha^{-1} d^{-1}	RNU
n_{tr}	total rate of nitrogen uptake by mass flow	135	kg ha^{-1} d^{-1}	TNUM
n_v	overall average concentration of available nitrogen in vegetative plant parts	72	kg kg^{-1}	FNVEG
n_{xm}	maximum nitrogen concentration in an organ for:	63	kg kg^{-1}	-
	leaf blades	17		FNMX
	stem			OFNST
	roots			OFNRT
n_{yx}	maximum nitrogen concentration in young tissue of an organ	64	kg kg^{-1}	-
N_e	translocatable nitrogen in vegetative plant parts	70	kg ha^{-1}	AVN
N_i	available mineral nitrogen per compartment	129	kg ha^{-1}	ASLT(I)
N_l	amount of nitrogen in the leaf tissue	74	kg ha^{-1}	ANLV
N_r	amount of nitrogen in the root	74	kg ha^{-1}	ANRT
N_s	available mineral nitrogen in the root zone	65	kg ha^{-1}	TNRT
N_{st}	amount of nitrogen in the stem	74	kg ha^{-1}	ANSTE

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
o_c	fraction of cellulose + hemicellulose in initial fresh organic material	121	kg kg^{-1}	FCELL
o_p	fraction of (proteins + carbohydrates) in initial fresh organic material	121	kg kg^{-1}	FCAPR
O_i	amount of fresh organic material per compartment	120	kg ha^{-1}	FOM(I)
O_i'	initial amount of fresh organic material per compartment	121	kg ha^{-1}	IFOM(I)
p	intermediate variable for calculation of canopy gross CO_2 assimilation	26	unitless	P
p'	intermediate variable for calculation of canopy gross CO_2 assimilation	32	unitless	P
p''	intermediate variable for calculation of canopy gross CO_2 assimilation	35	unitless	P
p_e	fraction of current assimilate allocated to the reserve pool	54	unitless	FTRL
p_l	fraction of current assimilate allocated to the leaf blades	49	kg kg^{-1}	FTLVS
p_r	fraction of current assimilate allocated to the roots	53	kg kg^{-1}	FDSR
p_{rr}	fraction of 'surplus' assimilate allocated to the roots	53	kg kg^{-1}	FSCHG
p_s	fraction of current assimilate allocated to the stem	51	kg kg^{-1}	FTSTE
P	density of an organ for:	76	no ha^{-1}	-
	tillers			TLN
	ears			EARN
	spikelets			NSPS
	florets			FFNR
	grains			GRN
P_e	assimilate 'surplus' due to water or nitrogen shortage	52	kg ha^{-1} d^{-1}	SCHFLV
P_{ec}	estimated daily gross CO_2 assimilation of the canopy under a clear sky	22	kg ha^{-1} d^{-1}	DGCC
P_{eo}	estimated daily gross CO_2 assimilation of the canopy under an overcast sky	21	kg ha^{-1} d^{-1}	DGCO

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
P_{esh}	contribution of shaded green area to daily gross canopy CO_2 assimilation	29	kg ha^{-1} d^{-1}	-
P_{esl}	contribution of sunlit green area to daily gross canopy CO_2 assimilation	29	kg ha^{-1} d^{-1}	PS
P_g	potential rate of gross canopy assimilation in CH_2O	20	kg ha^{-1} d^{-1}	PDTGAS
P_{gc}	total daily gross CO_2 assimilation under a clear sky	20	kg ha^{-1} d^{-1}	DGCCE
P_{go}	total daily gross CO_2 assimilation under an overcast sky	20	kg ha^{-1} d^{-1}	DGCOE
P_{gw}	total daily gross assimilation as influenced by moisture conditions in CH_2O	38	kg ha^{-1} d^{-1}	-
P_{gwr}	total daily gross assimilation in CH_2O as influenced by water, nitrogen and reserve level	42	kg ha^{-1} d^{-1}	DGAS
P_m	rate of reserve utilization for maintenance respiration if current assimilate supply is too low	54	kg ha^{-1} d^{-1}	CRMD
P_n	daily 'net' CO_2 assimilation, i.e. difference between gross assimilation and maintenance requirements	48	kg ha^{-1} d^{-1}	FCHN
P_{ng}	amount of carbohydrate translocated to the grains	54	kg ha^{-1} d^{-1}	ARTTG
P_{ne}	rate of change in size of the reserve pool	54	kg ha^{-1} d^{-1}	RCRES
P_{nl}	amount of assimilate allocated to the leaf blades	49	kg ha^{-1} d^{-1}	FCHTLV
P_{ns}	flow of assimilate to the stem	51	kg ha^{-1} d^{-1}	FCHST
P_{nr}	flow of assimilate to the roots	53	kg ha^{-1} d^{-1}	FCHTR
P_{nx}	flow of assimilate for growth of an organ	56	kg ha^{-1} d^{-1}	-
P_{tr}	rate of assimilate transfer from reserves to vegetative structures	49	kg ha^{-1} d^{-1}	TRFRS
P'	total number of dead tillers	84	no ha^{-1}	DTLN
P'_m	maximum number of dead tillers	84	no ha^{-1}	TNNR

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
q	factor accounting for the effect of temperature on turnover rate of nitrogen in vegetative tissue	71	unitless	TEF
q_a	leaf area index of the vegetation	5	$m^2\ m^{-2}$	LAI
q_t	total area index of green and dead leaf	106	$m^2\ m^{-2}$	ARLFE
r	factor accounting for effect of available carbohydrate reserves on nitrogen turnover	71	unitless	-
r_{bh}	boundary layer resistance for heat exchange	3	$s\ m^{-1}$	-
r_{bv}	boundary layer resistance for water vapour exchange	4	$s\ m^{-1}$	RA
r_c	weight to conductivity ratio of the root system	116	kg ha^{-1}/mm^{-1} d	WCRR
r_{dc}	rate of decline in leaf weight due to carbohydrate exhaustion	96	kg $ha^{-1}\ d^{-1}$	-
r_{dcr}	relative rate of decline in leaf weight due to carbohydrate exhaustion	96	d^{-1}	RDRCS
r_{dcrm}	maximum relative rate of decline in leaf weight due to carbohydrate exhaustion	97	d^{-1}	MXRDR
r_{dl}	rate of decline in leaf area due to shading	94	kg $ha^{-1}\ d^{-1}$	-
r_{dn}	rate of decline in leaf weight due to nitrogen shortage	90	kg $ha^{-1}\ d^{-1}$	-
r_{dpx}	energy contribution from degrading proteins to maintenance respiration of an organ in CH_2O	44	kg $ha^{-1}\ d^{-1}$	-
r_{ds}	potential rate of decline in leaf weight due to senescence	93	kg $ha^{-1}\ d^{-1}$	PDRLVS
r_{dt}	rate of decline in live leaf weight	67	kg $ha^{-1}\ d^{-1}$	DRLVS
r_{dw}	rate of decline in leaf weight due to water shortage	88	kg $ha^{-1}\ d^{-1}$	DRLVWS
r_f	basic multiplication factor for root extension rate	111	unitless	RTF
r_i	rate of inflow of moisture in a compartment	102	mm d^{-1}	RWF(I)

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
r_{lh}	boundary layer resistance for heat exchange	11	$s\ m^{-1}$	-
r_{lr}	current relative rate of decline in leaf weight due to shading	94	d^{-1}	RDRL
r_{lrm}	maximum relative rate of decline in leaf weight due to shading	95	d^{-1}	MRDRSH
r_{lv}	stomatal resistance for water vapour exchange	4	$s\ m^{-1}$	RS
r_{mx}	rate of maintenance respiration per organ for:	44	$kg\ ha^{-1}\ d^{-1}$	-
	roots			RMNR
	stems			RMNST
	leaves			RMNLVS
	grains			RMNG
r_{mb}	maximum relative growth rate of microbial population	134	d^{-1}	MRGRB
r_n	reduction factor for leaf growth due to nitrogen stress	89	unitless	RFNS
r_{nl}	rate of nitrogen loss from live leaf tissue	67	$kg\ ha^{-1}\ d^{-1}$	TRNLL
r_{nr}	relative rate of decline in leaf weight due to nitrogen shortage	90	d^{-1}	RDRN
r_{nrm}	maximum relative rate of decline in leaf weight due to nitrogen shortage	91	d^{-1}	RDRNX
r_{nfi}	rate of nitrogen mineralization due to decomposition of fresh organic material per compartment	124	$kg\ ha^{-1}\ d^{-1}$	RNRL(I)
r_{nsi}	rate of nitrogen mineralization due to decomposition of stable organic material per compartment	125	$kg\ ha^{-1}\ d^{-1}$	RHMIN(I)
r_{nw}	reduction factor for leaf growth due to water or nitrogen stress	49	unitless	RFSTRS
r_p	development rate of the canopy	80	d^{-1}	-
	in pre-anthesis phase			DVRV
	in post-anthesis phase			DVRR
r_{th}	turbulent resistance for water vapour exchange	12	$s\ m^{-1}$	RTURB

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
r_{ui}	current rate of moisture uptake per unit effective root length per compartment	112	mm mm^{-1}	TRR(I)
r_{up}	potential rate of moisture uptake per unit effective root length	112	mm mm^{-1}	TRPMM
r_w	reduction factor for leaf growth due to water stress	87	unitless	RFWS
r_{zi}	rate of change of moisture content per compartment due to infiltration	102	mm d^{-1}	-
R	absorbed total radiant flux	2	J m^{-2} s^{-1}	HZERO
R_c	average level of irradiance during daylight hours under a clear sky	33	J m^{-2} s^{-1}	RADC
R_g	measured daily total global radiation	5	J m^{-2} d^{-1}	DTR
R_{go}	daily total global radiation under an overcast sky	28	J m^{-2} d^{-1}	DTROV
R_l	net outgoing long wave radiation	5	J m^{-2} d^{-1}	ELWR
R_o	average level of irradiance during daylight hours under an overcast sky	27	J m^{-2} s^{-1}	RADO
s	slope of the saturated vapour pressure curve	2	mbar °C^{-1}	SLOPE
s_b	development stage at the beginning of an organ formation phase for:	78	unitless	-
	tillers			DVSTS
s_{sf}	stems	86		DVSST
s_{fi}	ears	Table 2	unitless	DVSSE
s_{fl}	spikelets			DVSSPS
s_{si}	florets			DVSFS
	grains			DVSGS
s_e	development stage at the end of an organ formation phase for:	78	unitless	-
	tillers			DVSPRE
	ears			DVSPRE
s_{ts}	spikelets			DVSSPE
	florets			DVSFE
s_{eg}	grains	64	unitless	DVSSGF
s_l	specific leaf area	86	m^2 kg^{-1}	FLFAR

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
s_n	rate of change in nitrogen content per compartment due to transport	139	kg ha^{-1} d^{-1}	-
s_{ni}	rate of inflow of nitrogen in compartment	139	kg ha^{-1} d^{-1}	SLTF(I)
s_{no}	rate of outflow of nitrogen from a compartment	139	kg ha^{-1} d^{-1}	-
s_o	overall development stage, defined as $(s_v + s_r)/2$	1	unitless	DVS
s_r	development stage of the vegetation in the post- anthesis phase	1	unitless	DVSR
s_{si}	development stage at onset of spikelet formation	Table 3	unitless	DVSSPS
s_{ts}	development stage at terminal spikelet formation	Table 3	unitless	DVSSPE
s_v	development stage of the vegetation in the pre-anthesis phase	1	unitless	DVSV
s_{vr}	development stage in either pre-anthesis or post-anthesis phase	78	unitless	-
S_i	weight of stable organic material per compartment	123	kg ha^{-1}	HUM(I)
S_{tr}	cumulative relative transpiration deficit	19	unitless	CTRDEF
t	actual rate of transpiration of the vegetation	18	mm d^{-1}	TRAN
t_c	cuticular water loss	73	mm d^{-1}	PCTRAN
t_e	end of an organ formation phase	76	unitless	-
t_i	beginning of an organ formation phase	76	unitless	-
t_o	potential rate of transpiration of the vegetation	18	mm d^{-1}	APTRAN
t_p	potential moisture uptake by the roots from the soil, as dictated by soil moisture status	115	mm d^{-1}	TRANW
t_r	ratio of current transpiration to potential transpiration	18	mm mm^{-1}	-
T_a	average daily air temperature	6	°C	TMPA
T_{ae}	'effective' air temperature during daylight hours	6	°C	EAVT

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
T_{an}	temperature sum required for anthesis	Table 2	d °C	-
T_c	canopy temperature	46	°C	TMPC
T_{de}	'effective' dew point temperature during daylight hours	8	°C	DPT14
T_f	time constant for the formation of plant organs for:	76	d	-
	tillers			TCTF
	ears			TCEF
	spikelets			TCSF
	florets			TCFF
	grains			TCGF
T_{fi}	temperature sum required for floral initiation	Table 2	d °C	-
T_i	temperature sum since initiation of leaf increment i	93	d °C	ALFT(I)
T_l	temperature sum from anthesis till end of lag phase	Table 5	d °C	-
T_{lf}	accumulative temperature sum for leaf senescence	93	d °C	-
T_m	temperature sum from anthesis till maturity	Table 5	d °C	-
T_{mn}	daily minimum air temperature	7	°C	TMIN
T_{mx}	daily maximum air temperature	7	°C	TMAX
u	average wind speed in daytime	11	$m\ s^{-1}$	WSA
u_c	maximum uptake rate of nitrogen by a closed canopy	66	$kg\ ha^{-1}\ d^{-1}$	UMXR
u_n	rate of nitrogen uptake by the vegetation	65	$kg\ ha^{-1}\ d^{-1}$	RNUV
u_x	maximum uptake rate of nitrogen by the vegetation	65	$kg\ ha^{-1}\ d^{-1}$	MXRUP
v	rate of translocation of nitrogen from the vegetative tissue to the grain	69	$kg\ ha^{-1}\ d^{-1}$	RNTG
v_c	carbohydrate flow needed to initiate one viable organ for:	79	$kg\ ha^{-1}\ d^{-1}$	-
	tillers			CFTUDM
	ears			CFEUDM
	spikelets			CFSUDM
	florets			CFFUDM
v_e	maximum rate of translocation of nitrogen from the vegetative tissue	69	$kg\ ha^{-1}\ d^{-1}$	RNEXP

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
v_p	potential rate of nitrogen accumulation in the grain	69	$\mathrm{kg\ ha^{-1}\ d^{-1}}$	PRNAGT
v_{pr}	rate of protein translocation from vegetative tissue to the grains	47	$\mathrm{kg\ ha^{-1}\ d^{-1}}$	SFPRD
v_r	potential rate of nitrogen accumulation per individual grain	75	$\mathrm{kg\ (grain)^{-1}\ d^{-1}}$	PRNAIG
w_a	rate of assimilate supply to the grains, expressed in terms of dry matter	58	$\mathrm{kg\ ha^{-1}\ d^{-1}}$	-
w_g	rate of increase in dry weight of the grains	58	$\mathrm{kg\ ha^{-1}\ d^{-1}}$	GRGR
w_i	rate of change in moisture content per compartment	119	$\mathrm{mm\ d^{-1}}$	DWAT(I)
w_{li}	growth rate of the leaves on day i	93	$\mathrm{kg\ ha^{-1}\ d^{-1}}$	GRLVS(DAYY)
w_p	potential rate of dry matter accumulation in the grains	58	$\mathrm{kg\ ha^{-1}\ d^{-1}}$	PGRRG
w_r	potential rate of dry matter accumulation per individual grain	59	$\mathrm{kg\ (grain)^{-1}\ d^{-1}}$	PGRIG
w_x	rate of increase in dry weight of a plant organ for:	56	$\mathrm{kg\ ha^{-1}\ d^{-1}}$	-
w_l	leaves	86		GRLVS
	stems			GRRSTE
	roots			GRRT
	grains			GRGR
W	minimum basic flow of carbohydrates needed to grow and maintain one viable organ for:	80	$\mathrm{kg\ ha^{-1}\ d^{-1}}$	-
	tillers			CHFTB
	ears			CHFEB
	spikelets			CHFSB
	florets			CHFFB
W_l	dry weight of leaf blades	47	$\mathrm{kg\ ha^{-1}}$	WLVS
W_{at}	average leaf weight per tiller at the end of ear formation		$\mathrm{kg\ tiller^{-1}}$	LADTWL
W_r	dry weight of the roots	47	$\mathrm{kg\ ha^{-1}}$	WRT
W_{rs}	dry weight of non-structural carbohydrates	55	$\mathrm{kg\ ha^{-1}}$	ARESP

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
W_{st}	dry weight of the stems	47	kg ha^{-1}	WSTE
W_x	dry weight of any plant organ as defined above	44	kg ha^{-1}	-
X	number of plant organs that can be maintained by the current assimilate supply for:	77	no ha^{-1}	-
	tillers			TLNM
	ears			MXNE
	spikelets			MXNSP
	florets			MXNFFL
Y_i	intermediate variable for calculation of moisture withdrawal for evaporation from various compartments	109	unitless	VAR(I)
z	length of an organ development stage in development units	80	unitless	-
z_{ai}	current moisture content in a compartment	102	mm	WATER(I)
z_{ap}	current moisture content in comparment where root tip is located	111	mm	-
z_{fi}	moisture content in a compartment at field capacity	102	mm	FLDCP(I)
z_o	roughness length	13	m	ZNOT
z_{wi}	moisture content in a compartment at wilting point	137	mm	WLTPT(I)
z_{wp}	moisture content at wilting point of compartment in which root tip is situated	111	mm	-
z'	dimensionless moisture number for calculation of soil evaporation	107	unitless	WCPR
α	proportionality factor for the calculation of the contribution of the drying power of the atmosphere to crop transpiration	10	unitless	ALPHA

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
α_{mx}	maintenance requirement per unit dry weight of organ x at maximum nitrogen concentration and 20 °C for:	44	kg kg^{-1} d^{-1}	-
	leaves			RMRESL
	stems			RMRESS
	roots			RMRESR
	grains			RMRESG
Δ	time step of integration	55	d	DELT
γ	psychrometric constant	4	mbar °C^{-1}	PSCH
γ^*	apparent psychrometric constant	2	mbar °C^{-1}	-
γ_g	fraction of proteins in the grain	62	kg kg^{-1}	FPGC
γ_x	fraction of proteins in a plant organ	57	kg kg^{-1}	-
δ	declination of the sun	24	degrees	DEC
δ_p	drying power of the atmosphere	2	J m^{-2}s^{-1} mbar °C^{-1}	-
δ_{pt}	daily total drying power of the atmosphere for the vegetation	10	J m^{-2}d^{-1} mbar °C^{-1}	-
ϵ	light use efficiency at the light compensation point	27	kg CO$_2$ ha^{-1} h^{-1}/(J m^{-2} s^{-1})	EFFE
ϵ_{cb}	growth efficiency of microbial biomass	132	unitless	YG
ϵ_{cg}	efficiency of conversion of primary photosynthates into grain dry matter	61	kg kg^{-1}	CEGR
ϵ_{ch}	efficiency of conversion of primary photosynthates into structural carbohydrates	57	kg kg^{-1} kg kg^{-1}	EFCCH
ϵ_{cx}	efficiency of conversion of primary photosynthates into structural plant material for organ x	56	kg kg^{-1}	-
ϵ_{pr}	efficiency of conversion of primary photosynthates into structural proteins	57	kg kg^{-1} kg kg^{-1}	EFCPR

Symbol	Definition	Equation in which it is first used	Units	Acronym in the model
ϵ_{prg}	efficiency of conversion of primary photosynthates into structural grain proteins	62	kg kg^{-1}	EFCPRG
λ	latent heat of vaporization of water	2	J kg^{-1}	LHVAP
λ_a	geographical latitude of the location	24	degrees	LAT
ψ	plant water potential		Pa	-
θ_a	volumetric soil moisture content of top soil compartment at air dryness	107	cm^3 cm^{-3}	WCLIM
θ_{ai}	volumetric soil moisture content of compartment i at air dryness	110	cm^3 cm^{-3}	-
θ_f	volumetric soil moisture content of top soil compartment at field capacity	107	cm^3 cm^{-3}	FLDCP(1)
θ_l	current volumetric soil moisture content of top soil compartment	107	cm^3 cm^{-3}	-
θ_{li}	current volumetric soil moisture content of compartment i	110	cm^3 cm^{-3}	-
ρ	reflection coefficient for total radiation	5	unitless	REFLC
ρ_{cp}	volumetric heat capacity of the air	3	J m^{-3} °C^{-1}	RHOCP
σ	Stefan-Boltzmann constant	6	J m^{-2} d^{-1} K^{-4}	STBC
τ_b	time constant for microbial growth	127	d	TCMG
τ_d	time constant for leaf death due to water shortage	88	d	TCDDH
τ_{nd}	time constant for nitrogen uptake by diffusion	136	d	TCUD
τ_u	time constant for nitrogen uptake	65	d	TCU
τ_{tr}	time constant for translocation of reserves	50	d	TCTR

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8 Listing of the model

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*           SIMULATION OF A SPRING WHEAT CROP
*                         BY
*       H VAN KEULEN                 N G SELIGMAN
*       CABO                         ARO
*       POSTBUS 14                   P.O.B  6
*       6700 AA WAGENINGEN           BET DAGAN  50-250
*       THE NETHERLANDS              ISRAEL

**********************************************************************
*             MARCH                     1986
*             ---------------

*                   MODEL COMPONENTS
*                   --------

* ================  SECTION 0  ======
*             DECLARATION AND TITLES
*             -----------

* ================  SECTION 1  ======
*                    INITIALISATION
*                    -------

* ================  SECTION 2  ======
*                   TIMER VARIABLES
*                   --------

* ================  SECTION 3  ======
*                     WEATHER DATA
*                     ------

* ================  SECTION 4  ======
*            SOIL MOISTURE PROCESSES
*            ------------

*  PARAMETERS AND FUNCTIONS FOR SOIL MOISTURE PROCESSES        SECT. 4A
*  CALCULATION OF POTENTIAL SOIL EVAPORATION(PENMAN)           SECT. 4B
*  CALCULATION OF ACTUAL SOIL EVAPORATION                      SECT. 4C
*  INFILTRATION                                                SECT. 4D
*  RATE OF WATER FLOW THROUGH THE TOP OF SOIL COMPARTMENTS     SECT. 4E
*  CHANGE IN WATER CONTENT, TRANSPIRATION AND SOIL EVAPORATION SECT. 4F

* ================  SECTION 5  ======
*            SOIL NITROGEN PROCESSES
*            ------------

*  DECOMPOSITION OF ORGANIC MATERIAL                           SECT. 5A
*  RATE OF CHANGE IN MICROBIAL BIOMASS IN KG N/HA/DAY          SECT. 5B
*  MOVEMENT AND AVAILABILITY OF INORGANIC N IN THE SOIL        SECT. 5C
*  FERTILIZER APPLICATION DURING THE GROWING PERIOD            SECT. 5D
*  VOLATILIZATION OF AMMONIA                                   SECT. 5E
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*  UPTAKE OF NITROGEN IN THE TRANSPIRATION STREAM           SECT. 5F
*  UPTAKE OF N BY DIFFUSION; RATE OF CHANGE OF SOIL MINERAL N  SECT. 5G
*  STATE VARIABLES AND TOTALS FOR THE WHOLE SOIL PROFILE       SECT. 5H

* ================  SECTION 6  ======
*             SOIL TEMPERATURE
*             --------

* ================  SECTION 7  ======
*                TRANSPIRATION
*                -------

*  POTENTIAL TRANSPIRATION                                  SECT. 7A
*  ACTUAL TRANSPIRATION                                     SECT. 7B

* ================  SECTION 8   =====
*       PHENOLOGICAL DEVELOPMENT OF THE VEGETATION
*       ---------------------

*  ================  SECTION 9   =====
*     GROWTH OF THE VEGETATION (DRY MATTER PRODUCTION)
*     ------------------------

*  DAILY GROSS CO2 ASSIMILATION                             SECT. 9A
*  RESPIRATION AND NET CARBOHYDRATE FLOW                    SECT. 9B
*  DRY MATTER ACCUMULATION IN LEAF BLADES                   SECT. 9C
*  SENESCENCE AND DEATH OF LEAVES                           SECT. 9D
*  DRY MATTER ACCUMULATION IN LEAF SHEATHS AND STEMS        SECT. 9E
*  DRY MATTER ACCUMULATION IN THE ROOT                      SECT. 9F
*  EXTENSION GROWTH OF ROOT SYSTEM                          SECT. 9G
*  RESERVES                                                 SECT. 9H
*  DRY MATTER ACCUMULATION IN THE GRAIN                     SECT. 9I

* ================  SECTION 10  =====
*           FORMATION OF PLANT ORGANS
*           ------------

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*  EAR FORMATION                                           SECT. 10B
*  SPIKELET FORMATION                                      SECT. 10C
*  FERTILE FLORET FORMATION                                SECT. 10D
*  GRAIN FORMATION                                         SECT. 10E

*  ================  SECTION 11  =====
*                   GREEN AREA
*                   -----

*  LEAF AREA DEVELOPMENT                                   SECT. 11A
*  EFFECT OF WATER STRESS ON LEAF AREA                     SECT. 11B
*  PHOTOSYNTHETICALLY ACTIVE AREA OF EARS AND STEMS        SECT. 11C

* ================  SECTION 12  =====
*            NITROGEN IN THE VEGETATION
*            -------------

*  NITROGEN IN LEAF BLADE TISSUE                           SECT. 12A
*  NITROGEN IN LIVE STEM AND SHEATH TISSUE                 SECT. 12B
*  ROOT NITROGEN                                           SECT. 12C
*  NITROGEN IN GRAIN                                       SECT. 12D
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* =================  SECTION 13  =====
*    WHOLE CANOPY PARAMETERS, VARIABLES AND BALANCES
*    ------------------------



*  ================  SECTION 14  =====
*               RUN AND OUTPUT CONTROL
*               -----------

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* ================= SECTION 0  ========================================
*             DECLARATION AND TITLES
*             -----------

/     DIMENSION W(11,13,7)
/     DIMENSION NAM1(13), NAM2(13), NAM3(13), NAM4(13)
/     DATA NAM1/4HGRAI,4HTOT ,4HGRAI,4HGRN ,4HNUMB,4HEAR ,
/    X        4HN-UP,4HTE T,4HWUE ,4HRAIN,4HANTH,4HGERD,
/    X        4HWAV /
/     DATA NAM2/4HN YL,4HDM  ,4HN WT,4HN-CO,4H  GR,4HE, E,
/    X        4HTAKE,4HOTRA,4HKG W,4H    ,4HESIS,4HAT  ,
/    X        4H /
/     DATA NAM3/4HD  K,4H   K,4H  MG,4HNC  ,4HAINS,4HARS/,
/    X        4H   K,4HN/TR,4HGR/H,4H    ,4H    ,4H    ,
/    X        4H /
/     DATA NAM4/4HG/HA,4HG/HA,4H/GRN,4HG/KG,4H/EAR,4HM**2,
/    X        4HG/HA,4HAIN%,4HA/MM,4H  MM,4H DAY,4H DAY,
/    X        4H  MM/
SYSTEM NPOINT=3000.
SYSTEM BCD
*  THIS ROUTINE MAY CONTAIN UNDETECTED ERRORS .
*  OUTPUT SHOULD ALWAYS BE EXAMINED CRITICALLY  !!
INITIAL
NOSORT


STORAGE ER(11),RTL(11),EDPTF(11),DISTF(11),FERTAP(11)
STORAGE AWATER(11),SLTF(11),RNUM(11),RNUDB(11),RNRL(11)
STORAGE RNAC(11),RHMIN(11),RVOL(11),DECR(11),NRDEC(11)
STORAGE FNOM(11),RNUD(11),CNR(11),THCKN(11),TDT(11),DRFA(11)
STORAGE DFFOM(11),MF(11),VAR(11),CONP(11),CONC(11),CNRF(11),WRED(11)
STORAGE RWF(11),TRR(11),RDECR(11),FOMRES(11)
STORAGE RNRLB(11),CADEC(11),CFBMG(11),BIOMXC(11),BIOMXN(11),BIOMX(11)
STORAGE PDBIOM(11),DBN(11),FLDCP(11),WLTPT(11),STORC(11),AWATF(11)

FIXED I,J,N,N1,K,L,LL,M,MY,NP,LG


* ================= SECTION 1  ========================================
*                  INITIALISATION
*                  --------




PARAM N=10, M=0, MY=1, L=0, NP=1, LG=0, I=1
*  NUMBER OF SOIL COMPARTMENTS AND PARAMETERS USED FOR MULTIPLE RUNS
 N1=N+1
*  TOTAL NUMBER OF BOUNDARIES, USED IN DO-LOOPS

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```
DO 1 I=1,N
 IWAT(I)=DRFA(I)*WLTPT(I)*THCKN(I)
 IFOM(I)=DFFOM(I)*FOMI
 IFON(I)=IFOM(I)*FRNF
 INHUM(I)=DFFOM(I)*NHUMI
 IHUM(I)=DFFOM(I)*HUMI
1  STORC(I)=FLDCP(I)-WLTPT(I)
*  INITIAL AMOUNTS OF: WATER, FRESH ORGANIC MATTER, NITROGEN IN FRESH
*  ORGANIC MATTER, NITROGEN IN STABLE ORGANIC MATTER, STABLE ORGANIC
*  MATTER AND NITROGEN IN MICROBIAL BIOMASS IN SOIL COMPARTMENTS,STORAGE
*  CAPACITY

*  CALCULATION OF DEPTHS OF TOP OF CONSECUTIVE COMPARTMENTS IN MM
 TDT(1) = 0.
DO 26 I =2,N1
26  TDT(I)=TDT(I-1)+THCKN(I-1)

*  CALCULATION OF INITIAL AMOUNT OF INORGANIC NITROGEN IN
*  TOTAL SOIL PROFILE
   TNINT = 0.
 DO 27 I=1,N
27   TNINT=TNINT+IAS(I)

*  CALCULATION OF TOTAL INITIAL AMOUNT OF NITROGEN IN MICROBIAL BIOMASS

   BIOMNI = 0.
 DO 28 I=1,N
28   BIOMNI = BIOMNI+IBIOMN(I)

*   STORE ORIGINAL PARAMETER VALUES FOR RERUNS OF SWDF(SOWING RATE)
 TLNIX  = TLNI
 WRTIX  ='WRTI
 WLVSIX = WLVSI
 TLNI = SWDF*TLNI
 WRTI = SWDF*WRTI
 WLVSI = SWDF*WLVSI

PARAM SWDF = 1.
* SOWING DENSITY FACTOR, TO ALLOW DIFFERENT PLANT NUMBERS

SORT

TABLE IAS(1-10)= (5.,10.,22.5,12.5,12.5,37.5,4*0.)
*  INITIAL AMOUNT OF INORGANIC NITROGEN IN SOIL COMPARTMENTS, KG/HA
*  VALUES USED IN ''STANDARD'' RUN

PARAM FOMI = 3000.,NHUMI = 2800.,HUMI = 28000.
*  INITIAL TOTAL AMOUNTS OF FRESH ORGANIC MATERIAL, NITROGEN IN STABLE
*  ORGANIC MATERIAL AND STABLE ORGANIC MATERIAL IN SOIL PROFILE, KG/HA

TABLE DFFOM(1-10)=.05,.075,.125,.21,.17,.37,4*0.
*  DISTRIBUTION OF ORGANIC MATTER IN THE SOIL
*  IDENTICAL FOR STABLE AND FRESH ORGANIC MATERIAL

TABLE THCKN(1-10)=20.,30.,50.,2*100.,5*300.
*  THICKNESS OF CONSECUTIVE COMPARTMENTS, MM

TABLE DRFA(1-10)=1.,1.5,2.5,5*3.0,2*1.
*  INITIAL DRYNESS FACTOR OF CONSECUTIVE COMPARTMENTS AS A FRACTION
*  OF MOISTURE CONTENT AT WILTING POINT
```

```
TABLE IBIOMN(1-10) = 6*1.,4*0.
*  INITIAL AMOUNT OF NITROGEN IN MICROBIAL BIOMASS PER COMPARTMENT


PARAM PI = 3.1416

PARAM LAT = 31.
*  LATITUDE OF LOCATION
 LATE = ABS(LAT)
*  ABSOLUTE VALUE OF LATITUDE, LOCATIONS ON SOUTHERN HEMISPHERE
*  HAVE NEGATIVE VALUES FOR LAT


*  INITIALIZATION OF CROP STATE VARIABLES TAKES PLACE AT
*  EMERGENCE,(PUSHD=1.), NOT NECESSARILY START OF THE SIMULATION

INCON WLVSI =45.,WRTI =45.
*  WEIGHT OF SHOOT AND ROOT AT EMERGENCE, KG/HA
 ARLFI = WLVSI*FLFARI
*  INITIAL LEAF AREA, M**2/HA
 ANLVI  =WLVSI*FRNVI
*  INITIAL AMOUNT OF NITROGEN IN LEAF BLADE TISSUE, KG/HA
 FRNVI = FNMXA+FNMXR
*  INITIAL FRACTION OF NITROGEN IN LEAVES, EQUAL TO MAXIMUM
 FNMAX = FNMXA+FNMXR
*  ABSOLUTE MAXIMUM FRACTION OF NITROGEN IN LEAF BLADES
PARAM FNMIN = 0.005
*  ABSOLUTE MINIMUM FRACTION OF NITROGEN IN LEAF BLADES
 RNFAC = FNMAX-FNMIN
*  RANGE OF NITROGEN FRACTIONS IN PLANT ORGANS, USED IN
*  CALCULATION OF MAINTENANCE RESPIRATION
 ANRTI =WRTI*IFNRT
*  INITIAL AMOUNT OF NITROGEN IN ROOT SYSTEM, KG/HA
 IFNRT = (1.-DVSI)*(FNRTMX-FNRTMN)+FNRTMN
*  INITIAL FRACTION OF NITROGEN IN THE ROOT
 ARESPI=RESLI*(WLVSI+WRTI)
*  INITIAL AMOUNT OF RESERVES IN THE PLANT, KG CH20/HA
PARAM RESLI =0.03
*  INITIAL FRACTION OF RESERVES IN PLANT ORGANS
 TSI   =5.*PARI*(AFGEN(MXTT,DAYNRO)+AFGEN(MNTT,DAYNRO))
* INITIAL SOIL TEMPERATURE, DEGREES C
 DAYNRO=1.+STDAY-FDAYN
*  DAY NUMBER AT TIME 0.

INCON PUSHD=0.,TGERD=0.,TSDAY=0.,SOWD=45.,GERDAT=365.
DYNAMIC
* ================== SECTION 2  ======================================
*                  TIMER VARIABLES
*                  --------

 DAYY  =1.+AMOD(STDAY+TIME,365.)
*  NUMBER OF DAY, JULIAN CALENDER
 NDAY = INSW(LAT,DAYYSL,DAYY)
 DAYYSL = 1.+AMOD(DAYY+180.,364.)
*  ''EQUIVALENT'' DAYNUMBER ON SOUTHERN HEMISPHERE
 DAYNR =1.+AMOD(STDAY+TIME-FDAYN,365.)
*  DAY NUMBER IN WEATHER TABLES, THESE TABLES CAN START FROM
*  ANY DAY AS DAY 1.
PARAM FDAYN = ~~273~~.  = 1.
*  DAY NUMBER AT WHICH TIME = 0. IN WEATHER TABLES
PARAM STDAY =273.
```

```
*  NO.OF DAY(JULIAN CALENDER) AT START OF SIMULATION MINUS 1 TO ACCOUNT
*  FOR AMOD FUNCTION

*  PROCEDURE TO ESTIMATE EMERGENCE DATE AS A FUNCTION OF SOIL WETNESS IN
*  TOP 3 SOIL LAYERS TO A DEPTH OF 100 MM.   PUSHD  IS A
*  SWITCH VARIABLE, ASSUMING VALUE 1. AT DAY OF EMERGENCE
*  OTHERWISE 0., USED FOR INITIALIZATION OF VEGETATION STATE VARIABLES

PROCEDURE PUSHD,GERDAT=PUSHB(WATER)
 IF (DAYNR.LT.SOWD)GO TO 95
 IF(PUSHD.LT.0.5.AND.TGERD.LT.9.)GO TO 94
 PUSHD=0.
 TGERD=100.
 IF(TGERD.GT.50.)GO TO 95
94     CONTINUE
 WGER=0.
 DO 98 I=1,3
98     WGER=WGER+WATER(I)
 SDAY=0.
 GERD=0.
 IF(WGER.GT.100.*WLTPT(1)*1.2)GERD=1.
 IF (GERD.LT.0.5.AND.TGERD.GT.4.)SDAY=1.
 TGERD=TGERD+GERD
 TSDAY=TSDAY+SDAY
 IF(TSDAY.GT.6.)GO TO 97
 IF(TGERD.GT.7.)GO TO 90
 GO TO 95
90     CONTINUE
 PUSHD=1.
 GERDAT=DAYNR
 GO TO 95
97     CONTINUE
 TGERD=0.
 TSDAY=0.
95     CONTINUE
ENDPRO

 PUSHDI = INTGRL(0.,PUSHD)
*  VARIABLE TO MONITOR END OF GERMINATION
 PUSHDF = INSW(PUSHDI-0.5,0.,1.)
*  VARIABLE USED TO PREVENT DEVELOPMENT BEFORE EMERGENCE
* ================= SECTION 3  ======================================
*                    WEATHER DATA
*                    ------

PARAM RADCF=4.182E4
*  PARAMETER TO CONVERT CAL/CM**2 TO J/M**2
*  IF OTHER UNITS ARE USED IN DTRT, RADCF MUST BE CHANGED
 DTR    = RADCF*AFGEN(DTRT,DAYNR)
*  DAILY TOTAL GLOBAL RADIATION IN J/M**
FUNCTION DTRT = 0., 500.,   365.,500.
*  DUMMY TABLE

PARAM FARI = 1.
*  PARAMETER TO ALLOW FOR DIFFERENT DIMENSIONS IN TEMP.TABLES
*  VALUE 1 ASSUMES DEGREES C IN TABLES

 DBT08 =PARI*AFGEN(DBT08T,DAYNR)
*  DRY BULB TEMPERATURE AT 800 HOURS, DEGREES C
FUNCTION DBT08T = 0.,25.,  365.,25.
*  DUMMY TABLE
```

```

WBT08 = PARI*AFGEN(WBT08T,DAYNR)
*  WET BULB TEMPERATURE AT 800 HOURS, DEGREES C
FUNCTION WBT08T = 0.,15.,  365.,15.
*  DUMMY TABLE

 DBT14 =PARI*AFGEN(DBT14T,DAYNR)
*  DRY BULB TEMPERATURE AT 1400 HOURS, DEGREES C
FUNCTION DBT14T = 0.,25.,   365.,25.
*  DUMMY TABLE

 WBT14 = PARI*AFGEN(WBT14T,DAYNR)
*  WET BULB TEMPERATURE AT 1400 HOURS, DEGREES C
FUNCTION WBT14T = 0.,15.,  365.,15.
*  DUMMY TABLE

*  CALCULATION OF DEW POINT TEMPERATURES FROM WET AND
*  DRY BULB TEMPERATURES
 EW08  = AMAX1(0.63*(DBT08-WBT08)+0.01,...
        6.11*EXP(17.4*WBT08/(239.+WBT08)))
 AG08  =ALOG((EW08-0.63*(DBT08-WBT08))/6.11)
 DPT08 =INSW(DEWSW,239.*AG08/(17.4-AG08),AFGEN(DP8T,DAYNR))
*  DEW POINT AT 800 HOURS, EITHER CALCULATED OR DIRECTLY
*  OBTAINED FROM TABULATED FUNCTIONS
FUNCTION DP8T = 0.,10., 365.,10.
*  DUMMY TABLE
 EW14  = AMAX1(0.63*(DBT14-WBT14)+0.01,...
        6.11*EXP(17.4*WBT14/(239.+WBT14)))
 AG14  =ALOG((EW14-0.63*(DBT14-WBT14))/6.11)
 DPT14 =INSW(DEWSW,239.*AG14/(17.4-AG14),AFGEN(DP2T,DAYNR))
*  DEW POINT TEMPERATURE AT 1400 HOURS, EITHER CALCULATED, OR
*  OBTAINED DIRECTLY FROM TABULATED FUNCTIONS
FUNCTION DP2T = 0.,3.5,365.,3.5
*  DUMMY TABLE

PARAM DEWSW=1.
*  PARAMETER TO ALLOW FOR THE USE OF EITHER DEW POINT OR WET/DRY BULB
*  TEMPERATURES IN TABLES

 DPT   =AMIN1((DPT08+DPT14)*0.5,TMPA)
*  AVERAGE DAILY VALUE OF DEW POINT, DEGREES C, AMIN1 TO AVOID
*  CONDENSATION CONDITIONS

 TMPA  =PARI*(AFGEN(MXTT,DAYNR)+AFGEN(MNTT,DAYNR))*0.5
*  AVERAGE AIR TEMPERATURE, DEGREES C

FUNCTION MXTT = 0.,25.,  365.,25.
*  TABULATED FUNCTION OF MAXIMUM AIR TEMPERAURE
*  DUMMY TABLE
FUNCTION MNTT = 0.,15.,  365.,15.
*  TABULATED FUNCTION OF MINIMUM AIR TEMPERATURE
*  DUMMY TABLE
 MNT = PARI * AFGEN(MNTT,DAYNR)
*  MINIMUM AIR TEMPERATURE, DEGREE C

 EAVT = PARI*(AFGEN(MXTT,DAYNR)-0.25*(AFGEN(MXTT,DAYNR)-MNT))
*  AVERAGE AIR TEMPERATURE DURING DAYLIGHT PERIOD

 TMPC = TMPA+CTEMPF*(1.-FTMPA*TMPA*TRAN/(EVAPR+NOT(EVAPR)))
 EVAPR =  EVAP*(1.-EXP(-0.5*GRAI))
PARAM CTEMPF=0.,  FTMPA=0.05
```

```
* CANOPY AND SOIL SURFACE TEMPERATURE INFLUENCED BY EVAPORATIVE COOLING
*  CTEMPF DETERMINES MAGNITUDE OF THE EFFECT

 WSR    =AFGEN(WSTB,DAYNR)
*  WIND RUN, KM/DAY
FUNCTION WSTB = 0.,350.,  365.,300.
*  DUMMY TABLE

 VPA = INSW(VPASW,4.58*EXP(17.4*DPT/(DPT+239.)), ...
                         AFGEN(AVPTB,DAYNR)*DIMSW)
 SVPA = 4.58*EXP(17.4*TMPA/(TMPA+239.))
*  ACTUAL AND SATURATED VAPOUR PRESSURE OF THE ATMOSPHERE, MM HG
FUNCTION AVPTB=0.,15.,365.,15.
* DUMMY TABLE
PARAM VPASW=-1., DIMSW=1.
* DIMENSION SWITCH (DIMSW) EQ 4.58/6.11=0.75 WHEN AVPTB GIVEN IN MBAR

 RAIN = PARI*AFGEN(RAINTB,DAYNR)*RAINF
*  DAILY RAINFALL, MM
PARAM   RAINF=1.
*  PARAMETER TO ALLOW FOR VARIATION IN RAINFALL INTENSITY
FUNCTION RAINTB = 0.,0.,   365.,0.
*  DUMMY TABLE
 TRAIN = INTGRL(0.,RAIN)
*  TOTAL SEASONAL RAINFALL, MM

*  TOTAL DAILY VISIBLE RADIATION ON COMPLETELY CLEAR DAYS
*  AS A FUNCTION OF LATITUDE AND DAY OF THE YEAR - CAL/CM**2

FUNCTION RADTB, 0.0 =   0.,340.,                                   ...
    15.,343.,46.,360.,74.,369.,105.,364.,135.,349.,166.,337.,   ...
    196.,342.,227.,357.,258.,368.,288.,365.,319.,349.,349.,337.,...
    365.,340.
FUNCTION RADTB,10.0 = 0.,295.,                                     ...
    15.,299.,46.,332.,74.,359.,105.,375.,135.,377.,166.,374.,   ...
    196.,375.,227.,377.,258.,369.,288.,345.,319.,311.,349.,291.,...
    365.,294.
FUNCTION RADTB,20.0 =   0.,243.,                                   ...
    15.,249.,46.,293.,74.,337.,105.,375.,135.,394.,166.,400.,   ...
    196.,399.,227.,386.,258.,357.,288.,313.,319.,264.,349.,239.,...
    365.,241.
FUNCTION RADTB,30.0 = 0.,185.,                                     ...
    15.,191.,46.,245.,74.,303.,105.,363.,135.,400.,166.,417.,   ...
    196.,411.,227.,384.,258.,333.,288.,270.,319.,210.,349.,179.,...
    365.,183.
FUNCTION RADTB,40.0 =   0.,124.,                                   ...
    15.,131.,46.,190.,74.,260.,105.,339.,135.,396.,166.,422.,   ...
    196.,413.,227.,369.,258.,298.,288.,220.,319.,151.,349.,117.,...
    365.,122.
FUNCTION RADTB,50.0 =   0.,67.,                                    ...
    15., 73.,46.,131.,74.,207.,105.,304.,135.,380.,166.,418.,   ...
    196.,405.,227.,344.,258.,254.,288.,163.,319., 92.,349., 61.,...
    365., 66.
FUNCTION RADTB,60.0 =     0., 18.,                                 ...
    15., 22.,46., 72.,74.,149.,105.,260.,135.,356.,166.,408.,   ...
    196.,389.,227.,309.,258.,201.,288.,103.,319., 37.,349., 14.,...
    365., 17.
FUNCTION RADTB,70.0 =    0.,0.,                                    ...
    15.,  0.,46., 20.,74., 89.,105.,209.,135.,331.,166.,408.,   ...
    196.,380.,227.,269.,258.,142.,288., 45.,319.,  2.,349.,  0.,...
    365.,  0.
```

```
FUNCTION RADTB,80.0 =        0.,0.,                                    ...
    15.,  0.,46.,  0.,74., 28.,105.,162.,135.,334.,166.,424.,     ...
    196.,380.,227.,248.,258., 81.,288.,  3.,319.,  0.,            ...
    365.,  0.
FUNCTION RADTB,90.0 =   0.,0.,                                         ...
    15.,  0.,46.,  0.,74.,  0.,105.,154.,135.,339.,166.,428.,     ...
    196.,393.,227.,252.,258., 40.,288.,0.,                        ...
    365.,0.
 DGRCL =2.*TWOVAR(RADTB,NDAY,LATE)*CONVER
*  TOTAL DAILY GLOBAL RADIATION ON COMPLETELY CLEAR DAY, J/M**2
PARAM CONVER=4.182E4
* CONVER CONVERTS CAL/CM**2 TO J/M**2
 DGROV =0.2*DGRCL
*  TOTAL DAILY GLOBAL RADIATION ON COMPLETELY OVERCAST DAY, J/M**2
 FOV   =1.-(DTR-DGROV)/(DGRCL-DGROV+NOT(DGRCL-DGROV))
*  FRACTION OF THE DAY, THAT THE SKY IS OVERCAST
 LFOV  =LIMIT(0.,1.,FOV)
*  FRACTION OF THE DAY THAT SKY IS OVERCAST, RESTRAINED BETWEEN
*  ZERO AND ONE


* ================ SECTION 4  ====================================
*           SOIL MOISTURE PROCESSES
*           ------------

*  PARAMETERS AND FUNCTIONS FOR SOIL MOISTURE PROCESSES       SECT. 4A
*  -------------------------

PARAM WCLIM =.025,    PROP =15.
TABLE WLTPT(1-10)=10*0.075
TABLE FLDCP(1-10)=10*0.23
*  FIELD CAPACITY, WILTING POINT, WATER CONTENT AT AIR DRYNESS,
*  CM**3/CM**3
*  PROPORTIONALITY FACTOR USED IN CALCULATION OF SOIL EVAPORATION
FUNCTION WREDT = 0.,0.,.1,.3,.15,.45,.3,.7,.5,.975,.75,1.,1.1,1.
*  FUNCTION RELATING ACTUAL RATE OF WATER UPTAKE
*  TO RELATIVE WATER CONTENT IN COMPARTMENT
FUNCTION EDPTFT = 0.,.15,.15,.6,.3,.8,.5,1.,1.1,1.
*  FUNCTION RELATING EFFECTIVINESS OF ROOTS TO MOISTURE
*  CONTENT IN COMPARTMENT
FUNCTION ROSPT = 0.,1.,45.,0.1,50.,0.,200.,0.
*  FUNCTION RELATING ROOT WATER UPTAKE TO OSMOTIC PRESSURE IN THE SOIL
FUNCTION MFT = 0.,0., .14,.002, .4,.32, .6,.65, .7,.8, .85,1., ...
        1.,.85, 1.1,.85
*  FUNCTION RELATING RATE OF DECOMPOSITION OF ORGANIC MATERIAL
*  TO MOISTURE CONTENT IN COMPARTMENT (ACCORDING TO BEEK & FRISSEL)


*  CALCULATION OF POTENTIAL SOIL EVAPORATION(PENMAN)          SECT. 4B
*  -------------------------

PROCEDURE EVAP =EPRO(DTR,LFOV,SVPA,VPA,WSR)

 LWR   =STBC*(TMPA+273.)**4*(0.58-0.09*SQRT(VPA))*(1.0-0.9*LFOV)
 HZERO =DTR*(1.-REFCF)-LWR
PARAM REFCF =0.05, STBC=4.93E-3
*  REFCF=REFLECTION COEFFICIENT FOR GLOBAL RADIATION
*  STBC=STEFAN-BOLZMANN CONSTANT
 EA    =0.35*(SVPA-VPA)*(0.5+WSR/1.6/100.)*LHVAP
 DELTA =17.4*SVPA*(1.-TMPA/(TMPA+239.))/(TMPA+239.)
PARAM GAMMA =0.49,LHVAP =2.390E6
```

```
*  PSYCHROMETRIC CONSTANT, MM HG/DEGREE C
*  LATENT HEAT OF VAPORIZATIUON, J/KG
 EVAP  =(HZERO*DELTA/GAMMA+EA)/(1.+DELTA/GAMMA)*1./LHVAP
ENDPRO


*  CALCULATION OF ACTUAL SOIL EVAPORATION                       SECT. 4C
*  ------------------

 PEVAP = EVAP*EXP(-5.E-5*ARLFE)
*  POTENTIAL SOIL EVAPORATION AS FUNCTION OF SOIL COVER
 AEVAP = PEVAP*AFGEN(REDFDT,WCPR)
*  POTENTIAL SOIL EVAPORATION AS FUNCTION OF SOIL COVER AND DRYNESS
*  OF TOP SOIL COMPARTMENT
FUNCTION REDFDT =-0.5,0.,0.,0.,.2,.05,.22,.27,.33,.9,1.,1.,1.1,1.
*  FUNCTION RELATING REDUCTION IN SOIL EVAPORATION TO DIMENSIONLESS
*  WATER CONTENT IN TOP SOIL COMPARTMENT
 WCPR = (WATER(1)/THCKN(1)-WCLIM)/(FLDCP(1)-WCLIM)
*  DIMENSIONLESS WATER CONTENT IN TOP COMPARTMENT
 TEVAP = INTGRL(0.,EVTOT)
*  TOTAL SEASONAL SOIL EVAPORATION, MM



*  INFILTRATION                                                 SECT. 4D
*  ------

 INFR  =RAIN+AFGEN(IRRT,DAYNR)
*  INFILTRATION RATE, MM/DAY(RAINFALL AND IRRIGATION)
*  NO ALLOWANCE BEING MADE FOR RUN-OFF HERE
FUNCTION IRRT = 0.,0.,365.,0.
 TOTINF=INTGRL(0.,INFR)
*  TOTAL INFILTRATION, MM
 TDRAIN=INTGRL(0.,RDRAIN)
*  TOTAL AMOUNT OF WATER DRAINED BELOW POTENTIAL ROOTING ZONE, MM



*  RATE OF WATER FLOW THROUGH THE TOP OF SOIL COMPARTMENTS      SECT. 4E
*  ----------------------------

PROCEDURE RWF,RDRAIN,K=CALRWF(INFR,STORC)
 RWF(1)=INFR
DO 10 I=2,N1
 RWF(I)=AMAX1(0.,RWF(I-1)-(FLDCP(I-1)*THCKN(I-1)-WATER(I-1))/DELT)
10 IF(TDT(I).GE.MXRTD.AND.TDT(I-1).LT.MXRTD) K=I
 RDRAIN=RWF(K)

ENDPRO


* CHANGE IN WATER CONTENT, TRANSPIRATION AND SOIL EVAPORATION   SECT. 4F
* ------------------------------

PROCEDURE TRR,RWRBT,ERLT,TRANW,SWPBT,EVTOT,AWATF,WAV,WAVT=...
    CALWAT(RWF,APTRAN,RTD,TEC,CONC,AEVAP)

 WAVT = 0.
 MWRTD=0.

DO 20 I=1,N
```

```
 AWATER(I)=AMAX1(0.,WATER(I)-THCKN(I)*WLTPT(I))
 RTL(I)=LIMIT(0.,THCKN(I),RTD-TDT(I))*INSW(TDT(I)-MXRTD,1.,0.)
 EDPTF(I)=AFGEN(EDPTFT,AWATER(I)/(THCKN(I)*STORC(I)))
 WRED(I)=AFGEN(WREDT,AWATER(I)/(THCKN(I)*STORC(I)))
 AWATF(I) = INSW(-AWATER(I),1.,0.)
 WAVT = WAVT+AWATER(I)*LIMIT(0.,1.,(MXRTD-TDT(I))/THCKN(I))
20 MWRTD=MWRTD+RTL(I)*STORC(I)

 WAV = INTGRL(0.,PUSHD*WAVT)
*  TOTAL AMOUNT OF WATER IN POTENTIAL ROOTING ZONE AT EMERGENCE, MM

 ERLT=0.
 RWRBT=0.
DO 21 I=1,N
 IF(TDT(I)+0.5.GT.MXRTD) GOTO 21
 ERLT=ERLT+RTL(I)*EDPTF(I)
21 RWRBT=RWRBT+RTL(I)/THCKN(I)*AWATER(I)/(MWRTD+NOT(MWRTD))

 TRPMM=APTRAN/(ERLT+NOT(ERLT))
 TRANW = 0.

DO 22 I=1,N
 TRR(I)=TRPMM*RTL(I)*EDPTF(I)*WRED(I)*AFGEN(ROSPT,CONC(I))
22 TRANW=TRANW+TRR(I)

 TRANW = INSW(TRP,APTRAN,TRANW)
PARAM TRP=1.
*  PARAMETER TO ALLOW FOR OPTIMUM MOISTURE SUPPLY THROUGHOUT(TRP = -1.)

 SUMT=0.
 SWPBT=0.
 EVTOT=0.

DO 23 I=1,N
 VAR(I)=AMAX1(WATER(I)/THCKN(I)-WCLIM,0.)*EXP(-PROP*0.001*  ...
        (TDT(I)+0.5*THCKN(I)))
23 SUMT=SUMT+VAR(I)*THCKN(I)

DO 24 I=1,N
 ER(I)=AMIN1(AMAX1(WATER(I)-WCLIM*THCKN(I),0.),AEVAP*THCKN(I)...
      *VAR(I) /(SUMT+NOT(SUMT)))
 SWPBT=SWPBT+AWATF(I)*AND(RTD-TDT(I),TDT(I+1)-RTD)
24 EVTOT = EVTOT+ER(I)

ENDPRO

PROCEDURE DWAT = CALWT1(RWF,TRR,ER,TRAN,TRANW)

DO 25 I=1,N
25 DWAT(I)=RWF(I)-RWF(I+1)-TRR(I)*TRAN/(TRANW+NOT(TRANW))-ER(I)

ENDPRO



* ================  SECTION 5====================================
*            SOIL NITROGEN PROCESSES
*            -----------

* DECOMPOSITION OF ORGANIC MATERIAL                          SECT. 5A
* ---------------
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```
PARAM RDLIGN = 0.0095,RDCELL = .05,RDCAPR = .8
*  RELATIVE RATE OF DECOMPOSITION OF COMPONENTS OF FRESH ORGANIC
*  MATERIAL UNDER OPTIMUM CONDITIONS, DAY**-1
PARAM FRNF = .01, FRC = 0.4
*  FRACTION OF NITROGEN IN FRESH ORGANIC MATERIAL, FRACTION OF
*  CARBON IN FRESH ORGANIC MATERIAL
PARAM FLIGN=0.1, FCELL=0.7,FCAPR=0.2
* COMPOSITION OF FRESH ORGANIC MATERIAL,LIGNIN,CELLULOSE/HEMICELLULOSE,
* CARBOHYDRATE/PROTEINS
PARAM CNRMIC = 8.
*  C/N RATIO OF MICROBIAL BIOMASS
PARAM TCMG = 2.
*  TIME CONSTANT FOR MICROBIAL GROWTH, DAY
PARAM RRMIC = 0.10,  MRGRB=1.
*  MAINTENANCE REQUIREMENT FOR MICROBIAL BIOMASS, KG/KG/DAY
*  MAX RGR FOR  MICROBIAL BIOMASS,    /DAY
PARAM NCH = .04
*  NITROGEN CONTENT OF STABLE ORGANIC MATERIAL
PARAM DMINR = 8.3E-5
*  RELATIVE DECOMPOSITION RATE OF STABLE ORGANIC MATERIAL
*  UNDER OPTIMUM CONDITIONS, DAY**-1

 YG = .25*EFCPR+.75*EFCCH
*  GROWTH EFFICIENCY OF MICROBIAL BIOMASS

*  CALCULATION OF RATE OF NITROGEN IMMOBILIZATION, NITROGEN MINERALIZATION
*  FROM FRESH ORGANIC MATERIAL AND NITROGEN MINERALIZATION FROM STABLE
*  ORGANIC MATERIAL, KG N/HA/DAY

PROCEDURE RNRL,RHMIN=CALNRC(TF,YG)

DO 30 I=1,N
FNOM(I) = FON(I)/(FOM(I)+NOT(FOM(I)))
CNR(I) = FRC*FOM(I)/(FON(I)+ASLT(I)+NOT(FON(I)+ASLT(I)))
CNRF(I) = AMIN1(1.,EXP(-.693*(CNR(I)-25.)/25.))
MF(I) = AFGEN(MFT,AWATER(I)/(STORC(I)*THCKN(I)))
FOMRES(I) = FOM(I)/(IFOM(I)+NOT(IFOM(I)))
RDECR(I) = INSW(FOMRES(I)-FLIGN,RDLIGN,     ...
           INSW(FOMRES(I)-(FLIGN+FCELL),RDCELL,RDCAPR))
LDEC = BIOMN(I)*CNRMIC/FRC*(MRGRB/YG+RRMIC)
DECR(I) = AMIN1(LDEC,FOM(I)*RDECR(I)*TF*CNRF(I)*MF(I))
RNRL(I) = DECR(I)*FNOM(I)
30 RHMIN(I) = NHUM(I)*DMINR*TF*MF(I)


ENDPRO


PROCEDURE DFON,DFOM = CALDFN(RNRL,RNLDR,DRRT)

DO 45 I = 1,N
    DFON(I) = -RNRL(I)+DFFOM(I)*RNLDR
45    DFOM(I) = -DECR(I)+DFFOM(I)*DRRT

ENDPRO

PROCEDURE DHUM = CALDHM(RNRL,RNRLB,RHMIN)

DO 46 I = 1,N
46    DHUM(I) = (FNIMH*(RNRL(I)+RNRLB(I))-RHMIN(I))/NCH*10.
```

```

ENDPRO

PARAM  FNIMH = 0.5
*  FRACTION OF N IN DECOMPOSING OM AND MICROBIOM IMMOBILISED IN THE HUMUS

PROCEDURE DNHUM = CALDNH(RNRL,RNRLB,RHMIN)
DO 47 I = 1,N
47     DNHUM(I) = FNIMH*(RNRL(I)+RNRLB(I))-RHMIN(I)

ENDPRO

*  RATE OF CHANGE IN MICROBIAL BIOMASS IN KG N/HA/DAY           SECT. 5B
*  -------------------------

PROCEDURE DBIOMN,RNRLB,RNAC = CALDBM(DECR,RHMIN,YG)

DO 60 I = 1,N
      CADEC(I) = 0.4*DECR(I)+RHMIN(I)*10.
      CFBMG(I) = INSW(DBIOMN(I),DBIOMN(I)*CNRMIC,...
                 DBIOMN(I)*CNRMIC/YG)
      BIOMXC(I) = AMAX1(CADEC(I)-CFBMG(I),0.5*CADEC(I))/RRMIC
      BIOMXN(I) = (ASLT(I)+BIOMN(I))*CNRMIC
      BIOMX(I) = AMIN1(BIOMXC(I),BIOMXN(I),  ...
                 BIOMN(I)*CNRMIC*(1.+MRGRB))
      DBN(I) = (BIOMX(I)/CNRMIC-BIOMN(I))/TCMG
      DBIOMN(I) = INSW(DBN(I),DBN(I)*DELT*RRMIC,DBN(I))
      RNRLB(I) = -1.*AMIN1(0.,DBIOMN(I))
60      RNAC(I) = AMAX1(0.,DBIOMN(I))

ENDPRO



*  MOVEMENT AND AVAILABILITY OF INORGANIC N IN THE SOIL       SECT. 5C
*  --------------------------

 NBR = RAIN*NCR
*  RATE OF INFLUX OF NITROGEN BY RAIN, KG N/HA/DAY

PARAM NCR = 0.02
*  CONCENTRATION OF NITROGEN IN RAINWATER, KG/MM/HA

*  FERTILIZER APPLICATION DURING THE GROWING PERIOD            SECT. 5D
*  ------------------------

TABLE DISTF(1-10) = 1.,9*0.
*  DISTRIBUTION OF FERTILIZER N OVER SOIL COMPARTMENTS
*  MIMICKING DISKING IN
PARAM NAPDAY = 0., NGIFT = 0.
*  DAY NUMBER OF NITROGEN APPLICATION
*  NITROGEN FERTILIZER APPLICATION RATE, KG N/HA/DAY
 TNGIFT = INTGRL(0.,APFERT)
*  TOTAL SEASONAL NITROGEN FERTILIZER APPLICATION, KG N/HA
 APFERT = FCNSW(TIME-NAPDAY,0.,NGIFT,0.)

*  VOLATILIZATION OF AMMONIA                                   SECT. 5E
*  -------------

 RVOLA=ASLT(1)*(1.-RANO3)/TCV*      ...
       LIMIT(0.,1.,ASLT(1)*(1.-RANO3)/LNH4)*NH4FP
```

```
*  RATE OF VOLATILIZATION OF AMMONIA FROM TOP COMPARTMENT, KG N/HA/DAY
PARAM NH4FP = 1.
*  PARAM TO DESIGNATE TYPE OF FERTILIZER: 1=NH4, 0=NO3
PARAM TCV = 10.,LNH4=2.2
*  TIME CONSTANT FOR AMMONIA VOLATILIZATION, DAYS
*  LIMITING CONCENTRATION FOR AMMONIA VOLATILIZATION
 RANO3 = INTGRL(0.,(1.-RANO3)/TCN)
*  RELATIVE AMOUNT OF NITRATE IN TOTAL INORGANIC N
PARAM TCN = 10.
*  TIME CONSTANT FOR NITRIFICATION, DAYS

*   UPTAKE OF NITROGEN IN THE TRANSPIRATION STREAM             SECT. 5F
*   ----------------------------------------

PROCEDURE TNRT,TNUM,RNUM,SLTFD,SLTF=             ...
              CALLT(AWATF,RWF,TRR,RNAC,NDEM,NDEMST,NBR,K)

 SLTF(1)=NBR
 CONP(1)=NCR
 TNRT = 0.
 TNUM =0.
DO 40 I = 1,N
 CONC(I) = (ASLT(I)+(RWF(I)*CONP(I)-RNAC(I))*DELT)/(WATER(I)+ ...
          RWF(I)*DELT)
 CONP(I+1) = CONC(I)
 SLTF(I+1) = RWF(I+1)*CONC(I)
 RNUM(I) = AMIN1(TRR(I)*CONC(I),ASLT(I)/DELT-RNAC(I))*...
          INSW(-(NDEM+NDEMST),1.,0.)
 TNRT = TNRT+(ASLT(I)-RNAC(I)*DELT)*RTL(I)/THCKN(I)* AWATF(I)
 FERTAP(I) = APFERT*DISTF(I)
40 TNUM = TNUM+RNUM(I)


 SLTFD = SLTF(K)

ENDPRO


*  UPTAKE OF N BY DIFFUSION; RATE OF CHANGE OF SOIL MINERAL N  SECT. 5G
*  ------------------------------------------

PROCEDURE DASLT,TNUDF =CALSLF(RNUM,RNRL,RHMIN,RVOLA,RNUDF,SLTF,AWATF)

 TNUDF=0.
DO 41 I=1,N
 RNUD(I)=RNUDF*(ASLT(I)-RNAC(I)*DELT)/(TNRT+NOT(TNRT))*RTL(I)/...
         THCKN(I)
 RNUDB(I)=AMIN1(RNUD(I),ASLT(I)/DELT-RNUM(I)-RNAC(I))* AWATF(I)
 TNUDF=TNUDF+RNUDB(I)
 RVOL(I)=0.
 IF(I.EQ.1) RVOL(I)=RVOLA
41  DASLT(I)=SLTF(I)-SLTF(I+1)-RNUM(I)-RNUDB(I)-RNAC(I)-RVOL(I)    ...
          +RHMIN(I)+(1.-FNIMH)*(RNRLB(I)+RNRL(I))+FERTAP(I)


ENDPRO


*  STATE VARIABLES AND TOTALS FOR THE WHOLE SOIL PROFILE          SECT. 5H
*  ----------------------------------------

```

```
*  DEFINITION OF STATE VARIABLES FOR VARIOUS COMPARTMENTS

 WATER = INTGRL(IWAT,DWAT,10)
*  AMOUNT OF WATER IN MM
 ASLT = INTGRL(IAS,DASLT,10)
*  AMOUNT OF MINERAL NITROGEN, KG/HA
 FOM = INTGRL(IFOM,DFOM,10)
*  AMOUNT OF FRESH ORGANIC MATTER KG DM/HA
 FON = INTGRL(IFON,DFON,10)
*  AMOUNT OF ORGANIC NITROGEN IN FRESH ORGANIC MATTER KG/HA
 HUM = INTGRL(IHUM,DHUM,10)
*  AMOUNT OF STABLE ORGANIC MATTER, KG DM/HA
 NHUM = INTGRL(INHUM,DNHUM,10)
*  AMOUNT OF ORGANIC NITROGEN IN STABLE ORGANIC MATTER, KG/HA
 BIOMN = INTGRL(IBIOMN,DBIOMN,10)
*  AMOUNT OF NITROGEN IN MICROBIAL BIOMASS, KG/HA


PROCEDURE WTOT,NTOT,TFON,NHUMT,TFOM,HUMT,BIOMNT=SUMPRO(...
                                WATER,ASLT,FON,NHUM,FOM)

 WTOT = 0.
 NTOT = 0.
 TFON = 0.
 TFOM = 0.
 NHUMT = 0.
 HUMT = 0.
 BIOMNT = 0.

DO 50 I=1,N
 IF(TDT(I)+0.5.GT.MXRTD) GOTO 50
 WTOT=WTOT+WATER(I)
*  TOTAL AMOUNT OF WATER IN THE PROFILE, MM
 NTOT=NTOT+ASLT(I)
*  TOTAL AMOUNT OF INORGANIC NITROGEN IN THE PROFILE, KG/HA
 TFON =TFON+FON(I)
*  TOTAL NITROGEN IN FRESH ORGANIC MATERIAL IN PROFILE, KG/HA
 NHUMT =NHUMT+NHUM(I)
*  TOTAL NITROGEN IN HUMUS IN PROFILE, KG/HA
 TFOM =TFOM+FOM(I)
*  TOTAL FRESH ORGANIC MATERIAL IN PROFILE, KG/HA
HUMT = HUMT+HUM(I)
*  TOTAL HUMUS IN PROFILE, KG/HA
50   BIOMNT = BIOMNT+BIOMN(I)
*  TOTAL NITROGEN IN MICROBIAL BIOMASS, KG/HA


ENDPRO


* ===========  SECTION 6  ================================================
*          SOIL TEMPERATURE
*          --------

 TS = 0.1*INTGRL(TSI,(TMPC-DTMPA)/DELT)
*  SOIL TEMPERATURE, RUNNING TEN-DAY AVERAGE OF AIR TEMPERATURE
 DTMPA = DELAY(20,10.,TMPC)+INSW(TIME-10.,0.1*TSI,0.)
*  AIR TEMPERATURE TEN TIME INTERVALS AGO
 TF = AFGEN(TFT,TS)
*  INFLUENCE OF SOIL TEMPERATURE ON DECOMPOSITION OF ORGANIC MATERIAL
```

```
FUNCTION TFT = 0.,0.001,5.,0.15,10.,.3,20.,.64,30.,.81,...
         40.,0.96,50.,1.
 TEC = AFGEN(TECT,TS)
*  INFLUENCE OF SOIL TEMPERATURE ON ROOT CONDUCTIVITY
FUNCTION TECT = 0.,0.06,3.,0.29,10.,0.85,16.,0.94,18.,1.,22.,1.,...
          31.,0.87,40.,0.6,50.,0.3


* ================ SECTION 7 ========================================
*                TRANSPIRATION
*                -------

*  POTENTIAL TRANSPIRATION                                     SECT. 7A
*  ------------

 CROPHT = AFGEN(CROHTB,DVS)
FUNCTION CROHTB = 0.,0.05,  0.5,1., 1.1,1.

PROCEDURE APTRAN,RA,RTURB,PCTRAN,VPAM,SVPAM,...
          ELWR,ALPHA,HRAD,SC,S,CC1,RS...
                      =PTRPRO(GRAI,DAYL,PDTGAS,...
          RFNS,CROPHT,EVAP,EAVT,FRNV,FNMX,FNMN)
 SVPAM =6.11*EXP(17.4*EAVT/(EAVT+239.))
*  ''EFFECTIVE'' SATURATED VAPOUR PRESSURE, MBAR
 VPAM  =AMIN1(SVPAM-0.1,INSW(VPASW,6.11*EXP(17.4*DPT14/...
        (DPT14+239.)),1.33*VPA))
*  ACTUAL VAPOUR PRESSURE IN DAYTIME
 WSA = 1.333E5*AFGEN(WSTB,DAYNR)
 RTURB = 0.
 IF(GRAI.LE.0.) GOTO 107
 LMIX = SQRT(4.*0.02*CROPHT/(PI*GRAI))
 ALPH = SQRT(DRAGC*GRAI*CROPHT/(2.*LMIX*IW))
 D = CROPHT-SQRT(LMIX*IW*CROPHT/ALPH)/KARMAN
 ZNOT = (CROPHT-D)*EXP(-CROPHT/(ALPH*(CROPHT-D)))
 LNREF = ALOG((REFHT-D)/ZNOT)
 REST = .74*LNREF*LNREF/(KARMAN*KARMAN*1.1574E-7*WSA)
 RTURB = REST/(864.E4)
107 CONTINUE
PARAM DRAGC = 0.2,KARMAN = .4,IW=.5,REFHT = 2.
 RA = 4.41E-3*SQRT(1./WSA)+RTURB*GRAI
PARAM RHOCP =12.4
 ELWR  =STBC*(EAVT+273.)**4*(0.58-0.09*SQRT(VPA))*        ...
 (1.0-0.9*LFOV)*DAYL/24.
 HNOT  =0.75*DTR-ELWR
 SLOPE =17.4*SVPAM*(1.-EAVT/(EAVT+239.))/(EAVT+239.)

 HRAD=(DTR/CONVER)/DAYL

 ALPHA = TWOVAR(ALPHAT,HRAD,LAI)

FUNCTION ALPHAT,0. = 0.,1.,   100.,1.
FUNCTION ALPHAT,0.2=0.,1.,   100.,1.
FUNCTION ALPHAT,2.0=0.,0.,10.,0.6,15.,.66,20.,.715,25.,.76,30.,.795,...
 35.,.835,40.,.87,45.,.91,50.,.94,60.,.97,100.,1.
FUNCTION ALPHAT,3.5=0.,0.,10.,.425,15.,.515,20.,.585,25.,.64,30.,.68,...
 35.,.715,40.,.745,45.,.77,50.,.795,60.,.845,100.,.875
FUNCTION ALPHAT,5.0=0.,0.,10.,.39,15.,.455,20.,.505,25.,.545,30.,.58,...
 35.,.61,40.,.635,45.,.66,50.,.685,60.,.74,100.,.775
FUNCTION ALPHAT,10.0=0.,0.,10.,.35,15.,.41,20.,.45,25.,.485,30.,.51,...
 35.,.53,40.,.55,45.,.565,50.,.585,60.,.61,100.,.65
```

```



PARAM SCM = 5.4E4
*  MINIMUM STOMATAL CONDUCTANCE , APPLICABLE UNDER OPTIMUM NITROGEN
*  CONDITIONS. SCM IS IN CM/D, VALUE IS EQUIVALENT TO 0.625 CM/S
 SC = SCM * RFNS
*  ACTUAL STOMATAL CONDUCTANCE, AS DETERMINED BY NITROGEN STATUS
*  OF THE VEGETATION
 RS = 1./(SC+NOT(SC))
*  ACTUAL STOMATAL RESISTANCE, APPLIED IN CALCULATION OF POTENTIAL CROP
*  TRANSPIRATION. (/RFNS, TO ACCOUNT FOR EFFECT OF N-DEFICIENCY ON RS
*  ACCORDING TO RADIN AND PARKER,1981)
S = (RA+RS)/RA
CC = 1./(SLOPE+S*PSCH)

PARAM PSCH  =0.67
*  PSYCHROMETRIC CONSTANT, MBAR/DEGREE C

* POTENTIAL CROP TRANSPIRATION IN MM/DAY.
 APTRAN = CC*((1.-EXP(-EXC*GRAI))*HNOT*SLOPE+ALPHA*GRAI*RHOCP...
         /RA*(SVPAM-VPAM)*DAYL/24.)/LHVAP

*  CALCULATION OF POTENTIAL CUTICULAR TRANSPIRATION, APPLIED IN
*  DETERMINING LEAF DEATH DUE TO WATER STRESS

PARAM RC = 1.15E-4 , EXC=0.5
*  CUTICULAR RESISTANCE FOR WATER FLOW, TWENTY TIMES STOMATAL RESISTANCE
*  EXTINCTION COEFFICIENT FOR GLOBAL RADIATION
 S1 = (RA+RC)/RA
 CC1 = 1./(SLOPE+S1*PSCH)
 PCTRAN = APTRAN*CC1/CC
*  POTENTIAL CUTICULAR TRANSPIRATION, UNDER THE ASSUMPTION OF FULLY CLOS
*  STOMATA

ENDPRO

*  ACTUAL TRANSPIRATION                                        SECT. 7B
*  ----------

 PCOND = WRT/WCRR
*  POTENTIAL CONDUCTIVITY OF THE ROOT SYSTEM, MM/DAY
PARAM WCRR = 200.
*  WEIGHT TO CONDUCTIVITY RATIO OF THE ROOT SYSTEM, ASSUMING AN AVERAGE
*  AGE DISTRIBUTION OF THE ROOT SYSTEM, 200 KG OF ROOT DRY MATTER IS
*  NEEDED PER HECTARE TO TAKE UP 1 MM OF WATER PER DAY

 ACOND = PCOND*TEC
*  ACTUAL CONDUCTIVITY OF THE ROOT SYSTEM, AS INFLUENCED BY SOIL TEMPERA
*  MM/DAY
 TRAN = AMIN1(TRANW,ACOND)
*  ACTUAL RATE OF TRANSPIRATION OF THE VEGETATION, MM/DAY


 RTRDEF = (APTRAN-TRAN)/(APTRAN+NOT(APTRAN))
*  RELATIVE TRANSPIRATION DEFICIT
 TOTRAN=INTGRL(0.,TRAN)
*  TOTAL SEASONAL TRANSPIRATION OF THE VEGETATION, MM

*  CALCULATION OF DEHYDRATION OF THE PLANT DUE TO CUTICULAR TRANSPIRATIO

```

```
 DEHYD = AMAX1(0.,1.E4*(PCTRAN-TRAN)*DELT)
*  DEHYDRATION OF PLANT TISSUE, KG H2O/HA



* ==================== SECTION 8  ======================================
*     PHENOLOGICAL DEVELOPMENT OF THE VEGETATION
*     ---------------------------------------

**PRE-ANTHESIS DEVELOPMENT


 DVSV = INTGRL(0.,DVRV+PUSHD*DVSI/DELT)
*  DEVELOPMENT STAGE IN THE PRE-ANTHESIS PHASE, 0. AT EMERGENCE,
*  1. AT ANTHESIS
 DVRV=CULTP*PUSHDF*AMAX1(0.,0.00094*TMPC-0.00046)...
      *(1.-DVSVF)*ABGDMF*NFD
*  RATE OF DEVELOPMENT IN THE PRE-ANTHESIS PHASE, DAY**-1
 NFD = INSW(DVSV-DVSFE, NFDEV+(1.-NFDEV)*RFNS, 1.)
*  EFFECT OF N DEFICIENCY ON DEVELOPMENT UP TO END OF FLOWER INITIATION
PARAM  NFDEV = 1.
*  MAXIMUM REDUCTION OF DEVELOPMENT RATE DUE TO N DEFICIENCY
PARAM CULTP = 1.
*  PARAMETER TO DEFINE CULTIVAR CHARACTERISTIC VEG PHASE DEVELOPMT RATES
 DVSVP = DELAY(5,DELT,DVSV)
*  DEVELOPMENT STAGE IN PRE-ANTHESIS PHASE, ONE TIME INTERVAL AGO
 ANTHES = INTGRL(0.,DAYNR*AND(DVS-0.5,0.5-DVSP)/DELT)
*  ANTHESIS  DAY
 DVSP = DELAY(5,DELT,DVS)
*  DEVELOPMENT STAGE  ONE TIME INTERVAL AGO

PARAM DVSI =0.  ,DVSTS = 0., DVSSE = 0.22, DVSSPS = 0.24, DVSST = 0.35
PARAM DVSFS = 0.40, DVSPRE = 0.50, DVSSPE = 0.52, DVSFE = 0.60
PARAM DVSAN = 1.00
*  RELEVANT DEVELOPMENT STAGES DURING PRE-ANTHESIS PHASE: AT EMERGENCE,
*  AT START OF TILLERING, AT EAR INITIATION, AT START OF SPIKELET
*  DIFFERENTIATION, AT START OF STEM ELONGATION,AT START OF FLORET FORMA-
*  TION AT END OF TILLERING, AT TERMINATION OF SPIKELET DIFFERENTIATION,
*  AT ANTHESIS, RESPECTIVELY
 DVSPRF = INSW(DVSV-DVSPRE,0.,1.)
*  FACTOR ACCOUNTING FOR END OF TILLERING AND EAR FORMATION
 DVSVF = INSW(DVSV-1.,0.,1.)
*  FACTOR ACCOUNTING FOR END OF PRE-ANTHESIS PHASE


**POST-ANTHESIS DEVELOPMENT


 DVSR = INTGRL(0.,DVRR)
*  DEVELOPMENT STAGE IN THE POST-ANTHESIS PHASE, 0. AT ANTHESIS,
*  1. AT DEAD RIPENESS
 DVRR = CULTM*PUSHDF*(0.000913*TMPC+0.003572)*DVSVF*ABGDMF
*  RATE OF DEVELOPMENT IN THE POST-ANTHESIS PHASE, DAY**-1
PARAM CULTM=1.
*  PARAMETER TO DEFINE CULTIVAR CHARACTERISTIC REPR PHASE DEVELOPMT RATE
PARAM DVSGS = 0.01, DVSSGF = 0.11, DVSEGF = 0.70, DVSDR = 1.00
*  RELEVANT DEVELOPMENT STAGES DURING POST-ANTHESIS PHASE:
*  AT START OF GRAIN SET, AT START OF GRAIN FILLING, AT END OF
*  EFFECTIVE GRAIN FILLING, AT DEAD RIPENESS, RESPECTIVELY
 SGFF = INSW(DVSR-DVSSGF,0.,1.)
*  FACTOR ACCOUNTING FOR START OF GRAIN FILL
```

```
 EGFF = INSW(DVSR-DVSEGF,0.,1.)
*  FACTOR ACCOUNTING FOR END OF GRAIN FILL
 DVS = 0.5 * (DVSV+DVSR)
*  DEVELOPMENT STAGE AS FRACTION OF TOTAL GROWTH CYCLE, USED IN
*  DETERMINATION OF ASSIMILATE PARTITIONING


*  ==================== SECTION  9  ===================================
*      GROWTH OF THE VEGETATION (DRY MATTER PRODUCTION)
*      ------------------------

*  DAILY GROSS CO2 ASSIMILATION                             SECT. 9A
*  -------------

*  PROCEDURE BASED ON GOUDRIAAN AND VAN LAAR (1978)

*  AMAX = LIGHT SATURATED CO2 ASSIMILATION RATE OF INDIVIDUAL LEAVES
*  IN KG CO2/HA LEAF/HOUR
*  EFFE = INITIAL LIGHT USE EFFICIENCY OF ASSIMILATION CURVE

 AMAXN = AMAX1(0.,(725.*EFRNV-2.75)*AFGEN(TMPFT,EAVT))
*  LIGHT SATURATED CO2 ASSIMILATION RATE AS A FUNCTION OF NITROGEN
*  CONCENTRATION IN THE LEAF BLADES

PARAM EFFE  =0.50
PROCEDURE PDTGAS,EDAYL,DAYL,PAMAX,AMAX = PHOTPR(DAYY,LFOV,GRAI,AMAXN)

 AMAX = INSW(AMAXN,PAMAX,AMAXN)

 DEC   =-23.4*COS(PI*(DAYY+10.173)/182.621)
 RAD   =PI/180.
 SSIN  =SIN(RAD*LAT)*SIN(RAD*DEC)
 CCOS  =COS(RAD*LAT)*COS(RAD*DEC)
 DAYL  =12.*(PI+2.*ASIN(SSIN/CCOS))/PI
 EDAYL =12.*(PI+2.*ASIN((-SIN(8.*RAD)+SSIN)/CCOS))/PI
 RADC  =0.5*DGRCL/(EDAYL*3600.)
 RADO  =0.2*RADC

 IF(AMAX.LE.0.001) GOTO 102
 IF(GRAI.LE.0.) GOTO 102

 SLLAE =SIN((90.+DEC-LAT)*RAD)
 X     =0.45*EFFE*RADC/(SLLAE*AMAX)
 P     =ALOG(1.+X)
 P     =P/(P+1.)
 PS    =SLLAE*P*EDAYL*AMAX
 X     =0.55*EFFE*RADC/(AMAX*(5.-SLLAE))
 P     =ALOG(1.+X)
 P     =P/(P+1.)
 DGCC  =PS+(5.-SLLAE)*AMAX*EDAYL*P
 DGCCE =0.95*DGCC+20.5
 X     =RADO*EFFE/(AMAX*5.)
 P     =X/(X+1.)
 DGCO  =5.*AMAX*EDAYL*P
 DGCOE =.9935*DGCO+1.1
 IF(GRAI.LT.5.) GOTO 100
 PDTGAS=(LFOV*DGCOE+(1.-LFOV)*DGCC)*CCO2TS
 GOTO 101
100  CONTINUE
 FINT  =(1.-EXP(-0.8*GRAI))
 C1    =FINT*DGCCE
```

```
 C2    =DAYL*GRAI*AMAX
 O1    =FINT*DGCOE
 O2    =C2
 IF(C1.GT.C2) GOTO 2
 CO    =C1
 C1    =C2
 C2    =CO
2   CONTINUE
 DGCCAE=C2*(1.-EXP(-C1/(C2+NOT(C2))))
 IF(O1.GT.O2) GOTO 3
 OO    =O1
 O1    =O2
 O2    =OO
3   DGCOAE=O2*(1.-EXP(-O1/(O2+NOT(O2))))
 PDTGAS=(LFOV*DGCOAE+(1.-LFOV)*DGCCAE)*CCO2TS
 GOTO 101
102 CONTINUE
 PDTGAS=0.
101 CONTINUE

 PAMAX = AMAX


ENDPRO

PARAM CCO2TS=0.6818
*  CONVERSION FROM CO2 TO CARBOHYDRATES

 DGAS = PDTGAS*TRAN/(APTRAN+NOT(APTRAN))*REDFRL
*  DAILY GROSS CO2 ASSIMILATION, KG CH2O/HA/DAY
 REDFRL = 1.-LIMIT(0.,1.,(RESL-TLRGA)/0.05)
*  REDUCTION FACTOR FOR GROSS ASSIMILATION DUE TO ACCUMULATION
*  OF RESERVE SUBSTANCES
PARAM   TLRGA=0.30
*  THRESHOLD LEVEL OF RESERVES FOR REDUCTION OF GROSS ASSIMILATION

FUNCTION TMPFT = 0.,0.,10.,1.,25.,1.,35.,0.01,50.,0.01
*  FUNCTION RELATING MAXIMUM PHOTOSYNTHETIC CAPACITY TO AVERAGE DAYTIME
*  AIR TEMPERATURE


*  RESPIRATION AND NET CARBOHYDRATE FLOW                           SECT. 9B
*  -------------------

 RMNLVS = WLVS*RMRESL*((FRNV-FNMIN)/RNFAC+1.)*TEF-...
          SFPRD*WLVS/(TVEGM+NOT(TVEGM))
*  RATE OF MAINTENANCE RESPIRATION OF LEAF TISSUE, KG CH2O/HA/DAY
 RMNST = WSTEM*RMRESS*((FRNST-FNMIN)/RNFAC+1.)*TEF       ...
                                - SFPRD*WSTEM/(TVEGM+NOT(TVEGM))
*  RATE OF MAINTENANCE RESPIRATION FOR STEM TISSUE, KG CH2O/HA/DAY
 RMNR = WRT*RMRESR*((FRNR-FNMIN)/RNFAC+1.)*TEF         ...
                                - SFPRD*WRT/(TVEGM+NOT(TVEGM))
*  RATE OF MAINTENANCE RESPIRATION FOR ROOT TISSUE, KG CH2O/HA/DAY
 RMNG = WGR*RMRESG*((FRNG-FNMIN)/RNFAC+1.)*TEF...
                         *LIMIT(0.,1.,3.-3*DVSR)
*  RATE OF MAINTENANCE RESPIRATION FOR GRAIN, KG CH2O/HA/DAY
PARAM RMRESL = 0.011, RMRESS=0.007, RMRESR=0.005, RMRESG=0.011
*  MAINTENANCE REQUIREMENT FACTOR, KG CH2O/KG DM/DAY AT 20 C
 TEF = Q10**(0.1*TMPC-2.0)
*  EFFECT OF TEMPERATURE ON MAINTENANCE RESPIRATION
PARAM Q10 = 2.
```

```
*  Q10-FACTOR FOR MAINTENANCE RESPIRATION

*  GROWTH RESPIRATION

PARAM EFCPR = 0.44, EFCCH = 0.825, EFCPRG=0.69
*  WEIGHT EFFICIENCIES FOR THE FORMATION OF PROTEINS (ASSUMING N AS NO3)
*  CARBOHYDRATES AND GRAIN PROTEINS FROM PRIMARY PHOTOSYNTHATES
*  COMPLEMENTARY FRACTION USED FOR GROWTH RESPIRATION



 FCHNX = DGAS-RMNLVS-RMNG-RMNR-RMNST
 FCHN  = AMAX1(0.,FCHNX)
*  ''NET'' FLOW OF CARBOHYDRATE IN KG CH2O/HA/DAY


*  DRY MATTER ACCUMULATION IN LEAF BLADES                          SECT. 9C
*  ------------------

 WLVS = INTGRL(0.,RCWLVS)
*  DRY WEIGHT OF LEAF BLADES, KG/HA
 RCWLVS = INSW(CRCWLV,AMAX1(-WLVS/DELT,CRCWLV),CRCWLV)
 CRCWLV= GRLVS-DRLVS+PUSHD*WLVSI/DELT
 GRLVS = FCHTLV*(EPVC*EFCPR+(1.-EPVC)*EFCCH)
*  RATE OF INCREASE IN WEIGHT OF LEAF BLADES, KG DM/HA/DAY
 FCHTLV = FTLVS*FCHN*RFSTRS+TRFRS
*  FLOW OF CARBOHYDRATE FOR GROWTH OF LEAF BLADES, KG CH2O/HA/DAY
 FTLVS = AFGEN(FTLVST,DVS)
*  FRACTION OF CURRENT NET ASSIMILATE AVAILABLE FOR GROWTH OF LEAF BLADES
FUNCTION FTLVST = 0.,0.475, .05,.475, .1,.575, .175,.755, .2,.755,...
            .25,.440, .3,.25, .35,.15,  ...
            .4,.12, .45,.06, .5,.0,  1.1,0.
*  FRACTION OF CURRENT ASSIMILATE TO LEAF BLADES, FUNCTION OF DEVELOPMENT
*  STAGE
 WLVSNT = WLVS+NOT(WLVS)
*  INTERMEDIATE VARIABLE USED TO AVOID ZERO DIVISION
 RFSTRS = AMIN1(RFWS,RFNS)
*  REDUCTION FACTOR FOR GROWTH OF LEAF BLADES, DUE TO EITHER WATER OR
*  NITROGEN STRESS
 RFWS = AFGEN(REDWST,RTRDEF)
*  REDUCTION FACTOR FOR GROWTH OF LEAF BLADES, DUE TO WATER STRESS
FUNCTION REDWST = 0.,1.,0.3,1.,0.8,0.,1.1,0.
*  REDUCTION FACTOR FOR GROWTH OF LEAF BLADES DUE TO WATER STRESS
*  AS A FUNCTION OF RELATIVE TRANSPIRATION DEFICIT
 RFNS = AFGEN(RFNST,FNC)
*  REDUCTION FACTOR FOR GROWTH OF LEAF BLADES DUE TO NITROGEN STRESS
FUNCTION RFNST = 0.,0., 0.8,0., 0.95,1., 1.1,1.
*  FUNCTION RELATING REDUCTION IN GROWTH OF LEAF BLADES TO NITROGEN
*  STATUS OF THE BLADES
 SCHFLV = (FTLVS+FTSTE)*FCHN*(1.-RFSTRS)
*  ''SURPLUS'' CARBOHYDRATES ORIGINATING FROM INHIBITION OF GROWTH OF
*  LEAF BLADES, KG/HA
 EPVC = 6.25*ANLV/WLVSNT
*  FRACTION OF PROTEINS IN LEAF BLADE TISSUE, VALUE ONE TIME
*  INTERVAL AGO USED

*  SENESCENCE AND DEATH OF LEAVES                                  SECT. 9D
*  ---------------

*   LEAF DEATH DUE TO WATER SHORTAGE (RDRW),SHADING (RDRL),
*   NITROGEN DEFICIENCY (RDRN), CARBOHYDRATE SHORTAGE(RDRCS),
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*   AND SENESCENCE (PDRLVS).

 RDRW = INSW(DVS-0.5,AMIN1(0.005,DRLVWS/WLVSNT)...
        ,DRLVWS/WLVSNT)
*  RELATIVE DEATH RATE OF LEAF BLADES DUE TO WATER SHORTAGE, DAY**-1
 DRLVWS = AMIN1(WLVS,DEHYD/(1.-FDM-FWDB)*WLVS/(WLVS+...
        0.5*WSTEM+NOT(WLVS)))/TCDDH
*  DEATH RATE OF LEAF BLADES DUE TO DEHYDRATION, KG/HA/DAY
PARAM TCDDH = 6.
*  TIME CONSTANT FOR DEATH OF PLANT TISSUE DUE TO WATER SHORTAGE
 FDM = AFGEN(FDMT,DVS)
*  FRACTION DRY MATTER IN PLANT TISSUE
FUNCTION FDMT = 0.,0.1, 1.,0.25,1.1,.25
*  CONCENTRATION OF DRY MATTER IN PLANT MATERIAL
PARAM FWDB = 0.1
*  FRACTION WATER IN DYING TISSUE

 RDRL = LIMIT(0.,MRDRSH,(LAI-LAILM)*MRDRSH/LAILM)
PARAM   MRDRSH=0.03,   LAILM=4.
*  MAX DEATH RATE DUE TO SHADING & THRESHOLD LAI FOR SHADING  EFFECT.
*  VALUES DERIVED FROM PUCKRIDGE & DONALD (1967)

*  RDRN - REL DEATH RT DUE TO N DEFICIENCY DEFINED IN SECTION 12A

 RDRCS = -MXRDR*AMIN1(0.,FCHNX/((DGAS-FCHNX)+NOT(DGAS-FCHNX)))
*   RELATIVE DEATH RATE OF LEAVES DUE TO CARBOHYDRATE SHORTAGE
PARAM   MXRDR = 0.3
 DRQ = RDR*WLVS+RWLLDT
 RWLLDT = AMIN1(WLVS/4.,DRNT*LWDTL)
*  RATE OF LOSS OF WEIGHT OF LEAF BLADES THROUGH DYING TILLERS, KG DM/HA
 DRLVS = AMAX1(0.,DRQ-DRQR,PDRLVS)
*  DEATH RATE OF LEAVES DUE TO ALL CAUSES ,    KG DM /HA/D
 RDR = AMAX1(RDRW,RDRL,RDRN,RDRCS)
*  RELATIVE DEATH RATE OF LEAVES,      /DAY
 RDRD = PDRLVS/WLVSNT
*  RELATIVE DEATH RATE OF LEAVES DUE TO AGEING,      /DAY

*  PROCEDURE TO CALCULATE LEAF DEATH DUE TO AGEING (PDRLVS) AS A FUNCTION
*  OF ACCUMULATED LEAF TEMPERATURE(ALFT) IN DAILY LEAF WEIGHT INCREMENTS
*  (LEAFW).   ALSO STORES APPROPRIATE LEAF AREA RATIO (LEAFA) AND
*  CALCULATES LEAF AREA REDUCTION(RDLFA)
 LEAFW = INTGRL(0.,DLEAF,110)
 ALFT  = INTGRL(0.,DALFT,110)
 LEAFA = INTGRL(0.,DLA,110)
PARAM AVLTLF = 50.
*  AVERAGE LIFE SPAN OF THE LEAVES AT 15 DEG C AVERAGE TEMP, DAYS

PROCEDURE DLEAF,DALFT,DLA,PDRLVS,RDLFA,DRQR=LEAFSN(GRLVS,TMPC,...
                                       PUSHD, FLFAR,DRQ,AVLTLF)
 PDRLVS = 0.
 RDLFA = 0.
 DRQR = 0.
 DO 2000 I=1,110
 DLEAF(I) = 0.
 DALFT(I) = 0.
2000  DLA(I) = 0.
 IF(GRLVS.LE.0..AND.PUSHD.EQ.0.)GO TO 2001
 LG = LG+1
 IF(LG.GT.110)LG=110
 DLEAF(LG) = GRLVS
 DLA(LG) = FLFAR
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 IF(PUSHD.EQ.0.)GO TO 2001
 DLEAF(1) = WLVSI/DELT
 DLA(1) = FLFARI/DELT
2001  CONTINUE
 IF(LG.EQ.0.)GO TO 2005
 DO 2002 I=1,LG
 DALFT(I) = TMPC
 IF(ALFT(I).LT.(15.0*AVLTLF))GO TO 2002
 DLEAF(I) = -LEAFW(I)/DELT
 PDRLVS = PDRLVS+LEAFW(I)/DELT
 RDLFA = RDLFA+LEAFW(I)*LEAFA(I)/DELT
2002  CONTINUE
 IF(PDRLVS.GE.DRQ)GO TO 2005
 RDLFA = 0.
 DRQX = DRQ
 DO 2003 I=1,LG
 LFD = LEAFW(I)/DELT
 IF(I.EQ.LG)LFD=LFD+GRLVS
 DLEAF(I) = AMIN1(LFD,DRQX)
 RDLFA = RDLFA+DLEAF(I)*LEAFA(I)
 DLEAF(I) = -DLEAF(I)
 DRQX = DRQX - LFD
 IF(I.NE.LG)GO TO 2004
 IF(DRQX.GT.0.)DRQR=DRQX
2004  IF(DRQX.LE.0.)GO TO 2005
2003  CONTINUE
2005  CONTINUE
ENDPROC



*  DRY MATTER ACCUMULATION IN LEAF SHEATHS AND STEMS          SECT. 9E
*  --------------------------

 WSTEM = INTGRL(0.,RCWST)
 CRCWST= GRRSTE-DRSTE-RWLSDT
 RCWST = INSW(CRCWST,AMAX1(-WSTEM/DELT,CRCWST),CRCWST)
*  WEIGHT OF STEM AND SHEATHS, KG DM/HA
 GRRSTE = FCHST*(FPST*EFCPR+(1.-FPST)*EFCCH)
*  RATE OF WEIGHT INCREASE OF THE STEM KG DM/HA/DAY
 FCHST = FTSTE*FCHN*RFSTRS
*  FLOW OF CARBOHYDRATES AVAILABLE FOR GROWTH OF STEM AND SHEATHS
*  LIMITED BY WATER & N STRESS WHEN LEAF GROWTH DOMINANT KG CH2O/HA/DAY
 FTSTE = AFGEN(FTSTET,DVS)
*  FRACTION OF CURRENT ASSIMILATE ALLOCATED TO STEM/SHEATHS, FUNCTION
*  OF DEVELOPMENT STAGE
FUNCTION FTSTET = 0.,0.,  .175,.0, .2,.045,...
             .25,.400, .3,.600, .35,.68,...
             .4,.65, .45,.60, .5,.45, .55,.19, .6,0., 1.1,0.
 WSTEMN = WSTEM+NOT(WSTEM)
*  INTERMEDIATE VARIABLE TO AVOID ZERO DIVISION
 FPST = 6.25*ANSTE/WSTEMN
*  FRACTION PROTEIN IN STEM/SHEATHS TISSUE, VALUE ONE TIME
*  INTERVAL AGO BEING USED
 DRSTE = RDRS*WSTEM
*  DEATH RATE OF STEM/SHEATH TISSUE, KG DM/HA/DAY
 RDRS = INSW(-DRLVS,RFST*RDR,RDRCS)
*  RELATIVE DEATH RATE OF STEM TISSUE, DUE TO EITHER WATER
*  SHORTAGE, NITROGEN DEFICIENCY, SENESCENCE OR CBHYDRATE EXHAUSTION
 RDRWS = DRSWS/WSTEMN
*  RELATIVE DEATH RATE OF STEM TISSUE DUE TO WATER SHORTAGE
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 DRSWS = AMIN1(WSTEM/DELT,DEHYD/(1.-FDM-FWDB)*0.5*WSTEM/...
        (WLVS+0.5*WSTEM+NOT(0.5*WSTEM+WLVS))/TCDDH)
*  DEATH RATE OF STEM TISSUE DUE TO DEHYDRATION, KG/HA/DAY
PARAM RFST = 0.60
*  STEM  DEATH LAG PARAMETER
 RWLSDT = AMIN1(DRNT*SWDTL,WSTEM/DELT-DRSTE)
*  RATE OF LOSS OF STEM WEIGHT THROUGH DYING TILLERS, KG DM/HA/DAY


*  DRY MATTER ACCUMULATION IN THE ROOT                              SECT. 9F
*  ------------------

 WRT = INTGRL(0.,RCWRT)
 CRCWR1 = GRRT-DRRT+WRTI*PUSHD/DELT
 CRCWRT=INSW(PUSHD-0.5,INSW(-(WSTEM/DELT+RCWST+WLVS/DELT+RCWLVS)...
          ,CRCWR1,-WRT/DELT),CRCWR1)
 RCWRT = INSW(CRCWRT,AMAX1(-WRT/DELT,CRCWRT),CRCWRT)
*  WEIGHT OF THE ROOT SYSTEM, KG DM/HA
 GRRT = FCHTR*(FPRT*EFCPR+(1.-FPRT)*EFCCH)
*  RATE OF INCREASE IN WEIGHT OF ROOT SYSTEM, KG DM/HA/DAY
 FCHTR = FDSR*FCHN+SCHFLV*FSCHG
*  FLOW OF CARBOHYDRATES AVAILABLE FOR GROWTH OF ROOT SYSTEM
*  KG CH2O/HA/DAY
PARAM  FSCHG = 0.8
*  FRACTION OF SURPLUS CARBOHYDRATE FLOW DIVERTED TO ROOT GROWTH
 FDSR  =AFGEN(FDSRT,DVS)
*  FRACTION OF CURRENT ASSIMILATE DIVERTED TO ROOT SYSTEM
*  UNDER OPTIMUM CONDITIONS
FUNCTION FDSRT = 0.,.5, .05,.5, .1,.4, .175,.22, .2,.175,...
          .25,.135, .3,.1, .35,.075,...
          .4,.05, .45,.03, .5,.02, .55,.01, .6,0., 1.1,0.
*  FUNCTION RELATING PARTITIONING FACTOR BETWEEN SHOOT AND ROOT
*  TO DEVELOPMENT STAGE ( BASIC DATA FROM JONKER,1966)
 FPRT = 6.25*ANRT/(WRT+NOT(WRT))
*  FRACTION PROTEIN IN THE ROOTS, VALUE ONE TIME INTERVAL AGO BEING USED
 DRRT = WRT*RDRS*RFRT
*  DEATH RATE OF THE ROOTS, KG/HA
PARAM RFRT = 0.8
*  PROPORTIONALITY BETWEEN RELATIVE DEATH RATE OF ROOT AND STEM


*   EXTENSION GROWTH OF ROOT SYSTEM                                 SECT. 9G
*   ----------------

 RTD   =INTGRL(0.,RGRRL+IRTD*PUSHD/DELT)
*  ROOTING DEPTH, MM
 RGRRL =SWPBT*DGRRT*RFRGT*INSW(RTD-MXRTD,1.,0.)...
*(RTF+1-RTF*RFSTRS)*INSW(WLVS-WLVSI,0.,1.)*INSW(-FDSR,1.,0.)
*  RATE OF EXTENSION GROWTH OF ROOT SYSTEM, MM/DAY
PARAM DGRRT =12., MXRTD =1800., IRTD=80.,  RTF=1.
*  EXTENSION RATE OF THE ROOTS UNDER OPTIMUM CONDITIONS,MM/DAY
*  MAXIMUM DEPTH OF ROOTING, MM
*  ROOTING DEPTH AT EMERGENCE, MM
*  FACTOR ACCOUNTING FOR INFLUENCE OF STRESS ON ROOT EXTENSION
 RFRGT =AFGEN(REDTTB,TS)
*  REDUCTION FACTOR FOR EXTENSION RATE, DUE TO SOIL TEMPERATURE
FUNCTION REDTTB=0.,.5,5.,.8,10.,.9,15.,1.,20.,0.97,35.,.97



*  RESERVES                                                         SECT. 9H
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*  ----

 ARESP =INTGRL(0.,RCRES+PUSHD*ARESPI/DELT)
*  AMOUNT OF RESERVES IN THE VEGETATION, KG CH2O/HA
 RCRES =FCHTRS-ARTTG/(CEGR+NOT(CEGR))-TRFRS-CRMR
*  RATE OF CHANGE IN AMOUNT OF RESERVES, KG CH2O/HA/DAY
 FCHTRS = FTRL*FCHN+SCHFLV*(1.-FSCHG)
*  RATE OF INCREASE IN WEIGHT OF RESERVES, KG CH2O/HA/DAY
 ARESPF = INSW(-ARESP,1.,0.)
*  FACTOR TO ACCOUNT FOR PRESENCE OF RESERVES IN VARIOUS PROCESSES
 FN= LIMIT(0.,1.,(FRNV-BN)/(FNMN-BN))
*  EFFECT OF NITROGEN STATUS OF LEAF BLADE TISSUE ON GROWTH RATE
*  OF SHOOT AND PARTITIONING BETWEEN LEAVES AND STEM
 TRFRS = AMAX1(0.,RESL-RESLL)*(WSTEM+WLVS+WRT)/TCTR*...
          INSW(FTLVS-0.10,0.,1.)*INSW(RFSTRS-0.99,0.,1.)
*  RATE OF TRANSLOCATION OF RESERVES TO VEGETATIVE TISSUE, FUNCTION
*  OF RESERVE LEVEL, NITROGEN STATUS OF THE LEAVES AND DEVELOPMENT
*  STAGE OF THE VEGETATION
 RESLL = INSW(DVSV-DVSFE,RESL1,RESL2)
PARAM  RESL1=0.05,  RESL2=0.15
*  LIMITING RESERVE CONCENTRATION FOR TRANSLOCATION TO VEGETATIVE TISSUE
PARAM TCTR = 2.
*  TIME CONSTANT FOR TRANSLOCATION OF RESERVES, DAY
 FTRL = AFGEN(FTRLT,DVS)
FUNCTION FTRLT = 0.,.025,  .2,.025,...
             .25,.025, .3,.050, .35,.095,...
             .4,.18, .45,.31, .5,.53, .55,.80, .6,1., 1.1,1.
*  FRACTION OF CURRENT ASSIMILATE TRANSFERRED TO THE RESERVES
*  FUNCTION OF DEVELOPMENT STAGE OF THE VEGETATION
 SFPRD = 0.5*RNTG*6.25
*  ENERGY GAIN FROM DEGRADATION OF PROTEINS PRIOR TO EXPORT, KG CH2O/HA/D
*  CF. PENNING DE VRIES, 1982
 CRMR = INSW(FCHNX,AMIN1(ARESP/DELT-(ARTTG/(CEGR+NOT(CEGR))+...
        TRFRS),-FCHNX),0.)
*  CONTRIBUTION OF RESERVES TO MAINTENANCE RESPIRATION,  WHEN FCHN 0.
 RESL  =ARESP/(ARESP+WLVS+WRT+WSTEM+NOT(ARESP+WLVS+WRT+...
        WSTEM))
*  RESERVE LEVEL IN THE PLANT( KG/KG)


*  DRY MATTER ACCUMULATION IN THE GRAIN                       SECT. 9I
*  -------------------

 WGR = INTGRL(0.,GRGR)
*  DRY WEIGHT OF THE GRAINS, KG DM/HA
 GRGR =ARTTG - LMR
*  RATE OF INCREASE IN WEIGHT OF THE GRAIN, KG DM/HA/DAY
 CEGR = (FPGC*EFCPRG+(1.-FPGC)*EFCCH)
*  EFFICIENCY OF CONVERSION OF PRIMARY PHOTOSYNTHATES IN GRAIN TISSUE
 FPGC = LIMIT(0.,1.,5.7*ANGR/(WGR+NOT(WGR)))
*  FRACTION OF PROTEINS IN GRAIN DRY WEIGHT, VALUE ONE TIME INTERVAL AGO
 ARTTG = AMIN1(PGRRG,AMAX1(0.,((ARESP-RESRES)/TCTR)*CEGR))
*  ACTUAL RATE OF TRANSLOCATION OF RESERVES TO THE GRAIN, KG DM/HA/DAY
 PGRRG = GRN*PGRIG*(1.-EGFF)*INSW(PUSHN-0.5,...
        (1.-LIMIT(0.,1.,(FRNGL-FRNG)/(FRNGL-FRNGL1))),1.)
*  POTENTIAL GROWTH RATE OF THE GRAINS, KG DM/HA/DAY
PARAM FRNGL = 0.01,FRNGL1 = 0.009
 PGRIG = AFGEN(PGRIGT,TMPC)*PGRIGF*SGFF
PARAM PGRIGF=1.
* PARAMETER TO TEST SENSITIVITY OF POTENTIAL GRAIN GROWTH RATE
*  POTENTIAL GROWTH RATE OF INDIVIDUAL GRAINS, KG DM/GRAIN/DAY
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FUNCTION PGRIGT = 0.,0.,8.,0.,10.,5.E-7,16.,1.35E-6,...
          20.,1.65E-6,25.,1.85E-6,30.,2.E-6,35.,2.E-6
*  POTENTIAL GROWTH RATE OF INDIVIDUAL GRAINS, KG DM/GRAIN/DAY,
*  FUNCTION OF AIR TEMPERATURE
*  DATA BASICALLY FROM SOFIELD ET AL, 1977
 LMR = (ARESPF-1.)*EGFF*LIMIT(0.,RMNG,...
                                    RMNG*(1.-(DVSR-0.4)/(0.7-0.4)))
*  GRAIN WEIGHT  LOSS BEFORE RIPENING  DUE TO MAINT RESP OF GRAIN  (RMNG)
*  WHEN OTHER CARBOHYDRATE SOURCES ARE EXHAUSTED  (ARESP=0)
 RESRES = RESLR*(WSTEM+WLVS+WRT)
*  RESIDUAL LEVEL OF RESERVES, NOT AVAILABLE FOR TRANSLOCATION TO GRAIN
PARAM RESLR = 0.01
*  RESIDUAL RESERVE CONCENTRATION IN THE TISSUE
 OTGW = WGR/(GRN+NOT(GRN))*1.E6
*  WEIGHT OF INDIVIDUAL GRAIN, MG


* ================ SECTION  10 =====================================
*            FORMATION OF PLANT ORGANS
*            ------------

*  TILLER FORMATION                                       SECT. 10A
*  -------

 TLN   =INTGRL(0.,GRNT-DRNT+PUSHD*TLNI/DELT)
*  TILLER NUMBER/HA
PARAM TLNI= 2.6E6
*  INITIAL NUMBER OF TILLERS (= MAIN STEMS)
 GRNT  =(1.-DVSPRF)*AMAX1(0.,(TLNM-TLN)/TCTF*FNC)
*  GROWTH RATE OF NUMBER OF TILLERS NO./HA/DAY
 TCTF  = AFGEN(TCTFT,TMPC)*LIMIT(0.3,1.,0.3+LAI*0.7)
*  TIME CONSTANT FOR TILLER FORMATION, DAY, FUNCTION OF AIR TEMPERATURE
FUNCTION TCTFT = 0.,20.,10.,10.,15.,4.,25.,3.,30.,4.5,50.,10.
*  DATA BASICALLY DERIVED FROM FRIEND, 1966
 TLNM  =(FCHTLV+FCHST+FCHTRS)/(CFTUDM+NOT(CFTUDM))
*  MAXIMUM NUMBER OF TILLERS, FUNCTION OF ASSIMILATE AVAILABILITY
 CFTUDM= CHFTB*DVRV/(DVSPRE-DVSTS)
*  CARBOHYDRATE FLOW REQUIRED TO MAINTAIN TILLER PER UNIT DEVELOPMENT
PARAM CHFTB = 7.0E-4
*  BASIC CARBOHYDRATE REQUIREMENT FOR TILLER FORMATION, STANDARD VALUE
 TLNIXX = TLNIX+NOT(TLNIX)
*  AUXILIARY VARIABLE USED TO AVOID ZERO DIVISION
 DRNT  =RDRT*DTLN*(1.-DTLN/(TNNR+NOT(TNNR)))
*  DEATH RATE OF NON-REPRODUCTIVE TILLERS
 DTLN = INTGRL(0.,PUSHT*(TLN-EARN)*0.01+DRNT)
*  TOTAL NUMBER OF DEAD TILLERS
 AWTL=(WLVS+WSTEM)/(TLN+NOT(TLN))
*  AVERAGE WEIGHT PER TILLER, KG
 TNNR  = INTGRL(0.,PUSHT*(TLN-EARN))
* TOTAL NUMBER OF NON-EARBEARING TILLERS  AT DVSPRE
 PUSHT = AND(DVSV-DVSPRE,DVSPRE-DVSVP)
*  PUSHT =1  AT END OF EAR FORMING PHASE, 0 OTHERWISE
 LWDTL = INTGRL(0.,PUSHT*WLVS/(TLN+NOT(TLN)))
*  LEAF WEIGHT OF AVERAGE NON-REPRODUCTIVE TILLER, KG
 SWDTL = INTGRL(0.,PUSHT*WSTEM/(TLN+NOT(TLN)))
*  STEM WEIGHT OF AVERAGE NON-EARBEARING TILLER, KG
PARAM RDRT = 0.2
*  RELATIVE DEATH RATE OF NON-EARBEARING TILLERS, DAY**-1


*  EAR FORMATION                                          SECT. 10B
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* ------

 EARN  =INTGRL(0.,REARF+PUSHE*TLNI)
*  TOTAL EARS, NO/HA
*  RATE OF EAR INITIATION, NO/HA/DAY
 REARF = INSW(DVSV-DVSSE,0.,(1.-DVSPRF)*REARF1)
 REARF1 = AMAX1(0.,(MXNE-EARN)/TCEF)*(1.-PUSHE)
 MXNE = LIMIT(0.,TLN,ALTN)
 ALTN = (FCHTLV+FCHST+FCHTRS)/(CFEUDM+NOT(CFEUDM))
 PUSHE = AND(DVSSE-DVSVP,DVSV-DVSSE)
*  MAXIMUM NUMBER OF EARS, FUNCTION OF ASSIMILATE AVAILABILITY
 TCEF = EB+AMAX1(0.,(TLN/TLNIXX-1.)*(STCEF-EB))
PARAM STCEF  =6.,   EB=3.
*  TIME CONSTANT FOR EAR INITIATION, DAYS
 CFEUDM = CHFEB*DVRV/(DVSPRE-DVSSE)

*  CARBOHYDRATE REQUIREMENT FOR EAR FORMATION PER UNIT DEVELOPMENT
PARAM CHFEB = 1.E-3
*  BASIC CARBOHYDRATE REQUIREMENT FOR EAR FORMATION, STANDARD VALUE


*   SPIKELET FORMATION                                         SECT. 10C
*   ---------

 NSPS = INTGRL(0.,RSPLF)
*  TOTAL SPIKELETS, NO/HA
 RSPLF=INSW(DVSV-DVSSPS,0.,INSW(DVSSPE-DVSV,0.,RSPLF1))
 RSPLF1 = AMAX1(0.,(MXNSP-NSPS)/TCSF)
 MXNSP = LIMIT(0.,EARN*25.,ALSN)
 ALSN  = (FCHTLV+FCHST+FCHTRS)/(CFSUDM+NOT(CFSUDM))
*  MAXIMUM NUMBER OF SPIKELETS, LIMITED BY ASSIMILATE AVAILABILITY

 TCSF = SB+AMAX1(0.,(EARN/TLNIXX-1.)*(STCSF-SB))
PARAM STCSF  =6.,   SB=3.
*  TIME CONSTANT FOR SPIKELET DIFFERENTIATION, DAYS
 CFSUDM = CHFSB*DVRV/(DVSSPE-DVSSPS)
*  CARBOHYDRATE REQUIREMENT FOR SPIKELET FORMATION PER UNIT DEVELOPMENT
PARAM CHFSB = 1.2E-4
*  BASIC CARBOHYDRATE REQUIREMENT FOR SPIKELET FORMATION, STANDARD VALUE


*  FERTILE FLORET FORMATION                                    SECT. 10D
*  ------------

 FFNR  =INTGRL(0.,RFFF)
*  FERTILE FLORETS, NO/HA
*  RATE OF FORMATION OF FERTILE FLORETS, NO/HA/DAY
 RFFF = INSW(DVSV-DVSFS,0.,INSW(DVSFE-DVSV,0.,RFFF1))
 RFFF1 = AMAX1(0.,(MXNFFL-FFNR)/TCFF)
 MXNFFL = LIMIT(0.,NSPS*4,ALFN)
 ALFN =(FCHTLV+FCHST+FCHTRS)/(CFFUDM+NOT(CFFUDM))
*  MAXIMUM NUMBER OF FERTILE FLORETS, LIMITED BY ASSIMILATE AVAILABILITY
 TCFF =FB+AMAX1(0.,(NSPS/TLNIXX-5.)*(STCFF-FB)/20.)
PARAM STCFF = 6.,   FB=3.
*  TIME CONSTANT FOR THE FORMATION OF FLORETS, DAYS
 CFFUDM = CHFFB*DVRV/(DVSFE-DVSFS)
*  CARBOHYDRATE REQUIREMENT FOR FLORET FORMATION PER UNIT
*  DEVELOPMENT
PARAM CHFFB = 4.5E-5
*  BASIC CARBOHYDRATE REQUIREMENT FOR FLORET FORMATION,
*  KG CH2O/FLORET/DAY, STANDARD VALUE
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*  GRAIN FORMATION                                                 SECT. 10E
*  --------


 GRN = INTGRL(0.,RGRN)
*  FILLED GRAINS, NO./HA
 RGRN = INSW(DVSR-DVSGS,0.,(1.-SGFF)*(FFNR-GRN)/TCGF*RFT)
*  RATE OF GRAIN SET
 TCGF = GB+AMAX1(0.,(FFNR/TLNIXX-10.)*(STCGF-GB)/90.)
PARAM STCGF = 4.,   GB=2.
 RFT = AFGEN(RFTT,MNT)
* EFFECT OF TEMPERATURE ON GRAIN SET
FUNCTION RFTT = 0.,0.,5.,1.,18.,1.,24.,1.,32.,0.,50.,0.
*  BASIC DATA FROM HOSHIKAWA(1960)


*  ================  SECTION   11  ==================================
*                     GREEN AREA
*                     -----

* LEAF AREA DEVELOPMENT                                            SECT. 11A
* ----------


 ARLF = INTGRL(0.,RCLFA)
 CRCLFA= GRLVS*FLFAR-RDLFA+ARLFI*PUSHD/DELT
 RCLFA = INSW(CRCLFA,AMAX1(-ARLF/DELT,CRCLFA),CRCLFA)
*  LEAF AREA OF THE VEGETATION, M**2/HA
 FLFAR = AMAX1(FLFARM,FLFARI-(FLFARI-FLFARM)*DVSV/DVSST)
PARAM FLFARM = 20.,  FLFARI=30.
*  FIRST LEAVES THINNER, LATER LEAVES THICKER.  WHEN DVSV GT DVSST,
*  THEN FLFAR=FLFARM
*  LEAF AREA RATIO , M**2/KG LEAF BLADE WEIGHT. DATA FROM AASE, 1976
*  AND OTHERS
 LAI  =  1.E-4*ARLF*STRESF
*  LEAF AREA INDEX IN M**2/M**2
 GRAI = 1.E-4*(ARLF*STRESF+EAF!-?E=JUT
*  TOTAL GREEN AREA, INCLUDING EARS AND STEMS

*  EFFECT OF WATER STRESS ON LEAF AREA                             SECT. 11B
*----------------


PROCEDURE STRESF = LEAFR(PTRN,PAPTRN)
 STRESF=MAXARR
 IF(PAPTRN.LE.0.)GO TO 268
 STRESF = MAXARR+LIMIT(0.,(1.-MAXARR),(PTRN/PAPTRN-0.1)* ...
                                      (1.-MAXARR)/0.8)
268  CONTINUE
ENDPROC
PARAM   MAXARR=1.0
*   STRESF MIMICS LEAF AREA REDUCTION DUE TO LEAF ROLLING UNDER MOISTURE
*   STRESS. MAX AREA REDUCTION FACTOR (MAXARR) SHOULD BE SET TO AN
*   ESTIMATED +/- 0.6 TO ACTIVATE THIS FUNCTION.

 PTRN = DELAY(5,DELT,TRAN)
 PAPTRN = DELAY(5,DELT,APTRAN)

 ARLFE = INTGRL(0.,GRLVS*FLFAR+ARLFI*PUSHD/DELT)
*  EFFECTIVE LEAF AREA FOR RADIATION INTERCEPTION, INCLUSIVE DEAD LEAVES
 SLWA=(WLVS+ARESP*WLVS/(TVEGM+NOT(TVEGM)))...
      /(ARLF+NOT(ARLF))
```

```
*  SPECIFIC LEAF WEIGHT, KG/M**2

*  PHOTOSYNTHETICALLY ACTIVE AREA OF EARS AND STEMS          SECT. 11C
*  ------------------------

 EARAR = EARN*ARPEAR*AGEF
PARAM ARPEAR = 2.5E-3
*  AREA PER INDIVIDUAL EAR AT MAXIMUM, M**2
 AGEF = AFGEN(AGEFT,DVS)
*  EFFECT OF AGE ON ACTIVE EAR AREA
FUNCTION AGEFT = 0.,0.,0.35,0.,0.4,1.,0.8,1.,0.85,0.,1.1,0.
*  CALCULATED BASICALLY FROM DATA BY STOY, 1965

  STAREA = WSTEM/5000.*CROPHT*MXSTAR
PARAM  MXSTAR = 3.E4
*  MAXIMUM STEM AREA,  M**2/M

* ==================  SECTION 12  ====================================
*             NITROGEN IN THE VEGETATION
*             -------------

*  NITROGEN IN LEAF BLADE TISSUE                             SECT. 12A
*  ---------------

 ANLV   =INTGRL(0.,RCANLV)
*  AMOUNT OF NITROGEN IN LIVE TISSUE OF LEAF BLADES, KG N/HA
 CRCANL   =RNUV-TRNLL+PUSHD*ANLVI/DELT
 RCANLV = INSW(CRCANL,AMAX1(-ANLV/DELT,CRCANL),CRCANL)
*   RATE OF CHANGE OF AMOUNT OF N IN LEAF BLADES,  KG /HA /DAY
 RNUV = RNUVP* NDEM/(NDEM+NDEMST+NOT(NDEM+NDEMST))
*  RATE OF UPTAKE OF NITROGEN BY LEAF BLADE TISSUE, KG N/HA/DAY
 NDEM = INSW(FRNV-FNMX,(ONLV-ANLV)/TCU,0.)*ARESPF
*  NITROGEN DEMAND OF LIVE LEAF BLADE TISSUE, KG N/HA/DAY
 ONLV   =(WLVS+GRLVS*DELT)*FNMX
*   MAXIMUM AMOUNT OF NITROGEN IN LEAF BLADE TISSUE, KG/HA
 FNMX = FNMXR+SONCT*FNMXA
*  MAXIMUM FRACTION OF NITROGEN IN LEAF BLADE TISSUE
 SONCT = AMAX1(0.,1.-DVS/((1.+DVSEGF)/2.))
*  SLOPE OF OPTIMUM NITROGEN CONCENTRATION IN TISSUE VS DEV. RATE
 FNMN  = FRNN*FNMX
*  MINIMUM FRACTION OF NITROGEN IN LIVE LEAF BLADE TISSUE
*  FOR TRANSPIRATION
PARAM FRNN = 0.33
*  FRACTION DERIVED FROM DATA BY YOSHIDA & CORONEL FOR RICE
 FNO3 = AFGEN(FNO3T,DVS)
*  FRACTION OF NITRATE IN LEAF BLADE TISSUE UNDER OPTIMUM N-SUPPLY
FUNCTION FNO3T = 0.,.01,.5,.005,1.,.001,1.1,.001
*  FRACTION NO3 IN LEAF BLADES AS FUNCTION OF DEVELOPMENT STAGE

 TRNLL = AMIN1(RNL+RNTLS,ANLV/DELT)
*  TOTAL RATE OF REMOVAL OF N FROM LEAF TISSUE
 RNL = DRLVS*(FRNV-(FRNV-BN)*(1.-RFNS))
*  RATE OF NITROGEN LOSS BY DYING LEAF BLADE TISSUE, KG N/HA/DAY
       RDRN = 0.2*AFGEN(RDRNT,FNC)
FUNCTION RDRNT = 0.,1., 0.65,1., 0.8,0., 1.1,0.
*  RELATIVE DEATH RATE OF LEAF BLADE TISSUE DUE TO N DEFICIENCY, DAY**-1
 RNTLS = RNTG*AVNLV/(AVN+NOT(AVN))
*  RATE OF TRANSFER OF NITROGEN FROM THE LEAVES TO THE GRAIN, KG N/HA/D
 FRNV = ANLV/WLVSNT
*  FRACTION OF NITROGEN IN LIVE LEAF BLADE TISSUE, KG N/KG DM
 EFRNV =INSW(DVSV-DVSAN,FRNV,INSW(NDPAR,FRNV,FRNV*HTFAC))
```

```
*  EFFECTIVE NITROGEN CONCENTRATION FOR ASSIMILATION
*  TAKING INTO ACCOUNT HETEROGENEOUS DISTRIBUTION IN THE PLANT
PARAM NDPAR=-1.,HTFAC=1.
* PARAMETER TO ACTIVATE UNEVEN NITROGEN DISTRIBUTION IN THE CROP
* 1 GIVES EVEN DISTRIBUTION, -1 HETEROGENEOUS
* PARAMETER TO INDICATE DEGREE OF HETEROGENEITY
PARAM TCU   =1.,FNMXA=.06,FNMXR=.01,FNMNA=.04,FNMNR=.0075
*  TIME CONSTANT FOR NITROGEN UPTAKE ( DAY),RANGE IN MAXIMUM FRACTION OF
*  N IN LEAF BLADE TISSUE, ABSOLUTE MINIMUM FRACTION OF N IN LEAF BLADE
 AVNLV = AMAX1(0.,ANLV-WLVS*BN)
*  ''AVAILABLE'' NITROGEN IN THE LEAVES
 BN = AFGEN(BNT,DVS)
*  RESIDUAL LEVEL OF NITROGEN IN LEAF BLADES, NOT TO BE TRANSLOCATED
FUNCTION BNT = 0.,0.015,0.26,0.006,0.555,0.006,0.75,0.0035,1.,0.003,...
         1.1,0.003
*  RESIDUAL LEVEL IN LEAF TISSUE AS FUNCTION OF DEVELOPMENT STAGE
 FNC = LIMIT(0.,1.,(FRNV-BN)/(FNMX-BN))
*  FACTOR TO ACCOUNT FOR NITROGEN SHORTAGE ON TILLER FORMATION
*  AND LEAF BLADE GROWTH


*  NITROGEN IN LIVE STEM AND SHEATH TISSUE                     SECT. 12B
*  ----------------------

 ANSTE = INTGRL(0.,RCANST)
 CRCANS = RNUST-TRNLS+TNLST-ANGRI
 RCANST = INSW(CRCANS,AMAX1(-ANSTE/DELT,CRCANS),CRCANS)
*  AMOUNT OF NITROGEN IN LIVE STEM AND LEAF SHEATHS, KG N/HA
 RNUST = RNUVP*NDEMST/(NDEM+NDEMST+NOT(NDEM+NDEMST))
*  RATE OF NITROGEN UPTAKE BY STEM AND SHEATHS, KG N/HA/DAY
 NDEMST = INSW(FRNST-OFNST,((WSTEM+GRRSTE*DELT)*OFNST     ...
                    -ANSTE)/TCU,0.)*ARESPF
*  NITROGEN DEMAND OF LIVE STEM AND SHEATH TISSUE, KG N/HA/DAY
 OFNST = FNMNSR+ SONCT*FNMXSA
*  MAXIMUM FRACTION OF NITROGEN IN STEM/SHEATH TISSUE
PARAM FNMXSA = 0.05, FNMNSR = 0.003
*  RANGE IN OPTIMUM NITROGEN CONCENTRATION IN THE STEM
*  LOWEST OPTIMUM NITROGEN CONCENTRATION IN THE STEM
 TNLST = AMIN1(PTNLST,RNL-DRLVS*BN)
*  RATE OF TRANSLOCATION OF NITROGEN FROM LEAF TO STEM
 PTNLST = AMAX1(0.,(WSTEM*OFNST-ANSTE-RNUST*DELT)/TCU)
*  POTENTIAL RATE OF NITROGEN ACCUMULATION IN THE STEM FROM TRANSLOCATION
 TRNLS = AMIN1(ANSTE/DELT,RNLDST+RNLSDT+RNTSS)
*  TOTAL RATE OF NITROGEN LOSS FROM STEM TISSUE
 RNLDST = DRSTE*INSW(WLVS-1.,FRNST,INSW(RDRWDS-RFST*RDRN,LN,FRNST))
*  RATE OF NITROGEN LOSS BY DYING OF STEMS/SHEATHS KG N/HA/DAY
 RDRWDS = AMAX1(RFST*RDRD,RDRWS)
*  RELATIVE DEATH RATE OF STEMS, MAXIMUM OF WATER AND SENESCENCE
 RNLSDT = RWLSDT*LN
*  RATE OF NITROGEN LOSS FROM STEMS/SHEATHS BY DYING TILLERS
 RNTSS = RNTG*AVNSTE/(AVN+NOT(AVN))
*  RATE OF TRANSFER OF NITROGEN FROM STEM/SHEATH TISSUE TO THE GRAINS
 FRNST = ANSTE/WSTEMN
*  FRACTION OF NITROGEN IN STEM/SHEATH TISSUE
 AVNSTE = AMAX1(0.,ANSTE-WSTEM*LN)
*  ''AVAILABLE'' NITROGEN IN THE STEM
 LN = AFGEN(LNT,DVS)
*  RESIDUAL FRACTION OF NITROGEN IN STEM TISSUE, NON-TRANSFERABLE
FUNCTION LNT = 0.,.008,0.26,0.005,0.555,0.003,1.,0.002,1.1,0.002
*  RESIDUAL FRACTION OF NITROGEN IN STEMS AS FUNCTION OF DEVELOPMENT
STAGE
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*  ROOT NITROGEN                                                 SECT. 12C
*  -------

 ANRT  =INTGRL(0.,RCANRT)
*  AMOUNT OF NITROGEN IN ROOT TISSUE, KG N/HA
 CRCANR = RNURT-RNLDR-RNTRS+PUSHD*ANRTI/DELT
 RCANRT = INSW(CRCANR,AMAX1(-ANRT/DELT,CRCANR),CRCANR)
 RNURT = RNU*DNRT/(TNDEM+NOT(TNDEM))
*  RATE OF NITROGEN UPTAKE BY THE ROOTS, KG N/HA/DAY
 DNRT = INSW(FRNR-OFNRT,((WRT+GRRT*DELT)*OFNRT-ANRT)/TCU,0.)...
                                     *ARESPF
*  NITROGEN DEMAND OF ROOT TISSUE, KG N/HA/DAY
 OFNRT =(1.-DVS)*(FNRTMX-FNRTMN)+FNRTMN
*  MAXIMUM FRACTION OF NITROGEN IN ROOT TISSUE
PARAM FNRTMX =0.030,FNRTMN=0.005
 RNTRS = RNTG*AVNRT/(AVN+NOT(AVN))
*  RATE OF TRANSLOCATION OF NITROGEN FROM ROOT TO GRAINS, KG N/HA/DAY
 FRNR  =ANRT/(WRT+NOT(WRT))
*  FRACTION OF NITROGEN IN ROOT TISSUE, KG N/KG DM
 RNLDR  = DRRT * RN
*  LOSS OF NITROGEN DUE TO DYING ROOTS
 AVNRT = AMAX1(0.,ANRT-WRT*RN)
*  ''AVAILABLE'' NITROGEN IN ROOTS
PARAM RN = 0.002
*  RESIDUAL CONCENTRATION OF NITROGEN IN THE ROOT SYSTEM


*  TOTAL NITROGEN DEMAND FOR ABOVE GROUND VEGETATIVE MATERIAL
*  IN RELATION TO UPTAKE

 TNDEM = DNRT+NDEM+NDEMST
*  TOTAL DEMAND FOR NITROGEN OF VEGETATIVE PLANT MATERIAL, KG N/HA/DAY
*  SINCE NITROGEN TO GRAINS IS TRANSLOCATED ONLY, THIS IS
*  THE TOTAL DEMAND OF THE VEGETATION
 PNUDP = AMIN1(TNDEM,TNRT/DELT,MXRUP*TCUD/DELT)
*  POTENTIAL RATE OF UPTAKE OF NITROGEN BY THE VEGETATION, DETERMINED
*  EITHER BY DEMAND, AVAILABILITY OR MAXIMUM UPTAKE RATE KG N/HA/DAY
 RNUDF = INSW(DVS-0.6,AMAX1(0.,(PNUDP-TNUM)*DELT/TCUD),0.)
PARAM   TCUD = 1.5
*  REQUIREMENT FOR NITROGEN UPTAKE BY DIFFUSION, DIFFERENCE BETWEEN
*  POTENTIAL RATE OF UPTAKE AND UPTAKE BY MASS FLOW, KG N/HA/DAY
*  TCUD IS A TIME CONSTANT FOR UPTAKE BY DIFFUSION
 RNU = TNUM+TNUDF
*  ACTUAL RATE OF NITROGEN UPTAKE BY THE VEGETATION, KG N/HA/DAY
*  SUM OF UPTAKE BY MASS FLOW AND DIFFUSION
 RNUVP = RNU-RNURT
*  RATE OF NITROGEN UPTAKE BY ABOVE GROUND VEGETATIVE PLANT MATERIAL
*  KG N/HA/DAY
 MXRUP = UMXR*(1.-EXP(-0.5*(WLVS+WSTEM)/CF))
*  MAXIMUM RATE OF UPTAKE BY THE VEGETATION, KG N/HA/DAY
PARAM UMXR = 6.,CF = 100.
*  ABSOLUTE MAXIMUM RATE OF UPTAKE BY THE VEGETATION,KG N/HA/DAY
*  CF IS A VALUE SET SO AS TO ALLOW THE PLANT TO MAINTAIN FRNV CLOSE TO
*  FNMX, IN THE EARLY STAGES OF GROWTH IF N SUPPLY IS ADEQUATE.



*  NITROGEN IN GRAIN                                             SECT. 12D
*  ---------

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 ANGR  =INTGRL(0.,RNTG+ANGRI)
*  AMOUNT OF NITROGEN IN THE GRAINS, KG N/HA
 PUSHN = AND(DVS-(DVSAN+DVSSGF)/2.,(DVSSGF+DVSAN)/2.-DVSP)
 ANGRI = PUSHN*GRGR*0.035

*  INITIAL AMOUNT OF NITROGEN IN THE GRAIN, KG N/HA
 RNTG = INSW(FRNG-0.035,AMIN1(PRNAGR,RNEXP),0.)*(1.-PUSHN)
*  RATE OF NITROGEN TRANSLOCATION TO THE GRAIN, KG N/HA/DAY
 PRNAGR = GRN * AFGEN(PRNAGT,TMPC)*SGFF
*  POTENTIAL RATE OF NITROGEN ACCUMULATION IN THE GRAIN, KG N/HA/DAY
FUNCTION PRNAGT = 0.,0.,7.,0.,10.,.025E-6,12.5,.034E-6,18.5,.045E-6,...
           27.5,.057E-6,35.,.075E-6
*  POTENTIAL RATE OF NITROGEN ACCUMULATION PER INDIVIDUAL GRAIN AS
*  FUNCTION OF AVERAGE AIR TEMPERATURE ( SOFIELD ET AL., 1977)
 RNEXP = AMAX1(0.,RTORT * AVN * AFGEN(FNEXT,FNVEG))
*  RATE OF NITROGEN EXPORT FROM VEGETATIVE TISSUE, KG N/HA/DAY
 AVN = AVNLV+AVNSTE+AVNRT
*  NITROGEN AVAILABLE FOR TURNOVER, KG N/HA
 RTORT = RRTORT * TEF * EFFWS * INSW(-ARESP,1.,1.2)
*  RELATIVE RATE OF NITROGEN TURNOVER IN VEGETATIVE TISSUE, DAY**-1
*  TURNOVER ASSUMED TO INCREASE AFTER EXHAUSTION OF RESERVES
PARAM RRTORT = 0.25
*  BASIC RELATIVE RATE OF TURNOVER OF NITROGEN IN VEGETATIVE TISSUE, DAY
 EFFWS = INSW(-TRAN,INSW(PCTRAN-TRAN,1.,2.),0.)
*  EFFECT OF MOISTURE STRESS ON RATE OF NITROGEN TURNOVER
*  DERIVED FROM LAL & SHARMA, 1973.
FUNCTION FNEXT = 0.,0.,  0.0025,0.,  0.007,0.15,  0.012,.25,...
          .016,.22, .02,.2, .025,.18, .0375,.12,.07,.08
*  FUNCTION RELATING FRACTION EXPORTED NITROGEN TO AVERAGE NITROGEN
*  CONCENTRATION IN VEGETATIVE TISSUE, DATA ADAPTED FROM DALLING, 1976

 FNVEG = (ANRT+ANSTE+ANLV)/(WRT+WSTEM+WLVS+NOT(WLVS+WRT+WSTEM))
*  AVERAGE FRACTION OF NITROGEN IN VEGETATIVE TISSUE
 FRNG  =ANGR/(WGR+NOT(WGR))
*  FRACTION OF NITROGEN IN THE GRAIN



* ===================  SECTION  13  ====================================
*    WHOLE CANOPY PARAMETERS, VARIABLES AND BALANCES
*    -------------------------------

 TADRW = WLVS+WSTEM+WGR+DSTR+ARESP*(1.-WRT/(TVEGM+NOT(TVEGM)))
*  TOTAL ABOVE GROUND DRY WEIGHT, EXCLUDING ROOT RESERVES,   KG DM/HA
 ABGDMF = INSW(-(WLVS+WSTEM+WGR),1.,0.)
*  FACTOR TO ACCOUNT FOR PRESENCE OF ABOVE GROUND MATERIAL
 TVEGM = WLVS+WSTEM+WRT
*  TOTAL WEIGHT OF VEGETATIVE ORGANS, KG/HA
 TNABM = ANLV+ANSTE+ANGR+NDSTR
*  TOTAL AMOUNT OF NITROGEN IN ABOVE GROUND MATERIAL, KG N/HA
 DSTR = INTGRL(0.,DRLVS+DRSTE+RWLSDT)
*     DSTR = INTGRL(0.,DRLVS+DRSTE+RWLLDT+RWLSDT)
*  TOTAL AMOUNT OF DEAD ABOVE GROUND VEGETATIVE MATERIAL KG DM/HA
 NDSTR = INTGRL(0.,RNL-TNLST+RNLDST+RNLSDT)
*  TOTAL AMOUNT OF NITROGEN IN DEAD ABOVE GROUND VEGETATIVE TISSUE,
*  KG N/HA
 SRR   =(WSTEM+WLVS+WGR+DSTR)/(WRT+NOT(WRT))
*  SHOOT TO ROOT RATIO


*  CARBON BALANCE
```

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 CARBAL = FCHN-FCHTR-FCHTLV-FCHST-ARTTG/...
                                (CEGR+NOT(CEGR))-CRMR-RCRES


*  NITROGEN BALANCE

 TNLCH = INTGRL(0.,SLTFD)
*  TOTAL NITROGEN LOST BY LEACHING, KG N/HA
 INIV = INTGRL(0.,PUSHD*(ANLVI+ANRTI)/DELT)
*  TOTAL INITIAL AMOUNT OF NITROGEN, KG N/HA
 TNVOL = INTGRL(0.,RVOLA)
*  TOTAL NITROGEN LOST BY VOLATILIZATION, KG N/HA

PROCEDURE NBAL = NPRO(NHUMT)
 NBAL = TNINT+TNGIFT+INIV+TRAIN*0.02+FRNF*FOMI+NHUMI+...
       BIOMNI-BIOMNT-NTOT-TFON-TNVOL-NHUMT-ANLV-ANSTE-ANRT-...
       ANGR-NDSTR-TNLCH
ENDPRO

*  NBAL SHOULD BE ZERO AT ANY MOMENT TO ENSURE NO LOSSES


*  ====================  SECTION 14  ==============================
*                  RUN AND OUTPUT CONTROL
*                  -----------

METHOD RECT
TIMER FINTIM=0.,DELT =1.,PRDEL =2.
FINISH WLVS =-1.,DVS =1.


PRINT   DAYNR,DVS,TADRW,WLVS,ARLF,SLWA,GRAI,WRT,RTD,WSTEM,DSTR,...
   WGR,GRN,OTGW,FFNR,NSPS,EARN,TLN,ARESP,RESL,TRFRS,ARTTG,...
   FCHN,AMAXN,PDTGAS,DGAS,APTRAN,TRAN,TOTRAN,EVTOT,TEVAP,...
   WTOT,TRAIN,TDRAIN,NTOT,BIOMNT,TNDEM,RNUV,TNABM,ANLV,ANGR,...
   ANSTE,NDSTR,FRNV,FRNR,FRNG,FN,RMNLVS,RMNST,RMNR,RMNG,...
   CARBAL,NBAL


PROCEDURE     Y=DBG(TIME)
IF(TIME.GE.SDBG1.AND.TIME.LE.EDBG1)CALL DEBUG(3,0.)
IF(TIME.GE.SDBG2.AND.TIME.LE.EDBG2)CALL DEBUG(3,0.)
ENDPROCEDURE
PARAM SDBG1=1., EDBG1=0.
PARAM SDBG2=1., EDBG2=0.
*   SDBG SETS START OF DEBUG CALLS; EDBG SETS END OF DEBUG CALLS
*   TO SUPPRESS DEBUG CALLS, SET SDBG   EDBG

PROCEDURE NCABM,RTADRW,RWLVS,RTABN,RNCBM,RLAI = RECORD(TNABM,TADRW)
 NCABM  = TNABM/(TADRW+NOT(TADRW))
 RTADRW = AFGEN(RTADWT,DAYNR)
 RWLVS  = AFGEN(RWLVST,DAYNR)
 RTABN  = AFGEN(RTABNT,DAYNR)
 RNCBM  = AFGEN(RNCBMT,DAYNR)
 RLAI   = AFGEN(RLAITB,DAYNR)
ENDPRO
FUNCTION RTADWT = 0.,0.,  365.,0.
FUNCTION RWLVST = 0.,0.,  365.,0.
FUNCTION RTABNT = 0.,0.,  365.,0.
FUNCTION RNCBMT = 0.,0.,  365.,0.
```

```
FUNCTION RLAITB = 0.,0.,  365.,0.

TERMINAL

PUSHD=0.
TGERD=0.
TSDAY=0.
LG=0
IF(TIME.EQ.0.) GO TO 9899
*   L IS USED TO MONITOR MULTIPLE PARAMETER RERUNS
IF(L.EQ.0)M=M+1
L=L+1
W(M,1,L)=WGR
W(M,2,L)=TADRW
W(M,3,L)=OTGW
W(M,4,L)=FRNG*1000.
W(M,5,L)=GRN/(EARN+NOT(EARN))
W(M,6,L)=EARN/10000.
W(M,7,L)=TNABM
W(M,8,L)=TOTRAN/(TOTINF+NOT(TOTINF))*100.
W(M,9,L)=WGR/(TOTINF+NOT(TOTINF))
W(M,10,L)=TRAIN
W(M,11,L)=ANTHES
W(M,12,L)=GERDAT
W(M,13,L)=WAV
IF(M.LT.MY)GO TO 9899
IF(L.LT.NP)GO TO 9899
DO 9898 LL=1,L
DO 9891 I=1,13
WRITE(24,110) NAM1(I),NAM2(I),NAM3(I),NAM4(I),(W(M,I,LL),M=1,MY)
**WRITE( 6,111) NAM1(I),NAM2(I),NAM3(I),NAM4(I),(W(M,I,LL),M=1,MY)
9891 CONTINUE
WRITE(24,112)
**WRITE( 6,112)
9898 CONTINUE
M = 0
9899 CONTINUE
IF(L.EQ.NP)L=0
GERDAT=365.
TLNI=TLNIX
WRTI=WRTIX
WLVSI=WLVSIX

110 FORMAT(2X,4A4,2X,'-',1X,21F6.0)
111 FORMAT(2X,4A4,2X,'-',1X,12F7.0)
112 FORMAT(2X,////)
END
STOP
ENDJOB
```

9 Wheat model directory

Acronym	Definition	Units	Variable type	Line no
ABGDMF	Switch variable assuming value 1 if dry matter is present above ground, otherwise 0	unitless	Auxiliary	01929
ACOND	Actual conductivity of the root system	mm d^{-1}	Auxiliary	01017
AEVAP	Potential rate of evaporation from soil surface as limited by canopy cover and moisture content of top soil compartment	mm d^{-1}	Auxiliary	00554
AGEF	Factor accounting for the effect of development stage on green ear area	unitless	Auxiliary	01710
AGEFT	Function describing the relation between development stage and relative green area of ears	–	Function	01712
AG08	Intermediate variable for calculation of dew point temperature at 8.00 hours	unitless	Auxiliary	00380
AG14	Intermediate variable for calculation of dew point temperature at 14.00 hours	unitless	Auxiliary	00388
ALFN	Maximum number of fertile florets that can be maintained by current carbohydrate supply	no ha^{-1}	Auxiliary	01630
ALFT*(I)	Accumulated temperature sum per leaf class	d °C	State	01317
ALPH	Intermediate variable for calculation of turbulent resistance above the crop	unitless	Auxiliary	00940
ALPHA	Proportionality factor for calculation of contribution	unitless	Auxiliary	00957

Acronym	Definition	Units	Variable type	Line no
	of drying power of the air to crop transpiration			
ALPHAT	Functions describing the relation between average hourly radiation intensity and the value of ALPHA for various values of LAI	–	Function till	00959 00968
ALSN	Maximum number of spikelets that can be maintained by current carbohydrate supply	no ha^{-1}	Auxiliary	01609
ALTN	Maximum number of tillers that can be maintained by current carbohydrate supply	no ha^{-1}	Auxiliary	01588
AMAX	Current maximum rate of gross CO_2 assimilation of a single leaf	kg ha^{-1} h^{-1}	Auxiliary	01119
AMAXN	Maximum rate of gross CO_2 assimilation of a single leaf in dependence of nitrogen concentration and temperature	kg ha^{-1} h^{-1}	Auxiliary	01112
ANGR	Weight of nitrogen in the grain	kg ha^{-1}	State	01885
ANGRI	Initial weight of nitrogen in the grain on the first day of grain growth	kg ha^{-1}	Initial state	01888
ANLV	Weight of nitrogen in the leaf blades	kg ha^{-1}	State	01726
ANLVI	Initial weight of nitrogen in the leaf blades at emergence	kg ha^{-1}	Initial state	00258
ANRT	Weight of nitrogen in the roots	kg ha^{-1}	State	01828
ANRTI	Initial weight of nitrogen in the roots at emergence	kg ha^{-1}	Initial state	00269
ANSTE	Weight of nitrogen in stem and leaf sheaths	kg ha^{-1}	State	01787
ANTHES	Anthesis date, julian calendar day	unitless	Output	01057
APFERT	Fertilizer application rate	kg ha^{-1} d^{-1}	Rate	00780

Acronym	Definition	Units	Variable type	Line no
APTRAN	Potential transpiration rate of the crop	mm d^{-1}	Auxiliary	00990
ARESP	Weight of reserve carbohydrates	kg ha^{-1}	State	01460
ARESPF	Factor indicating presence (1) or absence (0) of reserve carbohydrates	unitless	Auxiliary	01466
ARESPI	Initial weight of reserve carbohydrates at emergence	kg ha^{-1}	Initial state	00273
ARLF	Green area of the leaf blades	m^2 ha^{-1}	State	01665
ARLFE	Total area of green and senesced leaf blades	m^2 ha^{-1}	State	01698
ARLFI	Initial green area of leaf blades at emergence	m^2 ha^{-1}	Initial state	00256
ARPEAR	Maximum green area per individual ear	m^2	Parameter	01708
ARTTG	Rate of transfer of reserve carbohydrates from vegetative tissue to the grain	kg ha^{-1} d^{-1}	Rate	01509
ASLT(I)	Amount of mineral N per soil compartment	kg ha^{-1}	State	00853
AVLTLF	Average life span of the leaves, at standard temperature of 15 °C	d	Parameter	01319
AVN	Total amount of nitrogen in vegetative tissue available for translocation to the grain	kg ha^{-1}	Auxiliary	01901
AVNLV	Amount of nitrogen in leaf blades available for translocation to the grain	kg ha^{-1}	Auxiliary	01772
AVNRT	Amount of nitrogen in the roots available for translocation to the grain	kg ha^{-1}	Auxiliary	01846
AVNSTE	Amount of nitrogen in stem+sheaths available for translocation to the grain	kg ha^{-1}	Auxiliary	01817
AVPTB	Actual vapour pressure in the atmosphere as a function of day number	–	Function	00433

Acronym	Definition	Units	Variable type	Line no
AWATER (I)	Available water in a soil compartment	mm	Auxiliary	00604
AWATF(I)	Factor indicating presence (l) or absence (0) of moisture available to a plant in a soil compartment	unitless	Auxiliary	00608
AWTL	Average weight per tiller	kg	Output	01506
BIOMN(I)	Weight of nitrogen in microbial biomass in a soil compartment	kg ha^{-1}	State	00863
BIOMNI	Initial weight of nitrogen in microbial biomass in total soil profile, at start of simulation	kg ha^{-1}	Auxiliary	00204
	Set to zero			00202
BIOMNT	Total weight of nitrogen in microbial biomass in soil profile	kg ha^{-1}	Output	00892
	Set to zero			00876
BIOMX(I)	Maximum weight of carbon in microbial biomass in a soil compartment limited by either nitrogen or carbon availability	kg ha^{-1}	Auxiliary	00749
BIOMXC (I)	Maximum weight of carbon in microbial biomass in a soil compartment limited by carbon availability	kg ha^{-1}	Auxiliary	00747
BIOMXN (I)	Maximum weight of carbon in microbial biomass in a soil compartment limited by nitrogen availability	kg ha^{-1}	Auxiliary	00748
BN	Residual non-remobilizable concentration of nitrogen in leaf blades	kg kg^{-1}	Auxiliary	01774
BNT	Residual non-remobilizable concentration of nitrogen in leaf blades as a function of development stage of the crop	–	Function	01776
CADEC(I)	Rate of carbon release	kg ha^{-1}	Auxiliary	00744

Acronym	Definition	Units	Variable type	Line no
	through decomposition of organic material in a soil compartment	d^{-1}		
CARBAL	Carbon balance, should be zero throughout the simulation	kg ha^{-1}	Output	01947
CC	Intermediate variable in calculation of potential crop transpiration	° C $mbar^{-1}$	Auxiliary	00984
CCOS	Product of cosine of latitude and cosine of declination, used in calculation of daylength	cos^2	Auxiliary	01124
CCO2TS	Conversion factor from CO_2 to reduced sugars	kg kg^{-1}	Parameter	01178
CC1	Intermedidiate variable in calculation of cuticular water loss	°C $mbar^{-1}$	Auxiliary	01000
CEGR	Efficiency of conversion of primary assimilation products in grain dry matter	kg kg^{-1}	Auxiliary	01505
CF	Conversion factor from weight to relative root extension	kg ha^{-1}	Parameter	01875
CFBMG(I)	Rate of release or immobilization of carbon in a soil compartment due to changes in microbial biomass	kg ha^{-1} d^{-1}	Auxiliary	00745
CFEUDM	Current carbohydrate requirement for ear formation	kg ear^{-1} d^{-1}	Auxiliary	01594
CFFUDM	Current carbohydrate requirement for floret formation	kg $floret^{-1}$ d^{-1}	Auxiliary	01635
CFSUDM	Current carbohydrate requirement for spikelet formation	kg $spikelet^{-1}$ d^{-1}	Auxiliary	01615
CFTUDM	Current carbohydrate requirement for tiller formation	kg $tiller^{-1}$ d^{-1}	Auxiliary	01555

Acronym	Definition	Units	Variable type	Line no
CHFEB	Minimum carbohydrate requirement for completion of ear formation	kg ear^{-1}	Parameter	01597
CHFFB	Minimum carbohydrate requirement for completion of fertile floret formation	kg floret^{-1}	Parameter	01638
CHFSB	Minimum carbohydrate requirement for completion of spikelet formation	kg spikelet^{-1}	Parameter	01617
CHFTB	Minimum carbohydrate requirement for completion of tiller formation	kg tiller^{-1}	Parameter	01557
CNR(I)	Carbon to nitrogen ratio of fresh organic material in a soil compartment	kg kg^{-1}	Auxiliary	00699
CNRF(I)	Factor accounting for the effect of C/N ratio of fresh organic material on rate of decomposition in a soil compartment	unitless	Auxiliary	00700
CNRMIC	Carbon to nitrogen ratio of microbial biomass	kg kg^{-1}	Parameter	00675
CONC(I)	Concentration of mineral nitrogen in a soil compartment	kg mm^{-1}	Auxiliary	00809
CONP(I)	Concentration of mineral nitrogen in overlying soil compartment	kg mm^{-1}	Auxiliary	00811
CONVER	Conversion factor for radiation from cal cm^{-2} to J m^{-2}	J m^{-2}/cal cm^{-2}	Parameter	00492
CRCANL	Rate of change in amount of nitrogen in the leaf blades, not corrected	kg ha^{-1} d^{-1}	Auxiliary	01728
CRCANR	Rate of change in amount of nitrogen in the roots, not corrected	kg ha^{-1} d^{-1}	Auxiliary	01830
CRCANS	Rate of change in amount of nitrogen in stem and sheaths, not corrected	kg ha^{-1} d^{-1}	Auxiliary	01788
CRCLFA	Rate of change in leaf area, not corrected	m^2 ha^{-1} d^{-1}	Auxiliary	01666

Acronym	Definition	Units	Variable type	Line no
CRCWLV	Rate of change in weight of the leaf blades, not corrected	kg ha^{-1} d^{-1}	Auxiliary	01236
CRCWRT	Rate of change in weight of the roots, not corrected	kg ha^{-1} d^{-1}	Auxiliary	01411
CRCWR1	Auxiliary variable in calculation of rate of change in weight of the roots	kg ha^{-1} d^{-1}	Auxiliary	01410
CRCWST	Rate of change in weight of stem and sheaths, not corrected	kg ha^{-1} d^{-1}	Auxiliary	01371
CRMR	Rate of consumption of reserves for maintenance respiration	kg ha^{-1} d^{-1}	Auxiliary	01490
CROHTB	Height of the crop as a function of development stage of the crop	–	Function	00925
CROPHT	Height of the crop	m	Auxiliary	00924
CTEMPF	Maximum effect of evaporative cooling on canopy temperature	°C	Parameter	00420
CULTM	Cultivar-specific factor to account for differences in post-anthesis development rate	unitless	Parameter	01084
CULTP	Cultivar-specific factor to account for differences in pre-anthesis development rate	unitless	Parameter	01053
C0	Intermediate variable in calculation of canopy gross CO_2 assimilation	kg ha^{-1} d^{-1}	Auxiliary	01157
C1	Intermediate variable in calculation of canopy gross CO_2 assimilation	kg ha^{-1} d^{-1}	Auxiliary	01152
C2	Intermediate variable in calculation of canopy gross CO_2 assimilation	kg ha^{-1} d^{-1}	Auxiliary	01153
D	Zero plane displacement, used in calculation of turbulent resistance	m	Auxiliary	00941
DALFT(I)	Rate of change in cumula-	°C	Rate	01342

Acronym	Definition	Units	Variable type	Line no
	tive temperature sum per leaf class			
DASLT(I)	Rate of change in amount of mineral N per soil compartment	kg ha^{-1} d^{-1}	Rate	00838
DAYL	Astronomical daylength	h	Auxiliary	01125
DAYNR	Day number in weather tables and tables of observed data	unitless	Auxiliary	00293
DAYNRO	Day number in weather tables and tables of observed data at start of the simulation	unitless	Auxiliary	00279
DAYY	Day number in Julian calendar	unitless	Auxiliary	00288
DAYYSL	Equivalent day number on southern hemisphere	unitless	Auxiliary	00291
DBIOMN (I)	Rate of change in nitrogen in microbial tissue in a soil compartment	kg ha^{-1} d^{-1}	Rate	00752
DBN(I)	Rate of change in nitrogen in microbial tissue in a soil compartment, not corrected	kg ha^{-1} d^{-1}	Auxiliary	00751
DBT08	Dry bulb temperature at 8.00 hours	°C	Forcing	00356
DBT08T	Dry bulb temperature at 8.00 hours as a function of day number	–	Function	00358
DBT14	Dry bulb temperature at 14.00 hours	°C	Forcing	00366
DBT14T	Dry bulb temperature at 14.00 hours as a function of day number	–	Function	00368
DEC	Declination of the sun	degrees	Auxiliary	01121
DECR(I)	Rate of decomposition of fresh organic material in a soil compartment	kg ha^{-1} d^{-1}	Rate	00706
DEHYD	Rate of dehydration of plant tissue, difference between cuticular water loss and water uptake	kg ha^{-1} d^{-1}	Auxiliary	01031

Acronym	Definition	Units	Variable type	Line no
DELT	Time step of integration, 1 day in model	d	System	01918
DELTA	Slope of the saturated vapour pressure curve at air temperature	mm Hg °C^{-1}	Auxiliary	00541
DEWSW	Variable to indicate type of input data on atmospheric humidity: if −1 dry and wet bulb temperatures, if +1 dew point temperatures	unitless	Parameter	00395
DFFOM(I)	Distribution factor for fresh and stable organic material in soil profile	unitless	Table	00222
DFOM(I)	Rate of change in amount of fresh organic material in a soil compartment	kg ha^{-1} d^{-1}	Rate	00718
DFON(I)	Rate of change in amount of nitrogen in fresh organic material in a soil compartment	kg ha^{-1} d^{-1}	Rate	00717
DGAS	Rate of canopy gross assimilation in CH_2O	kg ha^{-1} d^{-1}	Auxiliary	01181
DGCC	Daily rate of gross CO_2 assimilation of a closed canopy under a clear sky	kg ha^{-1} d^{-1}	Auxiliary	01141
DGCCAE	Daily rate of gross CO_2 assimilation of the canopy under a clear sky	kg ha^{-1} d^{-1}	Auxiliary	01161
DGCCE	Estimated daily gross CO_2 assimilation of a closed canopy under a clear sky	kg ha^{-1} d^{-1}	Auxiliary	01142
DGCO	Daily rate of gross CO_2 assimilation of a closed canopy under an overcast sky	kg ha^{-1} d^{-1}	Auxiliary	01145
DGCOAE	Daily rate of gross CO_2 assimilation of the canopy under an overcast sky	kg ha^{-1} d^{-1}	Auxiliary	01166
DGCOE	Estimated daily gross CO_2 assimilation of the canopy under an overcast sky	kg ha^{-1} d^{-1}	Auxiliary	01146

Acronym	Definition	Units	Variable type	Line no
DGRCL	Daily total global radiation under a clear sky	J m^{-2} d^{-1}	Forcing	00490
DGROV	Daily total global radiation under an overcast sky	J m^{-2} d^{-1}	Forcing	00494
DGRRT	Maximum rate of root extension under optimum conditions	mm d^{-1}	Parameter	01446
DHUM(I)	Rate of change in amount of stable organic material in a soil compartment	kg ha^{-1} d^{-1}	Rate	00725
DIMSW	Variable to convert atmospheric humidity from mbar to mm Hg if AVPTB is given in mbar	mm Hg $mbar^{-1}$	Parameter	00435
DLA(I)	Specific leaf area of leaves in class I	m^2 kg^{-1} d^{-1}	Auxiliary	01330
	Zero setting of array			01330
DLA(LG)	Specific leaf area of leaves grown LG days after emergence	m^2 kg^{-1} d^{-1}	Auxiliary	01335
DLA(1)	Specific leaf area at emergence	m^2 kg^{-1} d^{-1}	Auxiliary	01338
DLEAF(I)	Rate of change of leaf weight in class I, used in procedure, redefined several times	kg ha^{-1} d^{-1}	Auxiliary	01356
DLEAF (LG)	Initial weight of LGth leaf increment	kg ha^{-1} d^{-1}	Auxiliary	01334
DLEAF(1)	Weight of leaf blades at emergence	kg ha^{-1} d^{-1}	Auxiliary	01337
DMINR	Relative rate of decomposition of stable organic material under optimum conditions	d^{-1}	Parameter	00684
DNHUM (I)	Rate of change in amount of nitrogen in stable organic material in a soil compartment	kg ha^{-1} d^{-1}	Rate	00734
DNRT	Nitrogen demand of the roots	kg ha^{-1} d^{-1}	Auxiliary	01834

Acronym	Definition	Units	Variable type	Line no
DPT	Average daily dew point temperature	°C	Forcing	00399
DPT08	Dew point temperature at 8.00 hours	°C	Forcing	00381
DPT14	Dew point temperature at 14.00 hours	°C	Forcing	00389
DP2T	Dew point temperature at 14.00 hours as a function of day number	–	Function	00392
DP8T	Dew point temperature at 8.00 hours as function of day number	–	Function	00384
DRAGC	Drag coefficient of the leaves	unitless	Parameter	00947
DRFA(I)	Factor defining initial soil moisture in a soil compartment, fraction of moisture content at wilting point	unitless	Table	00229
DRLVS	Current death rate of leaf blades	kg ha^{-1} d^{-1}	Auxiliary	01305
DRLVWS	Potential death rate of leaf blades due to water shortage	kg ha^{-1} d^{-1}	Auxiliary	01280
DRNT	Death rate of non-reproductive tillers	no ha^{-1} d^{-1}	Rate	01561
DRQ	Potential death rate of leaf blades due to water shortage, nitrogen shortage, shading or carbohydrate shortage	kg ha^{-1} d^{-1}	Auxiliary	01302
DRQR	Intermediate variable in calculation of potential death rate of leaf blades due to senescence	kg ha^{-1} d^{-1}	Auxiliary	01359
	Set to zero			01326
DRQX	Intermediate variable in calculation of potential death rate of leaf blades due to senescence	kg ha^{-1} d^{-1}	Auxiliary	01357
DRRT	Death rate of the roots	kg ha^{-1} d^{-1}	Rate	01432
DRSTE	Death rate of stem and sheaths	kg ha^{-1} d^{-1}	Rate	01390

Acronym	Definition	Units	Variable type	Line no
DRSWS	Potential death rate of stem and sheaths due to water shortage	kg ha^{-1} d^{-1}	Auxiliary	01397
DSTR	Total amount of dead material above ground	kg ha^{-1}	State	01935
DTLN	Total number of dead tillers	no ha^{-1}	State	01563
DTMPA	Average daily air temperature, ten days ago, used in calculation of soil temperature	°C	Auxiliary	00905
DTR	Daily total global radiation	J m^{-2} d^{-1}	Forcing	00347
DTRT	Daily total global radiation as a function of day number	–	Function	00349
DVRR	Development rate canopy in the post-anthesis phase	d^{-1}	Rate	01082
DVRV	Development rate canopy in the pre-anthesis phase	d^{-1}	Rate	01046
DVS	Overall development stage of the canopy	unitless	State	01094
DVSAN	Development stage of the canopy in the pre-anthesis phase at anthesis	unitless	Parameter	01064
DVSEGF	Development stage of the canopy in the post-anthesis phase at end of grain fill	unitless	Parameter	01063
DVSFE	Development stage of the canopy in the pre-anthesis phase at end of floret formation	unitless	Parameter	01063
DVSFS	Development stage of the canopy in the pre-anthesis phase at start of floret formation	unitless	Parameter	01063
DVSGS	Development stage of the canopy in the post-anthesis phase at start of grain set	unitless	Parameter	01086
DVSI	Development stage of the canopy in the pre-anthesis phase at emergence	unitless	Parameter	01062

Acronym	Definition	Units	Variable type	Line no
DVSP	Overall development stage of the canopy one time interval ago	unitless	Auxiliary	01059
DVSPRE	Development stage of the canopy in the pre-anthesis phase at end of tillering	unitless	Parameter	01063
DVSPRF	Factor indicating whether development stage is beyond the end of tiller formation (1) or not (0)	unitless	Auxiliary	01070
DVSR	Development stage of the canopy in the post-anthesis phase	unitless	State	01079
DVSSE	Development stage of the canopy in the pre-anthesis phase at start of floral initiation	unitless	Parameter	01062
DVSSGF	Development stage of the canopy in the post-anthesis phase at start of grain fill	unitless	Parameter	01086
DVSSPE	Development stage of the canopy in the pre-anthesis phase at terminal spikelet formation	unitless	Parameter	01063
DVSSPS	Development stage of the canopy in the pre-anthesis phase at start of spikelet differentiation	unitless	Parameter	01062
DVSST	Development stage of the canopy in the pre-anthesis phase at start of stem elongation	unitless	Parameter	01062
DVSTS	Development stage of the canopy in the pre-anthesis phase at start of tillering	unitless	Parameter	01062
DVSV	Development stage of the canopy in the pre-anthesis phase	unitless	State	01043
DVSVF	Variable indicating whether development stage is beyond anthesis (1) or not (0)	unitless	Auxiliary	01072

Acronym	Definition	Units	Variable type	Line no
DVSVP	Development stage of the canopy in the pre-anthesis phase, one time interval ago	unitless	Auxiliary	01055
DWAT(I)	Rate of change in amount of water in a soil compartment	mm d^{-1}	Rate	00653
EA	Drying power term in Penman equation	J m^{-2} d^{-1}	Auxiliary	00540
EARAR	Green area of the ears	m^2 ha^{-1}	Auxiliary	01707
EARN	Total number of ears	no ha^{-1}	State	01582
EAVT	Effective air temperature during daytime	°C	Auxiliary	00415
EB	Basic time constant for ear formation	d	Parameter	01592
EDAYL	Effective day length for assimilation, calculated for period that sun angle is above 8 degrees	h	Auxiliary	01126
EDBG1	Variable defining time at the end of the first DEBUG call	unitless	Parameter	01990
EDBG2	Variable defining time at the end of the second DEBUG call	unitless	Parameter	01991
EDPTF(I)	Reduction factor for soil moisture uptake due to low available moisture in a soil compartment	unitless	Auxiliary	00606
EDPTFT	Reduction factor for soil moisture uptake due to low available moisture as a function of fraction available moisture per soil compartment	–	Function	00519
EFCCH	Efficiency of conversion of primary assimilates into structural carbohydrates	kg kg^{-1}	Parameter	01218
EFCPR	Efficiency of conversion of primary assimilates into structural proteins	kg kg^{-1}	Parameter	01218

Acronym	Definition	Units	Variable type	Line no
EFCPRG	Efficiency of conversion of primary assimilates into structural grain proteins	kg kg^{-1}	Parameter	01218
EFFE	Initial light use efficiency at the light compensation point	kg ha^{-1} h^{-1}/J m^{-2} s^{-1}	Parameter	01116
EFFWS	Effect of water stress on turnover of nitrogen in vegetative tissue	unitless	Auxiliary	01908
EFRNV	'Effective' nitrogen concentration in leaf blade tissue, used in calculation of maximum assimilation rate	kg kg^{-1}	Auxiliary	01762
EGFF	Variable indicating whether development stage is beyond the end of grain fill (1) or not (0)	unitless	Auxiliary	01092
ELWR	Net outgoing long wave radiation	J m^{-2} d^{-1}	Auxiliary	00950
EPVC	Fraction of proteins in leaf blade tissue	kg kg^{-1}	Auxiliary	01266
ER(I)	Rate of moisture extraction from a soil compartment due to soil surface evaporation	mm d^{-1}	Rate	00643
ERLT	Total 'effective' root length	mm	Auxiliary	00619
EVAP	Potential rate of soil surface evaporation	mm d^{-1}	Rate	00545
EVAPR	Rate of soil surface evaporation from wet soil surface in presence of crop	mm d^{-1}	Auxiliary	00419
EVTOT	Current rate of soil surface evaporation	mm d^{-1}	Rate	00646
	Set to zero			00635
EW08	Intermediate variable for calculation of dew point temperature at 8.00 hours	unitless	Auxiliary	00378
EW14	Intermediate variable for calculation of dew point temperature at 14.00 hours	unitless	Auxiliary	00386

Acronym	Definition	Units	Variable type	Line no
EXC	Extinction coefficient for global radiation	unitless	Parameter	00996
FB	Basic time constant for floret formation	d	Parameter	01633
FCAPR	Fraction of easily decomposable carbohydrates and proteins in initial fresh organic material	kg kg^{-1}	Parameter	00672
FCELL	Fraction of cellulose and hemicellulose in original fresh organic material	kg kg^{-1}	Parameter	00672
FCHN	'Net' flow of carbohydrate, i.e. difference between gross assimilation and maintenance respiration, limited to positive values	kg ha^{-1} d^{-1}	Auxiliary	01226
FCHNX	'Net' flow of carbohydrate, i.e. difference between gross assimilation and maintenance respiration	kg ha^{-1} d^{-1}	Auxiliary	01225
FCHST	Current flow of carbohydrates to stem+sheaths	kg ha^{-1} d^{-1}	Rate	01376
FCHTLV	Current flow of carbohydrates to leaf blades	kg ha^{-1} d^{-1}	Rate	01239
FCHTR	Current flow of carbohydrates to roots	kg ha^{-1} d^{-1}	Rate	01417
FCHTRS	Current flow of carbohydrates to reserves	kg ha^{-1} d^{-1}	Rate	01464
FDAYN	Variable having number of Julian calendar day on which day number = 0 in weather tables and tables of observed data	unitless	Parameter	00296
FDM	Fraction dry matter in vegetative tissue, function of development stage	kg kg^{-1}	Auxiliary	01285
FDMT	Fraction dry matter in vegetative tissue as a function of development stage	–	Function	01287
FDSR	Fraction of current assimilate supply allocated to the	kg kg^{-1}	Auxiliary	01422

Acronym	Definition	Units	Variable type	Line no
	roots, function of development stage			
FDSRT	Fraction of current assimilate supply allocated to the roots as a function of development stage	–	Function	01425
FERTAP(I)	Rate of addition of mineral nitrogen by fertilizer application in a soil compartment	kg ha^{-1} d^{-1}	Rate	00816
FFNR	Number of fertile florets	no ha^{-1}	State	01624
FINT	Fraction of available energy intercepted by non-closed canopy	unitless	Auxiliary	01151
FINTIM	Number of days from beginning till end of the simulation	d	System	01918
FLDCP(I)	Volumetric moisture content at field capacity per soil compartment	cm^3 cm^{-3}	Table	00487
FLFAR	Current specific leaf area	m^2 kg^{-1}	Auxiliary	01669
FLFARI	Specific leaf area at emergence	m^2 kg^{-1}	Parameter	01670
FLFARM	Minimum value of specific leaf area, reached at start of stem extension	m^2 kg^{-1}	Parameter	01670
FLIGN	Fraction of lignin in initial fresh organic material	kg kg^{-1}	Parameter	00672
FN	'Relative' nitrogen concentration in leaf blades (redundant)	unitless	Auxiliary	01468
FNC	'Relative' nitrogen concentration in leaf blades, expressed as a fraction of difference between maximum concentration and residual concentration, used in calculation of growth of tillers, definition of relative death rate of leaf blades due to *nitrogen shortage, and definition of RFNS*	unitless	Auxiliary	01779

Acronym	Definition	Units	Variable type	Line no
FNEXT	Fraction of labile nitrogen exported from vegetative tissue to the grain, as a function of average nitrogen concentration in the vegetative tissue	–	Function	01911
FNIMH	Fraction of nitrogen in decomposing fresh organic material and microbial biomass immobilized in stable organic material	kg kg^{-1}	Parameter	00729
FNMAX	Maximum nitrogen concentration in young leaf blades	kg kg^{-1}	Auxiliary	00262
FNMIN	Absolute minimum nitrogen concentration in leaf blades	kg kg^{-1}	Parameter	00264
FNMN	Minimum nitrogen concentration in leaf blades for unrestricted transpiration	kg kg^{-1}	Auxiliary	01741
FNMNA	Absolute minimum nitrogen concentration in leaf blades	kg kg^{-1}	Parameter	01769
FNMNR	Absolute minimum nitrogen concentration in roots	kg kg^{-1}	Parameter	01769
FNMNSR	Maximum nitrogen concentration in mature stem and sheaths	kg kg^{-1}	Parameter	01798
FNMX	Maximum nitrogen concentration in leaf blades, function of development stage	kg kg^{-1}	Auxiliary	01737
FNMXA	Range in maximum nitrogen concentration between young and mature leaf blades	kg kg^{-1}	Parameter	01769
FNMXR	Maximum nitrogen concentration in mature leaf blades	kg kg^{-1}	Parameter	01769
FNMXSA	Range in maximum nitrogen concentration between young and mature stem and sheaths	kg kg^{-1}	Parameter	01798
FNOM(I)	Fraction of nitrogen in fresh organic material in a soil compartment	kg kg^{-1}	Auxiliary	00698
FNO3	Fraction of nitrate in leaf	kg kg^{-1}	Auxiliary	01746

Acronym	Definition	Units	Variable type	Line no
	blades, function of development stage			
FNO3T	Nitrate concentration in leaf blades as a function of development stage	–	Function	01748
FNRF	Fraction of nitrogen in fresh organic material	kg kg^{-1}	Parameter	00669
FNRTMN	Maximum nitrogen concentration in mature roots	kg kg^{-1}	Parameter	01839
FNRTMX	Maximum nitrogen concentration in young roots	kg kg^{-1}	Parameter	01839
FNVEG	Overall average nitrogen concentration in vegetative material	kg kg^{-1}	Auxiliary	01916
FOMI	Total initial weight of fresh organic material in soil profile, i.e. at start of the simulation	kg ha^{-1}	Parameter	00223
FOM*(I)	Weight of fresh organic material in a soil compartment	kg ha^{-1}	State	00855
FOMRES (I)	Fraction of fresh organic material not yet decomposed in a soil compartment	kg kg^{-1}	Auxiliary	00702
FON*(I)	Nitrogen in fresh organic material in a soil compartment	kg ha^{-1}	State	00857
FOV	Fraction of the day the sky is overcast	unitless	Auxiliary	00496
FRC	Fraction of carbon in fresh organic material	kg kg^{-1}	Parameter	00669
FRNGL	Minimum nitrogen concentration in the grain	kg kg^{-1}	Parameter	01514
FRNGL1	Nitrogen concentration in the grain at which dry matter accumulation starts to be affected	kg kg^{-1}	Parameter	01514
FRNN	Ratio between minimum concentration of nitrogen for unrestricted transpiration and maximum nitrogen con-	unitless	Parameter	01744

Acronym	Definition	Units	Variable type	Line no
	centration in leaf blades			
FPGC	Fraction of protein in the grain	kg kg^{-1}	Auxiliary	01507
FPRT	Fraction of protein in the roots	kg kg^{-1}	Auxiliary	01430
FPST	Fraction of protein in stem + sheaths	kg kg^{-1}	Auxiliary	01387
FRNG	Fraction of nitrogen in the grain	kg kg^{-1}	Auxiliary	01918
FRNR	Fraction of nitrogen in the roots	kg kg^{-1}	Auxiliary	01842
FRNST	Fraction of nitrogen in stem+sheaths	kg kg^{-1}	Auxiliary	01815
FRNV	Fraction of nitrogen in leaf blades	kg kg^{-1}	Auxiliary	01760
FRNVI	Initial fraction of nitrogen in leaf blades at emergence	kg kg^{-1}	Auxiliary	00260
FSCHG	Fraction of 'surplus' carbohydrate, originating from growth check of leaf blades and stems due to water or nitrogen shortage, allocated to the roots	unitless	Parameter	01420
FTLVS	Fraction of current assimilate supply allocated to leaf blades, function of development stage	kg kg^{-1}	Auxiliary	01241
FTLVST	Fraction of current assimilate supply allocated to leaf blades as a function of development stage	–	Function	01482
FTMPA	Reciprocal of mean standard canopy temperature (= 1/15)	° C^{-1}	Parameter	00420
FTRL	Fraction of current assimilate supply allocated to the reserve pool, function of development stage	kg kg^{-1}	Auxiliary	01481
FTRLT	Fraction of current assimilate supply allocated to the reserve pool as a function of development stage	–	Function	01382

Acronym	Definition	Units	Variable type	Line no
FTSTE	Fraction of current assimilate supply allocated to stem and sheaths, function of development stage	kg kg^{-1}	Auxiliary	01379
FTSTET	Fraction of current assimilate supply allocated to stem and sheaths as a function of development stage	–	Function	01382
FWDB	Fraction of water left in dying plant tissue	kg kg^{-1}	Parameter	01289
GAMMA	Psychrometric constant	mm Hg $°C^{-1}$	Parameter	00542
GB	Basic time constant for grain formation	d	Parameter	01651
GERD	Day on which conditions are favourable (1) or unfavourable (0) for germination	unitless	Auxiliary	00319
	Set to zero			00318
GERDAT	Day number on which germination is completed	unitless	Auxiliary	00328
GRAI	Green area index of the canopy	m^2 m^{-2}	Auxiliary	01677
GRGR	Rate of increase in dry weight of the grain	kg ha^{-1} d^{-1}	Rate	01503
GRLVS	Rate of increase in dry weight of the leaf blades	kg ha^{-1} d^{-1}	Rate	01237
GRN	Grain density	no ha^{-1}	State	01646
GRNT	Rate of increase in tiller density	no ha^{-1} d^{-1}	Rate	01547
GRRSTE	Rate of increase in dry weight of stem and sheaths	kg ha^{-1} d^{-1}	Rate	01374
GRRT	Rate of increase in dry weight of the roots	kg ha^{-1} d^{-1}	Rate	01415
HNOT	Net global radiation	J m^{-2} d^{-1}	Auxiliary	00952
HRAD	Average hourly radiation intensity during daylight hours	J m^{-2} h^{-1}	Auxiliary	00955
HTFAC	Multiplication factor used to convert average nitrogen concentration in leaf blades to 'effective' concentration	unitless	Parameter	01765

Acronym	Definition	Units	Variable type	Line no
	used in calculation of maximum assimilation rate			
HUMI	Initial total weight of stable organic material in soil profile	kg ha^{-1}	Parameter	00223
HUM*(I)	Weight of stable organic material in a soil compartment	kg ha^{-1}	State	00859
HUMT	Total weight of stable organic material in soil profile	kg ha^{-1}	Output	00890
	Set to zero			00875
HZERO	Net absorbed radiation by open water surface	J m^{-2} d^{-1}	Auxiliary	00536
I	Counter used in DO loops	unitless	Auxiliary	-
IAS(I)	Initial weight of mineral nitrogen in a soil compartment	kg ha^{-1}	Initial state	00216
IBIOMN(I)	Initial weight of nitrogen in microbial biomass in a soil compartment	kg ha^{-1}	Initial state	00233
IFNRT	Initial fraction of nitrogen in the roots at emergence	kg kg^{-1}	Auxiliary	00271
IFOM(I)	Initial weight of fresh organic material in a soil compartment at start of the simulation	kg ha^{-1}	Initial state	00179
IFON(I)	Initial weight of nitrogen in fresh organic material in a soil compartment at start of the simulation	kg ha^{-1}	Initial state	00180
IHUM(I)	Initial weight of stable organic material in a soil compartment at start of the simulation	kg ha^{-1}	Initial state	00182
INFR	Rate of infiltration	mm d^{-1}	Rate	00570
INHUM(I)	Initial weight of nitrogen in stable organic material in a soil compartment at the start of the simulation	kg ha^{-1}	Initial state	00181
INIV	Initial weight of nitrogen in the vegetation at emergence	kg ha^{-1}	Initial state	01955

Acronym	Definition	Units	Variable type	Line no
IRRT	Effective irrigation as a function of day number	–	Function	00573
IRTD	Initial rooting depth at emergence	mm	Initial state	01446
IW	Turbulence intensity	unitless	Parameter	00947
IWAT(I)	Initial amount of soil moisture in a compartment at start of the simulation	mm	Initial state	00178
K	Counter used to indicate last soil compartment of the potential root zone (integer)	unitless	Auxiliary	00588
KARMAN	Von Karman's constant	unitless	Parameter	00947
L	Counter used in definition of output for multiple runs (integer)	unitless	Auxiliary	02018
	Set to zero			00172
LAI	Leaf area index (area of green leaf blades)	$m^2\ m^{-2}$	Auxiliary	01675
LAIM	Threshold value of LAI beyond which death due to shading starts	$m^2\ m^{-2}$	Auxiliary	01293
LAT	Latitude of location	degrees	Parameter	00244
LATE	Absolute value of latitude of location, used to define locations in southern hemisphere degrees	degrees	Auxiliary	00246
LDEC	Maximum rate of decomposition of fresh organic material, as dictated by maximum growth rate of microbial biomass per soil compartment	$kg\ ha^{-1}\ d^{-1}$	Auxiliary	00705
LEAFA*(I)	Leaf area per leaf class	$m^2\ ha^{-1}$	State	01318
LEAFW*(I)	Leaf weight per leaf class	$kg\ ha^{-1}$	State	01316
LFD	Rate of change in leaf weight per leaf class	$kg\ ha^{-1}\ d^{-1}$	Rate	01352
LFOV	Fraction of the day the sky is overcast, constrained between 0 and 1	unitless	Auxiliary	00498

Acronym	Definition	Units	Variable type	Line no
LG	Counter used to designate leaf classes by day of initiation (integer)	unitless	Auxiliary	01332
	Set to zero			00172
	Must be reset in TERMINAL section for multiple runs			02014
LHVAP	Latent heat of vapourization	J kg^{-1}	Parameter	00542
LL	Counter used in organization of selected output (array W) (integer)	unitless	Auxiliary	02034
LMIX	Mixing length used in calculation of turbulent resistance	unitless	Auxiliary	00939
LMR	Rate of weight loss of the grain, due to maintenance respiration, if current supply of assimilates is insufficient	kg ha^{-1} d^{-1}	Auxiliary	01524
LN	Residual non-remobilizable concentration of nitrogen in stem and sheaths, function of development stage	kg kg^{-1}	Auxiliary	01819
LNH4	Threshold concentration of NH4 below which no ammonia volatilization occurs	kg mm^{-1}	Parameter	00790
LNT	Residual non-remobilizable concentration of nitrogen in stem and sheaths as a function of development stage	–	Function	01821
LNREF	Intermediate variable in calculation of turbulent resistance	unitless	Auxiliary	00943
LWDTL	Average weight of leaf blades of non-reproductive tiller at end of ear formation	kg $tiller^{-1}$	Auxiliary	01571
LWR	Net outgoing long wave radiation used in Penman equation	J m^{-2} d^{-1}	Auxiliary	00535
M	Counter used for organization of output in case of multiple runs (integer)	unitless	Auxiliary	02042

Acronym	Definition	Units	Variable type	Line no
	set to zero			00172
	Must be reset in TERMINAL section for multiple runs			02042
MAXARR	Maximum area reduction factor due to leaf rolling: value 1 gives no effect	unitless	Parameter	01690
MF(I)	Factor accounting for the effect of soil moisture on decomposition of organic material in a soil compartment	unitless	Auxiliary	00701
MFT	Function relating factor accounting for the effect of soil moisture on decomposition of organic material to fraction available soil moisture per soil compartment	–	Function	00524
MNT	Daily minimum air temperature	°C	Forcing	00412
MNTT	Daily minimum air temperature as a function of day number	–	Function	00409
MRDRSH	Maximum relative death rate of leaf blades due to shading	d^{-1}	Parameter	01293
MRGRB	Maximum relative growth rate of microbial biomass	d^{-1}	Parameter	00679
MWRTD	Maximum amount of water that can be stored in rooted depth	mm	Auxiliary	00610
	Set to zero			00601
MXNE	Maximum number of ears that can be formed	no ha^{-1}	Auxiliary	01587
MXNFFL	Maximum number of fertile florets that can be formed	no ha^{-1}	Auxiliary	01629
MXNSP	Maximum number of spikelets that can be formed	no ha^{-1}	Auxiliary	01608
MXRDR	Maximum relative death rate of leaf blades due to carbohydrate shortage	d^{-1}	Parameter	01301

Acronym	Definition	Units	Variable type	Line no
MXRTD	Maximum rooting depth	mm	Parameter	01446
MXRUP	Maximum rate of nitrogen uptake by the vegetation	kg ha^{-1} d^{-1}	Auxiliary	01873
MXSTAR	Maximum green area of stem and sheaths	m^2 ha^{-1}	Auxiliary	01716
MXTT	Maximum daily air temperature as a function of day number	–	Function	00406
MY	Variable indicating number of years to be run in case of multiple runs (integer)	unitless	Parameter	00172
N	Number of soil compartments considered (integer)	unitless	Parameter	00172
NAM1(I)	Array containing first four letter part of description of variables stored in Array W	alphanumeric	Auxiliary	00133
NAM2(I)	Array containing second four letter part of description of variables stored in Array W	alphanumeric	Auxiliary	00136
NAM3(I)	Array containing third four letter part of description of variables stored in Array W	alphanumeric	Auxiliary	00139
NAM4(I)	Array containing fourth four letter part of description of variables stored in Array W	alphanumeric	Auxiliary	00142
NAPDAY	Day number at which fertilizer application takes place	unitless	Parameter	00775
NBAL	Nitrogen balance, should be zero throughout the simulation	kg ha^{-1}	Output	01961
NBR	Contribution of nitrogen by rain and free living micro organisms	kg ha^{-1} d^{-1}	Auxiliary	00763
NCABM	Overall nitrogen concentration in above ground material	kg kg^{-1}	Output	01996
NCH	Nitrogen concentration in stable organic material	kg kg^{-1}	Parameter	00682
NCR	Nitrogen concentration in rain water, taking also into	kg ha^{-1} mm^{-1}	Parameter	00766

Acronym	Definition	Units	Variable type	Line no
	account fixation by free living micro organisms			
NDAY	Day number in Julian calendar, for southern hemisphere equal to DAYY+180	unitless	Auxiliary	00290
NDEM	Nitrogen demand of leaf blades	kg ha^{-1} d^{-1}	Auxiliary	01733
NDEMST	Nitrogen demand of stem and sheaths	kg ha^{-1} d^{-1}	Auxiliary	01738
NDPAR	Variable indicating whether even (+1) or uneven (-1) nitrogen distribution is assumed	unitless	Parameter	01765
NDSTR	Weight of nitrogen in dead above ground material	kg ha^{-1}	Output	01938
NGIFT	Rate of fertilizer nitrogen application	kg ha^{-1} d^{-1}	Auxiliary	00775
NFD	Factor accounting for the effect of crop nitrogen status on phenological development	unitless	Auxiliary	01049
NFDEV	Variable indicating degree of influence of nitrogen status on crop development	unitless	Auxiliary	01051
NHUMI	Initial total weight of nitrogen in stable organic material in soil profile	kg ha^{-1}	Parameter	00223
NHUM*(I)	Weight of nitrogen in stable organic material in a soil compartment	kg ha^{-1}	State	00861
NHUMT	Total weight of nitrogen in stable organic material in soil profile	kg ha^{-1}	Output	00886
	Set to zero			00874
NH4FP	Variable indicating fraction of ammoniacal compounds in fertilizer (1:all ammonium)	unitless	Auxiliary	00788
NP	Variable indicating number of values for parameter in case of multiple runs (integer)	unitless	Auxiliary	00172

Acronym	Definition	Units	Variable type	Line no
NSPS	Total number of spikelets	no ha^{-1}	State	01604
NTOT	Total weight of inorganic nitrogen in soil profile	kg ha^{-1}	Output	00882
	Set to zero			00871
N1	Total number of compartment boundaries distinguished in the model (number of compartments plus 1, integer)	unitless	Auxiliary	00174
OFNRT	Maximum nitrogen concentration in the roots, function of development stage	kg kg^{-1}	Auxiliary	01837
OFNST	Maximum nitrogen concentration in stem and sheaths, function of development stage	kg kg^{-1}	Auxiliary	01796
ONLV	Maximum nitrogen content of leaf blades	kg ha^{-1}	Auxiliary	01735
OTGW	Individual grain weight	mg grain^{-1}	Output	01532
O0	Intermediate variable in calculation of canopy gross CO_2 assimilation	kg ha^{-1} d^{-1}	Auxiliary	01163
O1	Intermediate variable in calculation of canopy gross CO_2 assimilation	kg ha^{-1} d^{-1}	Auxiliary	01154
O2	Intermediate variable in calculation of canopy gross CO_2 assimilation	kg ha^{-1} d^{-1}	Auxiliary	01155
P	Intermediate variable in calculation of canopy gross CO_2 assimilation (Note that P is redefined several times during execution)	unitless	Auxiliary	01093
PAMAX	Value of light saturated assimilation rate of an individual leaf, one time interval ago	kg ha^{-1} h^{-1}	Auxiliary	01173
PAPTRN	Potential crop transpiration rate, one time interval ago	mm d^{-1}	Auxiliary	01696

Acronym	Definition	Units	Variable type	Line no
PARI	Variable accounting for non-standard units in weather tables	unitless	Auxiliary	00352
PCOND	Potential conductivity of the root system	mm d^{-1}	Auxiliary	01010
PCTRAN	Rate of cuticular water loss with fully closed stomata	mm d^{-1}	Auxiliary	01001
PDRLVS	Potential death rate of leaf blades due to senescence	kg ha^{-1} d^{-1}	Auxiliary	01345
	Set to zero			01324
PDTGAS	Potential daily gross assimilation of the canopy expressed in CH_2O	kg ha^{-1} d^{-1}	Auxiliary	01148
	Set to zero			01170
PEVAP	Potential rate of soil evaporation as limited by canopy cover	mm d^{-1}	Auxiliary	00552
PGRIG	Potential rate of dry matter accumulation of an individual grain, function of canopy temperature	kg $grain^{-1}$ d^{-1}	Auxiliary	01515
PGRIGF	Factor accounting for cultivar-specific difference in potential growth rate of individual grain	unitless	Auxiliary	01516
PGRIGT	Potential rate of dry matter accumulation of an individual grain as a function of canopy temperature	–	Function	01519
PGRRG	Potential rate of dry matter accumulation in the grains	kg ha^{-1} d^{-1}	Auxiliary	01511
PI	Circumference of a circle divided by its diameter	unitless	Parameter	00242
PNUDP	Maximum rate of nitrogen uptake by the canopy, determined by either demand, uptake capacity or nitrogen availability	kg ha^{-1} d^{-1}	Auxiliary	01859
PRDEL	Time interval for printing	d	System	01918
PRNAGR	Potential rate of nitrogen accumulation in the grains	kg ha^{-1} d^{-1}	Auxiliary	01893

Acronym	Definition	Units	Variable type	Line no
PRNAGT	Potential rate of nitrogen accumulation in the grains as a function of canopy temperature	–	Function	01895
PROP	Proportionality factor for calculation of soil moisture contribution to soil surface evaporation by soil compartment	unitless	Parameter	00510
PS	Intermediate variable in calculation of canopy gross CO_2 assimilation	kg ha^{-1} d^{-1}	Auxiliary	01137
PSCH	Psychrometric constant	mbar $°C^{-1}$	Parameter	00986
PTNLST	Potential rate of nitrogen transfer from dying leaf blades to stem and sheaths	kg ha^{-1} d^{-1}	Auxiliary	01803
PTRN	Actual canopy transpiration, one time interval ago	mm d^{-1}	Auxiliary	01695
PUSHD	Switch variable: 1 at emergence; otherwise 0. Used to initialize crop state variables	unitless	Auxiliary	00327
	Set to zero			00310
	Must be reset in TERMINAL section for multiple runs			02010
PUSHDF	Factor indicating whether germination is completed (1) or not (0)	unitless	Auxiliary	00338
PUSHDI	Integrated value of PUSHD, used to define PUSHDF	unitless	Auxiliary	00336
PUSHE	Switch variable that assumes value 1 on the day of start of floral initiation and is otherwise 0	unitless	Auxiliary	01589
PUSHN	Switch variable that assumes value 1 on the day that grain fill starts and is otherwise 0. Used to initialize grain state variables	unitless	Auxiliary	01887

Acronym	Definition	Units	Variable type	Line no
PUSHT	Switch variable that assumes value 1 on the day that tillering ceases, and is otherwise 0. Used to define size of non-reproductive tillers	unitless	Auxiliary	01569
RA	Total resistance for water vapour transport from canopy to the atmosphere, sum of laminar resistance and turbulent resistance	d cm^{-1}	Auxiliary	00948
Q10	Factor accounting for effect of temperature on maintenance respiration	unitless	Parameter	01213
RAD	Conversion factor from degrees to radians	rad $degr^{-1}$	Auxiliary	01122
RADC	Total visible radiation under a clear sky	J m^{-2} s^{-1}	Forcing	01127
RADCF	Factor to convert from any units in measured radiation table to J m^{-2} d^{-1}	–	Parameter	00344
RADO	Total visible radiation under an overcast sky	J m^{-2} s^{-1}	Forcing	01128
RADTB	Total visible radiation as a function of day of the year and geographical latitude	–	Function	00450
RAIN	Rain intensity	mm d^{-1}	Forcing	00438
RAINF	Factor enabling variation of rainfall amount	unitless	Parameter	00440
RAINTB	Daily rainfall as a function of day number	–	Function	00442
RANO3	Relative amount of nitrate in total inorganic nitrogen store in top soil compartment	unitless	Auxiliary	00793
RC	Cuticular resistance for water vapour exchange	d cm^{-1}	Parameter	00996
RCANLV	Current rate of change in amount of nitrogen in leaf blades, limited to amount present	kg ha^{-1} d^{-1}	Rate	01729
RCANRT	Current rate of change in amount of nitrogen in the	kg ha^{-1} d^{-1}	Rate	01831

Acronym	Definition	Units	Variable type	Line no
	roots, limited to amount present			
RCANST	Current rate of change in amount of nitrogen in stem and sheaths, limited to amount present	kg ha^{-1} d^{-1}	Rate	01789
RCLFA	Current rate of change in green leaf area, limited to amount present	m^2 ha^{-1} d^{-1}	Rate	01667
RCRES	Rate of change in amount of non-structural carbohydrates	kg ha^{-1} d^{-1}	Rate	01462
RCWLVS	Current rate of change in weight of live leaf blades, limited to amount present	kg ha^{-1} d^{-1}	Rate	01235
RCWRT	Current rate of change in weight of the roots, limited to amount present	kg ha^{-1} d^{-1}	Rate	01413
RCWST	Current rate of change in weight of stem and sheaths, limited to amount present	kg ha^{-1} d^{-1}	Rate	01372
RDCAPR	Relative rate of decomposition of easily decomposable carbohydrates and proteins under optimum conditions	d^{-1}	Parameter	00666
RDCELL	Relative rate of decomposition of cellulose and hemicellulose under optimum conditions	d^{-1}	Parameter	00666
RDECR(I)	Rate of decomposition of fresh organic material per soil compartment	kg ha^{-1} d^{-1}	Rate	00703
RDLFA	Rate of decline in leaf area due to senescence	m^2 ha^{-1} d^{-1}	Rate	01346
				01355
	Set to zero			01325
				01349
RDLIGN	Relative rate of decomposition of lignin under optimum conditions	d^{-1}	Parameter	00666

Acronym	Definition	Units	Variable type	Line no
RDR	Overall relative death rate of leaf blades	d^{-1}	Auxiliary	01307
RDRAIN	Rate of drainage of soil moisture beyond potential rooting zone	mm d^{-1}	Rate	00589
RDRCS	Relative death rate of leaf blades due to carbohydrate exhaustion	d^{-1}	Auxiliary	01299
RDRD	Relative death rate of leaf blades due to senescence	d^{-1}	Auxiliary	01309
RDRL	Relative death rate of leaf blades due to shading	d^{-1}	Auxiliary	01292
RDRN	Relative death rate of leaf blades due to nitrogen shortage	d^{-1}	Auxiliary	01755
RDRNT	Relative death rate of leaf blades due to nitrogen shortage as a function of 'relative' nitrogen concentration	–	Function	01756
RDRS	Relative death rate of stem and sheaths	d^{-1}	Auxiliary	01392
RDRT	Relative death rate of non-fertile tillers	d^{-1}	Parameter	01575
RDRW	Relative death rate of leaf blades due to water shortage	d^{-1}	Auxiliary	01277
RDRWDS	Relative death rate of stem and sheaths due to either water shortage or senescence	d^{-1}	Auxiliary	01809
RDRWS	Relative death rate of stem and sheaths due to water shortage	d^{-1}	Auxiliary	01395
REARF	Current rate of increase in ear number, limited to appropriate phenological phase	no ha^{-1} d^{-1}	Rate	01585
REARF1	Potential rate of increase in ear number as determined by assimilate supply	no ha^{-1} d^{-1}	Auxiliary	01586
REDFRL	Factor accounting for the effect of carbohydrate accumulation on gross canopy assimilation	unitless	Auxiliary	01183

Acronym	Definition	Units	Variable type	Line no
REDFDT	Reduction in soil surface evaporation as a function of dimensionless moisture content in top soil compartment	–	Function	00557
REDTTB	Reduction factor for root extension as a function of soil temperature	–	Function	01453
REDWST	Reduction factor for leaf blade growth as a function of relative transpiration deficit	–	Function	01255
REFCF	Reflection coefficient of open water for short wave radiation	unitless	Parameter	00537
REFHT	Reference height for measuring wind speed	m	Parameter	00947
RESL	Current concentration of non-structural carbohydrates (reserves) in the canopy	kg kg^{-1}	Auxiliary	01493
RESLI	Initial concentration of non-structural carbohydrates in the canopy	kg kg^{-1}	Parameter	00275
RESLL	Non-remobilizable concentration of reserves in the vegetation for transfer to vegetative structures	kg kg^{-1}	Auxiliary	01476
RESLR	Residual non-remobilizable concentration of reserves for translocation to the grain	kg kg^{-1}	Parameter	01530
RESL1	Residual non-remobilizable concentration of reserves for translocation to vegetative structures before end of floret formation	kg kg^{-1}	Parameter	01477
RESL2	Residual non-remobilizable concentration of reserves for translocation to vegetative structures after end of floret formation	kg kg^{-1}	Parameter	01477
RESRES	Weight of non-remobilizable reserves in the canopy	kg ha^{-1}	Auxiliary	01528

Acronym	Definition	Units	Variable type	Line no
REST	Intermediate variable in calculation of turbulent resistance	unitless	Auxiliary	00944
RFFF	Current rate of fertile floret formation, limited to appropriate phenological phase	no ha^{-1} d^{-1}	Rate	01627
RFFF1	Rate of fertile floret formation as determined by assimilate availability	no ha^{-1} d^{-1}	Auxiliary	01628
RFNS	Factor accounting for the effect of nitrogen shortage on leaf growth, stomatal conductance, phenological development and nitrogen loss from dying leaf blades	unitless	Auxiliary	01258
RFNST	Factor accounting for the effect of nitrogen shortage on leaf growth as a function of 'relative' nitrogen concentration in leaf blades (FNC)	–	Function	01260
RFRGT	Factor accounting for the effect of low soil temperatures on root growth	unitless	Auxiliary	01451
RFRT	Proportionality factor between relative death rate of roots and stem and sheaths	unitless	Parameter	01434
RFST	Proportionality factor between relative death rate of stem and sheaths and leaf blades	unitless	Parameter	01400
RFSTRS	Factor accounting for the effect of either water shortage or nitrogen shortage on leaf growth	unitless	Auxiliary	01250
RFT	Factor accounting for the effect of temperature on grain set, function of minimum temperature	unitless	Auxiliary	01652

Acronym	Definition	Units	Variable type	Line no
RFTT	Factor accounting for the effect of temperature on grain set as a function of minimum temperature	–	Function	01654
RFWS	Factor accounting for the effect of water shortage on growth of leaf blades	unitless	Auxiliary	01253
RGRN	Rate of increase in grain density	no ha^{-1} d^{-1}	Rate	01648
RGRRL	Rate of increase in rooting depth	mm d^{-1}	Rate	01443
RHMIN(I)	Rate of nitrogen mineralization from stable organic material in a soil compartment	kg ha^{-1} d^{-1}	Rate	00708
RHOCP	Volumetric heat capacity of the air	J m-3 K^{-1}	Parameter	00949
RLAI	Observed leaf area index of the canopy	m^2 m^{-2}	Output	02001
RLAITB	Observed leaf area index of the canopy as a function of day number	–	Function	02007
RMNG	Rate of maintenance respiration of the grain	kg ha^{-1} d^{-1}	Rate	01206
RMNLVS	Rate of maintenance respiration of leaf blades	kg ha^{-1} d^{-1}	Rate	01197
RMNR	Rate of maintenance respiration of the roots	kg ha^{-1} d^{-1}	Rate	01203
RMNST	Rate of maintenance respiration of stem and sheaths	kg ha^{-1} d^{-1}	Rate	01200
RMRESG	Relative maintenance respiration rate of the grains	d^{-1}	Parameter	01209
RMRESL	Relative maintenance respiration rate of the leaf blades	d^{-1}	Parameter	01209
RMRESR	Relative maintenance respiration rate of the roots	d^{-1}	Parameter	01209
RMRESS	Relative maintenance respiration rate of stem and sheaths	d^{-1}	Parameter	01209

Acronym	Definition	Units	Variable type	Line no
RNAC(I)	Rate of nitrogen immobilization by soil microbes in a soil compartment	$kg\ ha^{-1}\ d^{-1}$	Rate	00754
RNCBM	Observed average nitrogen concentration in above ground biomass	$kg\ kg^{-1}$	Output	02000
RNCBMT	Observed average nitrogen concentration in above ground biomass as a function of day number	–	Function	02006
RNEXP	Rate of nitrogen export from vegetative tissue to the grain	$kg\ ha^{-1}\ d^{-1}$	Auxiliary	01890
RNFAC	Range in nitrogen concentration between maximum and minimum concentration	$kg\ kg^{-1}$	Auxiliary	00266
RNL	Rate of loss of nitrogen from dying leaf blades	$kg\ ha^{-1}\ d^{-1}$	Rate	01753
RNLDR	Rate of nitrogen loss from dying roots	$kg\ ha^{-1}\ d^{-1}$	Rate	01844
RNLDST	Rate of nitrogen loss from dying stem and sheaths	$kg\ ha^{-1}\ d^{-1}$	Rate	01807
RNLSDT	Rate of nitrogen loss from stem and sheaths of dying tillers	$kg\ ha^{-1}\ d^{-1}$	Rate	01811
RNRL(I)	Rate of nitrogen mineralization through decomposing fresh organic material in a soil compartment	$kg\ ha^{-1}\ d^{-1}$	Rate	00707
RNRLB(I)	Rate of nitrogen mineralization from dying microorganisms in a soil compartment	$kg\ ha^{-1}\ d^{-1}$	Rate	00753
RNTG	Rate of nitrogen accumulation in the grain	$kg\ ha^{-1}\ d^{-1}$	Rate	01891
RNTLS	Rate of translocation of nitrogen from leaf blades to the grain	$kg\ ha^{-1}\ d^{-1}$	Rate	01758
RNTRS	Rate of translocation of nitrogen from roots to the grain	$kg\ ha^{-1}\ d^{-1}$	Rate	01840

Acronym	Definition	Units	Variable type	Line no
RNTSS	Rate of translocation of nitrogen from stem and sheaths to the grain	$kg\ ha^{-1}\ d^{-1}$	Rate	01813
RNU	Total rate of nitrogen uptake by the vegetation	$kg\ ha^{-1}\ d^{-1}$	Rate	01867
RNUD(I)	Current rate of nitrogen uptake by diffusion in a soil compartment	$kg\ ha^{-1}\ d^{-1}$	Rate	00832
RNUDB(I)	Potential rate of nitrogen uptake by diffusion in a soil compartment	$kg\ ha^{-1}\ d^{-1}$	Auxiliary	00834
RNUDF	Required contribution from diffusion to nitrogen supply of the canopy	$kg\ ha^{-1}\ d^{-1}$	Auxiliary	01862
RNUM(I)	Rate of nitrogen uptake by mass flow in a soil compartment	$kg\ ha^{-1}\ d^{-1}$	Rate	00813
RNURT	Rate of nitrogen uptake by the roots	$kg\ ha^{-1}\ d^{-1}$	Rate	01832
RNUST	Rate of nitrogen uptake by stem and sheaths	$kg\ ha^{-1}\ d^{-1}$	Rate	01791
RNUV	Rate of nitrogen uptake by leaf blades	$kg\ ha^{-1}\ d^{-1}$	Rate	01731
RNUVP	Rate of nitrogen uptake by above ground organs	$kg\ ha^{-1}\ d^{-1}$	Rate	01870
ROSPT	Reduction factor for root moisture uptake as a function of nitrogen concentration per soil compartment	–	Function	00522
RRMIC	Relative rate of maintenance respiration of microbial biomass	d^{-1}	Parameter	00679
RRTORT	Basic relative rate of nitrogen turnover in vegetative biomass	d^{-1}	Parameter	01906
RS	Stomatal resistance for water vapour exchange	$d\ cm^{-1}$	Auxiliary	00979
RSPLF	Current rate of spikelet formation, limited to appropriate phenological phase	$no\ ha^{-1}\ d^{-1}$	Rate	01606

Acronym	Definition	Units	Variable type	Line no
RSPLF1	Rate of spikelet formation, as determined by assimilate availability	no ha^{-1} d^{-1}	Auxiliary	01607
RTABN	Observed value of total above ground nitrogen uptake	kg ha^{-1}	Output	01999
RTABNT	Observed value of total above ground nitrogen uptake as a function of day number	–	Function	02005
RTADRW	Observed value of total above ground dry weight	kg ha^{-1}	Output	01997
RTADWT	Observed value of total above ground dry weight as a function of day number	–	Function	02003
RTD	Rooting depth	mm	State	01441
RTF	Factor accounting for the effect of stress on the rate of root extension	unitless	Parameter	01446
RTL(I)	Root length in a soil compartment	mm	Auxiliary	00605
RTORT	Rate of nitrogen turnover in vegetative tissue	kg ha^{-1} d^{-1}	Auxiliary	01903
RTRDEF	Relative transpiration deficit	unitless	Auxiliary	01024
RTURB	Turbulent resistance for water vapour exchange	d cm^{-1}	Auxiliary	00945
	Set to zero			00937
RVOL(I)	Rate of ammonia volatilization in a soil compartment, only effective in top soil compartment	kg ha^{-1} d^{-1}	Rate	00837
	Set to zero			00836
RVOLA	Rate of ammonia volatilization from top soil compartment	kg ha^{-1} d^{-1}	Rate	00785
RWF(I)	Rate of water flow into a soil compartment	mm d^{-1}	Rate	00587
RWF(1)	Rate of water flow into top soil compartment	mm d^{-1}	Rate	00585
RWLLDT	Rate of weight loss of leaf blades through dying of leaf	kg ha^{-1} d^{-1}	Rate	01303

Acronym	Definition	Units	Variable type	Line no
	blades of non-reproductive tillers			
RWLSDT	Rate of weight loss of stem and sheaths through dying of stem and sheaths of non-reproductive tillers	kg ha^{-1} d^{-1}	Rate	01402
RWLVS	Observed value of weight of green leaves	kg ha^{-1}	Output	01998
RWLVST	Observed value of weight of green leaves as a function of day number	–	Function	02004
RWRBT	Relative amount of available water in the root zone	unitless	Auxiliary	00620
	Set to zero			00616
S	Intermediate variable in calculation of potential crop transpiration	unitless	Auxiliary	00983
SB	Basic time constant for spikelet formation	d	Parameter	01613
SC	Actual stomatal conductance as influenced by the nitrogen status of the canopy	cm d^{-1}	Auxiliary	00976
SCM	Maximum stomatal conductance for water vapour exchange	cm d^{-1}	Parameter	00973
SCHFLV	'Surplus' carbohydrate flow due to growth check of leaves and stems under influence of water or nitrogen stress	kg ha^{-1} d^{-1}	Auxiliary	01263
SDAY	Variable indicating whether a day counts for deterioration of germinating seeds (1) or not (0)	unitless	Auxiliary	00320
	Set to zero			00317
SDBG1	Variable indicating time at the start of the first DEBUG call	unitless	Parameter	01990
SDBG2	Variable indicating time at the start of the second DEBUG call	unitless	Parameter	01991

Acronym	Definition	Units	Variable type	Line no
SFPRD	Rate of energy contribution from catabolyzed proteins, available for maintenance respiration	kg ha^{-1} d^{-1}	Auxiliary	01487
SGFF	Variable indicating whether development stage is beyond start of grain fill (1) or not (0)	unitless	Auxiliary	01090
SLLAE	Sunlit leaf area	m^2 ha^{-1}	Auxiliary	01133
SLOPE	Slope of saturated vapour pressure curve at 'effective' day time temperature	mbar C^{-1}	Auxiliary	00953
SLTF(I)	Rate of inflow of nitrogen in a soil compartment	kg ha^{-1} d^{-1}	Rate	00812
SLTF(1)	Rate of inflow of nitrogen in top soil compartment	kg ha^{-1} d^{-1}	Rate	00804
SLTFD	Rate of leaching of nitrogen beyond potential rooting zone	kg ha^{-1} d^{-1}	Rate	00820
SLWA	Leaf weight ratio, i.e. leaf weight as a fraction of total above ground weight	kg kg^{-1}	Output	01700
SONCT	Intermediate variable used to calculate maximum nitrogen concentration in plant organs as a function of development stage	unitless	Auxiliary	01739
SRR	Shoot root ratio	kg kg^{-1}	Output	01941
SSIN	Product of sine of latitude and sine of declination, used in calculation of daylength	sin^2	Auxiliary	01123
STAREA	Green area of stem and sheaths	m^2 ha^{-1}	Auxiliary	01715
STBC	Stefan-Boltzmann constant	J m-2 s^{-1} K^{-4}	Parameter	00537
STCEF	Maximum value of time constant for ear formation	d	Parameter	01592
STCFF	Maximum value of time constant for floret formation	d	Parameter	01633
STCGF	Maximum value of time constant for grain formation	d	Parameter	01651

Acronym	Definition	Units	Variable type	Line no
STCSF	Maximum value of time constant for spikelet formation	d	Parameter	01613
STDAY	Day number on first day of simulation	unitless	Parameter	00298
STORC(I)	Storage capacity for available water in a soil compartment	$m^3\ m^{-3}$	Auxiliary	00183
STRESF	Factor accounting for the effect of leaf rolling on effective leaf area	unitless	Auxiliary	01686
SUMT	Intermediate variable for calculation of soil surface evaporation	cm	Auxiliary	00640
	Set to zero			00633
SVPA	Average daily saturated vapour pressure	mm Hg	Forcing	00431
SVPAM	Average saturated vapour pressure during daylight hours	mbar	Forcing	00931
SWDF	Variable used to set different sowing densities	unitless	Parameter	00214
SWDTL	Final weight of stem and sheaths of non-reproductive tiller, i.e. the end of ear formation	kg $tiller^{-1}$	Auxiliary	01573
SWPBT	Switch variable to indicate whether root tip is in wet soil compartment (1) or not (0)	unitless	Auxiliary	00645
	Set to zero			00634
S1	Intermediate variable in calculation of cuticular water loss	unitless	Auxiliary	00999
TADRW	Total above ground dry weight	kg ha^{-1}	Output	01927
TCDDH	Time constant for dehydration of plant tissue	d	Parameter	01283
TCEF	Time constant for ear formation	d	Auxiliary	01591

Acronym	Definition	Units	Variable type	Line no
TCFF	Time constant for fertile floret formation	d	Auxiliary	01632
TCGF	Time constant for grain formation	d	Auxiliary	01650
TCSF	Time constant for spikelet formation	d	Auxiliary	01612
TCTF	Time constant for tiller formation	d	Auxiliary	01549
TCMG	Time constant for microbial growth	d	Parameter	00677
TCN	Time constant for nitrification	d	Parameter	00795
TCTFT	Time constant for tiller formation as a function of canopy temperature	–	Function	01551
TCTR	Time constant for translocation of reserves	d	Parameter	01479
TCU	Time constant for uptake of nitrogen	d	Parameter	01769
TCUD	Time constant for uptake of nitrogen by diffusion	d	Parameter	01863
TCV	Time constant for volatilization of ammonia	d	Parameter	00790
TDRAIN	Total water loss by drainage beyond potential rooting zone	mm	Output	00576
TDT(I)	Depth of upper boundary of soil compartment below soil surface	mm	Auxiliary	00192
TDT(1)	Depth of upper boundary of first soil compartment below soil surface	mm	Auxiliary	00190
TEC	Factor accounting for the effect of soil temperature on root conductivity	unitless	Auxiliary	00911
TECT	Factor accounting for the effect of soil temperature on root conductivity as a function of soil temperature	–	Function	00913
TEF	Factor accounting for the effect of canopy temperature	unitless	Auxiliary	01211

Acronym	Definition	Units	Variable type	Line no
	on maintenance respiration			
TEVAP	Total seasonal soil surface evaporation	mm	Output	00562
TF	Factor accounting for the effect of soil temperature on decomposition of organic material	unitless	Auxiliary	00907
TFT	Factor accounting for the effect of soil temperature on decomposition of organic material as a function of soil temperature	–	Function	00909
TFOM	Total weight of fresh organic material in soil profile	kg ha^{-1}	Output	00888
	Set to zero			00873
TFON	Total weight of nitrogen in fresh organic material in soil profile	kg ha^{-1}	Output	00884
	Set to zero			00872
TGERD	Cumulative number of days with favourable conditions for germination	d	Auxiliary	00321
	Set to zero			00282
	Must be reset in TERMINAL section for multiple runs			02012
TLN	Tiller density	no ha^{-1}	State	01543
TLNI	Initial tiller density, i.e. at emergence	no ha^{-1}	Initial state	00210
	Must be reset in TERMINAL section for multiple runs			02046
TLNIX	Auxiliary variable to save original value of TLNI	no ha^{-1}	Auxiliary	00207
TLNIXX	Auxiliary variable to avoid zero division	no ha^{-1}	Auxiliary	01549
TLNM	Maximum number of tillers that can be maintained by current assimilate supply	no ha^{-1}	Auxiliary	01553
TLRGA	Threshold concentration of reserves beyond which as-	kg kg^{-1}	Parameter	01186

Acronym	Definition	Units	Variable type	Line no
	similation is affected			
TMPA	Average daily air temperature	°C	Forcing	00403
TMPC	Average daily canopy temperature	°C	Auxiliary	00418
TMPFT	Reduction factor for gross CO_2 assimilation as a function of temperature	–	Function	01189
TNABM	Total weight of nitrogen in above ground material	kg ha^{-1}	Output	01933
TNDEM	Total nitrogen demand of the canopy	kg ha^{-1} d^{-1}	Auxiliary	01855
TNGIFT	Total nitrogen fertilizer application	kg ha^{-1}	Output	00778
TNINT	Total amount of inorganic nitrogen in soil profile	kg ha^{-1}	Output	00198
	Set to zero			00196
TNLCH	Total nitrogen loss by leaching	kg ha^{-1}	Output	01953
TNLST	Rate of nitrogen transfer from dying leaf blades to stem and sheaths	kg ha^{-1} d^{-1}	Rate	01801
TNNR	Total number of non-reproductive tillers	no ha^{-1}	Auxiliary	01567
TNRT	Total available mineral nitrogen in wet rooted zone	kg ha^{-1}	Output	00815
	Set to zero			00806
TNUDF	Total rate of nitrogen uptake by diffusion	kg ha^{-1} d^{-1}	Auxiliary	00835
	Set to zero			00830
TNUM	Total rate of nitrogen uptake by mass flow	kg ha^{-1} d^{-1}	Auxiliary	00817
	Set to zero			00807
TOTINF	Total seasonal infiltration	mm	Output	00574
TOTRAN	Total seasonal crop transpiration	mm	Output	01026
TRAIN	Total seasonal rainfall	mm	Output	00444
TRAN	Rate of canopy transpiration as dictated by actual soil moisture conditions	mm d^{-1}	Auxiliary	01020
TRANW	Actual rate of canopy tran-	mm d^{-1}	Rate	00627

Acronym	Definition	Units	Variable type	Line no
	spiration, equal to APTRAN if TRP.LT.0, equal to TRAN if TRP.GT.0			00629
	Set to zero			00623
TRFRS	Rate of translocation of reserves to vegetative structures	kg ha^{-1} d^{-1}	Rate	01471
TRNLL	Rate of nitrogen loss from live leaf blades	kg ha^{-1} d^{-1}	Rate	01751
TRNLS	Rate of nitrogen loss from live stem and sheaths	kg ha^{-1} d^{-1}	Rate	01805
TRP	Variable indicating whether transpiration is gouverned by current soil moisture conditions (+1) or set equal to potential (-1)	unitless	Parameter	00630
TRPMM	Potential rate of moisture uptake per unit 'effective' root length	mm d^{-1} mm^{-1}	Auxiliary	00622
TRR(I)	Actual rate of moisture uptake for transpiration in a soil compartment	mm d^{-1}	Rate	00626
TS	Soil temperature	°C	State	00903
TSDAY	Total number of consecutive days with conditions conducive for seed deterioration	d	Auxiliary	00322
	Set to zero			00332
	Must be reset in TERMINAL section for multiple runs			02013
TSI	Initial soil temperature at start of the simulation	°C	Initial state	00277
TVEGM	Total weight of vegetative crop organs	kg ha^{-1}	Output	01931
UMXR	Maximum rate of nitrogen uptake by a closed canopy	kg ha^{-1} d^{-1}	Parameter	01875
VAR(I)	Auxiliary variable in calculation of moisture uptake for soil surface evaporation in a soil compartment	cm^3 cm^{-3}	Auxiliary	00638

Acronym	Definition	Units	Variable type	Line no
VPA	Actual average daily vapour pressure	mm Hg	Forcing	00429
VPAM	Actual vapour pressure during daylight hours	mbar	Forcing	00933
VPASW	Variable indicating whether vapour pressure is calculated from dew point (-1) or given directly as input (1)	unitless	Parameter	00435
W(M,I,L)	Array containing selected output variables for summary of model performance	–	Auxiliary	02019 till 02031
WATER*(I)	Amount of soil moisture in a soil compartment	mm	State	00851
WAV	Total available soil moisture in the potential root zone at emergence	mm	Output	00612
WAVT	Available soil moisture at emergence per soil compartment	mm	Output	00609
	Set to zero			00600
WBT08	Wet bulb temperature at 8.00 hours	°C	Forcing	00361
WBT08T	Wet bulb temperature at 8.00 hours as a function of day number	–	Function	00363
WBT14	Wet bulb temperature at 14.00 hours	°C	Forcing	00371
WBT14T	Wet bulb temperature at 14.00 hours as a function of day number	–	Function	00373
WCLIM	Volumetric soil moisture content at air dryness	$cm^3\ cm^{-3}$	Parameter	00510
WCPR	Dimensionless moisture number for calculation of reduction in soil surface evaporation due to dry soil surface	unitless	Auxiliary	00560
WCRR	Weight to conductivity ratio of the roots	$kg\ mm^{-1}\ d^{-1}$	Parameter	01012

Acronym	Definition	Units	Variable type	Line no
WGER	Total amount of soil moisture in potential germination zone	mm	Auxiliary	00316
	Set to zero			00314
WGR	Dry weight of the grain	kg ha^{-1}	State	01501
WLTPT(I)	Volumetric soil moisture content at wilting point per soil compartment	cm^3 cm^{-3}	Table	00486
WLVS	Dry weight of live leaf blades	kg ha^{-1}	State	01233
WLVSI	Initial dry weight of live leaf blades, i.e. at emergence	kg ha^{-1}	Initial state	00212
	Must be reset in TERMINAL section for multiple runs			02048
WLVSIX	Auxiliary variable to save value of WLVSI for resetting in TERMINAL section	kg ha^{-1}	Auxiliary	00209
WLVSNT	Auxiliary variable to avoid zero division in case no live leaf blades are present	kg ha^{-1}	Auxiliary	01248
WRED(I)	Factor accounting for the effect of low soil moisture on moisture uptake for crop transpiration in a soil compartment	unitless	Auxiliary	00607
WREDT	Factor accounting for the effect of low soil moisture on moisture uptake for crop transpiration per soil compartment as function of fraction available moisture	–	Function	00516
WRT	Dry weight of live roots	kg ha^{-1}	State	01409
WRTI	Initial dry weight of live roots at emergence	kg ha^{-1}	Initial state	00211
	Must be reset in TERMINAL section for multiple runs			02047
WRTIX	Auxiliary variable to save value of WRTI for resetting in TERMINAL section	kg ha^{-1}	Auxiliary	00208

Acronym	Definition	Units	Variable type	Line no
WSA	Average daily wind speed during daylight hours	cm d^{-1}	Forcing	00936
WSR	Daily wind run	km d^{-1}	Forcing	00424
WSTB	Daily wind run as a function of day number	–	Function	00426
WSTEM	Dry weight of live stem and sheaths	kg ha^{-1}	State	01370
WSTEMN	Auxiliary variable to avoid zero division in case no live stems and sheaths are present	kg ha^{-1}	Auxiliary	01385
WTOT	Total amount of soil moisture in potential root zone	mm	Output	00880
	Set to zero			00870
X	Auxiliary variable used in calculation of canopy gross CO_2 assimilation	kg ha^{-1} d^{-1}	Auxiliary	01134
	Variable is redefined several times during execution			01138 01143
YG	Efficiency of conversion of primary assimilates into grain dry matter	kg kg^{-1}	Auxiliary	00688
ZNOT	Zero plane displacement	m	Auxiliary	00942

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