

# CROPSIM — WHEAT: A model describing the growth and development of wheat

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Hunt, L. A. and Pararajasingham, S. 1995. CROPSIM — WHEAT: A model describing the growth and development of wheat. *Can. J. Plant Sci.* 75: 619–632. Crop simulation models consolidate mathematical representations of the various physiological processes underlying crop growth and development into an entity that can be used to predict the outcome of various crop, soil and weather scenarios. For wheat, a number of simulation models are already available, but most of these do not appear to be set-up to facilitate easy comparison of model outputs with experimental data, to allow easy modification for new cultivars, and to facilitate the addition of disease routines, an aspect necessary for models to be useful in the general field situation. Cropsim-wheat was developed to help overcome some of these deficiencies.

The model assumes that a crop consists of a collection of uniform plants, and performs calculations on a daily basis. It is driven by daily weather data dealing with solar radiation receipt, maximum and minimum temperatures, and precipitation. Water and nitrogen balance subroutines are included, and the rate of various crop processes is modulated through the use of multipliers that reflect the water and nitrogen states of the crop. Developmental processes are simulated using the concept of "biological days", a time measure that equates to chronological days under optimum conditions. The phases into which the life-cycle is broken relate closely to those in the widely used "Zadoks" scale. Dry matter accumulation is calculated from intercepted radiation, and distributed largely on the basis of demand. A minimum fraction of daily assimilate, however, is reserved for root growth. Leaf area is computed on the basis of potential leaf size and available dry matter, whereas stem and spike areas are calculated from the stem and spike weights. Both leaf and stem area are used in calculating radiation interception. Critical stresses, water saturation during early seedling growth and low temperature during the winter period, can result in plant death. Low temperatures, when they occur around heading, can also result in sterility and reduced grain number.

The model performance has been compared with datasets from North America and Europe, and results of these comparisons will be conveyed in companion publications. The model has been set-up, however, on the premise that model development should be a continuing process as new datasets become available and new applications are contemplated. With this in mind, it has been built to use file structures that facilitate the handling and storage of field data, and the easy comparison of field and simulated data. It should thus be useable by experimenters as a tool to help in the analysis of field studies.

**Key words:** Wheat, simulation, nitrogen, water, development, growth

Hunt, L. A. et Pararajasingham, S. 1995. CROPSIM — Blé: modèle décrivant la croissance du blé. *Can. J. Plant Sci.* 75: 619–632. Les modèles de culture en simulation intègrent par représentation mathématique les divers processus physiologiques sous-tendant la croissance et le développement en un ensemble qu'on peut utiliser pour prédire l'évolution de divers scénarios culturels, édaphiques et météorologiques. Dans le cas du blé, il existe déjà un certain nombre de modèles en simulation, mais la plupart ne se prête pas facilement face à une comparaison des sorties modélisées avec les données expérimentales ni à l'introduction de modifications pour les adapter aux nouveaux cultivars ni à la prise en compte des maladies, aspect nécessaire pour rendre ces modèles pleinement applicables dans les situations agronomiques complètes. Le modèle Cropsim-blé a été conçu particulièrement pour surmonter quelques-unes de ces lacunes. Le modèle s'appuie sur la considération qu'une culture est une collection de plantes homogènes et ces calculs sont exécutés sur une base journalière. Il est actionné par les données météorologiques quotidiennes: rayonnement solaire incident, température maximum et minimum et précipitations. Il compte des sous-programmes pour les bilans de l'eau et de l'azote, ces deux éléments étant exprimés sous forme de multiplicateurs qui servent à moduler le rythme des divers processus physiologiques de la culture. Les processus phénologiques sont simulés au moyen de «jours de croissance» mesure du temps correspondant aux jours chronologiques en conditions optimales. Les diverses phases du cycle de croissance correspondent étroitement à celles largement utilisées dans l'échelle de Zadok. L'accumulation de la matière sèche est calculée d'après le rayonnement intercepté et est répartie pour une grande part selon les besoins de la culture. Une fraction minimum de l'assimilat quotidien est toutefois réservée pour la croissance racinaire. La surface foliaire est calculée en fonction de la taille potentielle des feuilles ainsi que de la matière sèche disponible, tandis que les surfaces des tiges et des épis sont calculées à partir du poids de ces organes. Les surfaces foliaires et caulinaires sont toutes deux utilisées dans le calcul du rayonnement intercepté. Des stress

**Abbreviations:** CAID, canopy area index; Bd, biological days; IBT, increments in biological time; PAR, photosynthetically active radiation; VF, vernalization factor

critiques comme la saturation d'eau durant les débuts de la croissance et les basses températures durant l'hiver peuvent occasionner la mort des plantes. Les basses températures, lorsqu'elles surviennent à l'époque de l'épiaison, peuvent entraîner la stérilité et, par conséquent, diminuer le nombre de grains par épi. La performance du modèle est comparée avec les bases de données provenant d'Amérique du nord et d'Europe. Les résultats de ces comparaisons feront l'objet de publications corollaires. Il faut préciser que le modèle est conçu sur le principe que l'élaboration d'un modèle est un processus continu, capable d'accueillir les nouvelles bases de données à mesure qu'elles deviennent disponibles, ainsi que les nouvelles utilisations envisagées. À partir de ce principe, il a été conçu pour utiliser des fichiers qui facilitent la manipulation et le stockage de données sur le terrain et la comparaison de ces données avec les données en simulation. Ainsi conçu, il devrait rendre de précieux services aux chercheurs comme auxiliaires dans l'analyse des études sur le terrain.

**Mots clés:** Blé, simulation, azote, eau, développement, croissance

A crop simulation model is a consolidation of mathematical representations of the various physiological processes that underlie crop growth and development. Models are available for many crops, with each one being unique in the number of processes included, in the assumptions made as to how processes interact with each other and with the environment, and in the way that processes and their control factors are represented in the model.

For wheat, over 70 models have been developed over the past 20 yr (McMaster 1993). Not all of these models have been based on the physiological processes of the crop, however, and the number of process oriented models developed lies somewhere between 10 and 20. Prominent examples of such models, reflecting a variety of approaches to the representation of wheat growth and development, but all being useable on PCs, are: Ceres (Ritchie and Otter 1984), Simtag (Stapper 1984), Arcwheat1 (Porter 1984; Weir et al. 1984), Swheat and Sucros (van Keulen and Seligman 1987; van Laar et al. 1992), and the models developed by Amir and Sinclair (1991a,b) and Sinclair and Amir (1992). Of these models, the Swheat and Sinclair models have been developed specifically for spring wheat; the others are able to handle fall planted wheat, and most have water and nitrogen subroutines. The original Arcwheat model assumed no water or nitrogen limitations, but a recent update (Afrwheat 2) includes subroutines to simulate the effect of these environmental variables on crop performance (Porter 1993). Other models that have similarities with the ones already mentioned, but that may not be known to as wide an audience, are also available (e.g. Demeter: Matthaus et al. 1991; Nwheat: Groot 1987; Putu: Singles and de Jager 1991a,b,c; and Sirius: Jamieson 1993, personal communication).

The number of wheat simulation models available suggests that it should be possible to use one or more of them as tools to aid the evaluation and interpretation of field experiments, and the formulation of management regimes for specific field situations. Unfortunately, most available models are not set up to facilitate both easy comparison of model outputs with experimental data, and easy modification for new cultivars. New data standards to facilitate the handling of experimental data and the comparison of model outputs with measured data have recently been elaborated (Hunt et al. 1994), and software to simplify the computation of genotype specific characteristics has also been released (Hunt et al. 1993). The model documented here was developed to conform to the above-mentioned data standards, to be useable with the genotype characteristic software, and, to allow easy addition of disease routines, an aspect not covered in the current wheat models.

A further aim was to build on progress made in existing models by adding extra capabilities, for example, capabilities to deal separately with cultivar differences in tiller death and tiller production, and to allow for water supply from a water table. This paper presents a first description of the model; subsequent papers will deal with the performance of the model relative to field data.

### PREVIOUS WHEAT MODELS

In many current process based wheat models, Ceres, Afrc, and Putu to name a few, it is assumed that crop development rate is dependent critically on temperature. Generally, accumulated thermal time (cumulative day degrees above a critical base temperature) is used as a means of measuring the progress of development. McMaster et al. (1992), however, in their phenology model, used phyllochron (the accumulated thermal time between successive leaf appearances) as the measure of thermal time between developmental stages.

In models in which the effect of photoperiod on development rate is considered (the Swheat and Sinclair models are exceptions), photoperiod is taken to modify the length of the vegetative phase. Further, models capable of simulating winter wheat growth often contain constraints on development caused by vernalization. The effect of too short a photoperiod, or lack of vernalization, on development rate is normally included as a factor modifying the thermal time (e.g., Ceres, Afrwheat) or daily development rate (e.g., Putu). Genotypic variability in the sensitivity of photoperiod, or vernalization, is taken into account in models such as Ceres, Simtag and Putu.

The simulation of growth processes generally revolves around the simulation of three phenomena: interception of solar radiation and dry matter production, dry matter partitioning, and leaf area expansion. Interception is commonly estimated as a function of leaf area index, generally using an extinction coefficient, the value of which varies between models from 0.44 in the Afrwheat model to 0.85 in the Ceres model. The solar radiation is, in many models, converted to dry matter by use of an overall conversion factor. The value of this factor varies among models (e.g., 2.9 g dry matter MJ<sup>-1</sup> PAR in Ceres when incident PAR is between 10 and 11 MJ m<sup>-2</sup>d<sup>-1</sup>; and 1.1 g dry matter MJ<sup>-1</sup> solar radiation in the Sinclair model during the vegetative stage), and in some cases has been varied with developmental phase (e.g. in Simtag, 2.9 g dry matter MJ<sup>-1</sup> in the pre-anthesis period, down to 2.3 g dry matter MJ<sup>-1</sup> in the post-anthesis period). In the Sinclair model, the conversion factor

was computed as a function of thermal time during the grain filling phase. In other models (e.g., Swheat) intercepted radiation is converted to gross photosynthesis by making use of the photosynthesis–light response curve of individual leaves and a complex photosynthesis model (Goudriaan and van Laar 1978). The dry matter production from intercepted radiation is assumed to be affected by temperature (e.g., Ceres, Simtag, Swheat), drought stress (e.g. Ceres, Simtag, Swheat) and/or nitrogen and reserve levels of leaves (e.g., Ceres, Swheat).

Dry matter distribution is usually simulated by specifying the fraction of total dry matter allocated to each growing organ, with the magnitude of the fraction allocated being determined by thermal time (e.g., Ceres, Simtag) or growth stage (e.g., Afrc, Swheat, Simtag). In the Sinclair model, however, dry matter partitioning is simulated for grain growth only.

In some wheat models, leaf area development is modelled as the production, growth and death of leaves on the main stem and tillers, an approach that necessitates the simulation of tiller production (e.g., Ceres, Simtag, Afrc and Sinclair models). The rate of tiller formation in these models is driven by accumulated thermal time and closely related to phyllochron interval. In the Swheat model, although leaf area development is handled independently of tiller formation, the latter is simulated to set the number of spikes per unit area. Rate of tiller formation in this latter model is simulated from emergence to the onset of the stem elongation stage, and is controlled by assimilate flow to the sites of tiller formation and crop development rate. The tiller formation rate is assumed to be slowed by soil water and nitrogen deficiencies. In Ceres, tiller formation in the period between the beginning of spike growth and anthesis is assumed, as in the Swheat model, to be dependent upon assimilate supply modified by soil water and nitrogen contents. Cessation of tiller formation in Ceres and Swheat models is influenced by environmental and genetic factors as well as developmental status, whereas the latter aspect is of major significance in the Afrc, Simtag or Sinclair models.

Not all the tillers formed grow into mature, spike bearing tillers in wheat. Tiller death is mainly the result of competition between and within tillers for environmental resources such as light, water and nutrients. Excess tillers are lost based on tiller density (e.g., Ceres, Afrc), leaf area index (e.g., Swheat), soil water (e.g., Ceres, Simtag), soil nitrogen (e.g., Ceres) and radiation (e.g., Simtag). The effect of cold temperature on tiller death at early developmental stages is also simulated in Ceres. Not all wheat models simulate tiller death, however (e.g., Sinclair model).

In those models in which the growth of individual leaves on tillers is simulated, leaf appearance rate is generally handled as a function of cumulative thermal time (e.g., Ceres, Simtag, Afrc, Sinclair), with the interval between the appearance of successive leaves (the phyllochron interval) being assumed constant. In the Afrc model, following Baker et al. (1980), phyllochron interval is calculated based on the rate of change of daylength at crop emergence to account for the observed variability in the interval with respect to latitude and date of planting. Variability due to genotype as well as

latitude and date of planting in phyllochron interval is accounted for in the Simtag model through the introduction of two factors, phyllochron and daylength factors, respectively.

Following the appearance of a leaf, the increase in leaf area has been modelled in a variety of ways: as growth to a potential maximum size (e.g., Afrc), as a function of preceding leaf size (e.g., Simtag) or as a function of main stem or tiller number (e.g., Sinclair model). In the Ceres model, the increase in leaf area is calculated on the basis of an individual plant using information on main stem leaf appearance rate, tiller number, and relative leaf growth rate. Leaf area growth in Ceres is reduced by assimilate supply, water and nitrogen stresses. Leaf area expansion rate per plant in the Putu model is considered to be a function of effective temperature (mean of daily maximum and minimum temperatures), crop stage, plant population, inter-leaf competition expressed in terms of leaf area index, and water stress. In Swheat, leaf area increase is modelled without regard to tiller formation as the product of rate of increase in dry matter of the leaf blades and specific leaf area (leaf surface area/leaf dry matter). The influence of soil water and nitrogen shortages on leaf area expansion is taken into account.

Leaf senescence is related to one or more of the following: leaf age in cumulative thermal time (e.g., Afrc, Swheat, Ceres, Simtag), freezing (e.g., Ceres), frost (e.g., Simtag), water stress (e.g., Ceres, Swheat, Putu), nitrogen stress (e.g., Ceres, Swheat) and leaf area index (e.g., Ceres, Swheat, Putu).

Grain number and growth rate may need to be simulated to determine final grain yield. These aspects are usually simulated by reducing a potential grain number and/or a potential grain growth rate based on temperature, water stress and/or assimilate availability. The potential grain growth parameters are genetic inputs in the Ceres and Simtag models whereas in the Swheat and Putu models the potential grain growth rate is calculated. In the Afrc model all net assimilate between anthesis and maturity plus 30% of stem weight at anthesis are made available for grain growth. In the Sinclair model grain growth is simulated in a different manner by assuming that harvest index increases linearly during the grain growth period.

### THE CROPSIM — WHEAT MODEL

Cropsim — wheat simulates growth and development on the assumption that the crop is comprised of uniform plants. It does not address the problem of variation among plants within a stand, as attempted by McMaster et al. (1992) in their wheat phenology model. However, the model has been built for future use along with various weed species models. Structures to permit such use, which would have to facilitate the sequential operation of different models, would also permit the handling of heterogeneous wheat stands.

The model works using a daily time step and does not attempt to account for minute to minute variations in input environmental and simulated crop and soil variables. It is driven by four "prime" weather variables: daily solar radiation receipt, maximum and minimum daily temperature, and daily precipitation. A number of other environmental

variables, however, are derived from these primary variables, and/or other inputs that specify the site. Such "derived" variables, used to modulate the rate of plant or root processes, include daylength and soil temperatures by layer. This latter is calculated in a manner similar to that used both in the EPIC (Erosion-Productivity Impact Calculator) model of Sharpley and Williams et al. (1990) and in Ceres (see Jones and Kiniry 1986). It is calculated as a function of the average annual air temperature ( $^{\circ}\text{C}$ ), the annual amplitude in mean monthly air temperature ( $^{\circ}\text{C}$ ), the soil depth at which temperature is assumed constant, and the date of the warmest day of the year.

In operation, the model performs a number of operations sequentially each day. These will be described in the following sections.

### Water Balance

Water balance components are calculated for a multi-layered soil with the layer thickness being the same as for the soil and initial conditions data. Preferred layer thicknesses, from the surface down are 5, 10, 15, 15, 15 and then 30 cm for all remaining layers. Maximum layer number is 15.

**RUNOFF.** Runoff is calculated using a simple relationship to the water retention capacity of the uppermost three (or as specified) layers of the soil. Water does not run off until these layers are saturated, and all water runs off once they are saturated. Maximum retention thus occurs when the soil is dry.

**DRAINAGE.** Each soil layer, which can be filled to saturation, will drain if the water content is above the lower limit. The amount is determined either by a layer specific drainage constant, or by the amount that the next layer can hold before becoming saturated. The layer specific drainage constant is input in the soil file; if it is missing, an overall constant is used for each layer. Drainage does not occur from, nor into, a frozen layer.

**EVAPORATION.** Potential evapotranspiration is computed using an adaptation of the Priestley and Taylor (1972) equation similar to that used in Ceres (Ritchie and Otter 1985). The approach hinges on a calculation of the fraction of absorbed solar radiation used for evaporation, a fraction which is assumed to be dependent on the mean daily temperature. This latter is calculated giving more weight to the maximum than to the minimum ( $0.6 * T_{\text{MAX}} + 0.4 * T_{\text{MIN}}$ ). If mean temperatures are between  $5^{\circ}\text{C}$  and  $-24^{\circ}\text{C}$ , the fraction used increases linearly from 0.45 at  $5^{\circ}\text{C}$  to 0.70 at  $24^{\circ}\text{C}$ . If mean temperatures are above  $24^{\circ}\text{C}$ , the fraction increases linearly from the value of 0.70 at  $24^{\circ}\text{C}$  to 1.0 at  $30^{\circ}\text{C}$  and, with the same slope, to 1.5 at  $40^{\circ}\text{C}$ . Below  $5^{\circ}\text{C}$ , the fraction decreases from 0.45 at  $5^{\circ}\text{C}$  to 0.44 at  $1^{\circ}\text{C}$ , and to yet lower values as mean temperature falls to zero and below, but with the slope being the same as between  $5^{\circ}\text{C}$  and  $1^{\circ}\text{C}$ . The energy equivalents of evapotranspiration calculated using the fractions determined as above are converted to quantities of water by use of a constant latent heat of evaporation of  $2450 \text{ J g}^{-1}$ .

The absorbed solar radiation is determined from incoming solar radiation using an albedo that varies from the value input for the soil when there is no crop cover, to 0.23 for a complete active crop cover, and to 0.33 for a complete, mature crop cover. The crop cover, assumed equal to the fractional interception of solar radiation, is determined using a canopy extinction coefficient for short wave radiation. This is computed from the extinction coefficient for photosynthetically active radiation, an input variable, assuming that the leaf transmission coefficients for photosynthetically active and infra-red radiation are 0.1 and 0.4, respectively.

Potential transpiration is calculated by multiplying the potential evapotranspiration by the fractional interception of solar radiation. Actual transpiration is the same as potential transpiration when adequate water is present, but is reduced as the amount of water available on any day drops below that required to meet potential transpiration requirements. The amount of water available on any day is calculated by summing the immediately available water in the rooting zone. Immediately available water is set equal to available water content multiplied by a relative availability factor, where the latter has a value of 1.0 when the ratio between actual and maximum available water is greater than 0.4, and a value that decreases linearly from 1.0 to 0.0 as the actual/maximum ratio falls from 0.4 to 0.0.

Soil evaporation is calculated using the concepts developed by Ritchie (1972). Evaporation from the soil surface is considered separately for constant rate and falling rate phases. In the former, the soil is sufficiently wet for water to be transported to and lost from the surface at a rate equal to the soil evaporation potential. In the falling rate phase, the surface soil water content is below a threshold value, such that soil evaporation depends on the flux of water through the upper layer of soil to the evaporating surface. Following wetting of the soil surface the amount of drying required before evaporation falls below the potential rate is input with other soil information. Values generally fall between 6 and 12 mm for different soils (Ritchie 1972). Cumulative evaporation during the second phase is a square root function of time, with the proportionality constant being related to the available energy at the soil surface, to a maximum of  $3.5 \text{ mm d}^{-1}$ , as in the Simtag model (Stapper 1984).

**UPTAKE.** Water uptake is set equal to the actual transpiration, and distributed down the profile in a manner determined by the amount of water available in each layer. Water is used from the uppermost layers first so that a drying front will progress down the profile. The water content of each layer is then adjusted to account for that taken up by the plant. These calculations are continued when the roots reach a permanent water table, but in this case, the water content of the lowermost layer is reset to saturation each day.

**REDISTRIBUTION.** Water movement is allowed to occur between soil layers in which the water content is below the drained upper limit in proportion to the water content of the respective layers. To avoid instability, however, no more than 5% of the water in one layer is allowed to move in any one day.

### Nitrogen Balance

Nitrogen balance components are calculated using the same layering as for the water balance calculations. Required data, organic carbon content of the different layers for example, thus must be provided using the same vertical breakdown as for water balance aspects. The conceptual framework is similar, but somewhat simpler, than that used in Ceres (see Godwin et al. 1986).

**MINERALIZATION.** Two pools of organic matter are assumed to occur in each soil layer. One of these is the fresh organic matter pool, composed of the root and shoot residues of the previous crop, and its rapidly decomposing products; the other is the stable organic matter or "humus" pool composed of all other organic matter in the soil. Nitrogen can be released from both pools in direct proportion to their sizes. The maximum rate at which this can occur is set at 5% per day for the fresh organic matter, and slightly under 0.01% per day for the humus. This latter value, however, is multiplied by a 0 to 1 factor that is input along with other soil information, to reflect the actual mineralization capabilities of the soil in question. These maximum rates are multiplied by the product of factors that summarize the effects of soil temperature, soil moisture and, for the humus only, the overall C:N ratio of the layer. The temperature factor increases linearly from zero at 5°C to 1.0 at 30°C; the water factor increases from zero at the lower limit to 1.0 at the upper limit, and then decreases to zero for a saturated soil; the C:N factor decreases exponentially from a maximum of 1.0 at a C:N ratio of 25 to 0.1 at a ratio of 100.

The decay of fresh organic matter results not only in the release of nitrogen, but also in the release of CO<sub>2</sub> and the production of new stable organic matter. The distribution of carbon between CO<sub>2</sub> and stable organic matter is controlled by an empirical factor that is currently set to deliver 20% to the stable organic pool. Accumulation of carbon in this pool is generally associated with a build-up of stable nitrogen. This "immobilization" of available nitrogen is set to equal either the mineral nitrogen content of the layer, or the amount of nitrogen needed to establish a standard C:N ratio in the newly produced humus. The standard C:N ratio in the humus is set to a value of 10.

**DENITRIFICATION.** Denitrification rate, calculated whenever soil water in a layer is greater than the drained upper limit, is determined as a function of the water content, the carbon concentration, and the temperature of the soil layer in question, following an approach similar to that used in Ceres (see Jones and Kiniry 1986; Godwin and Jones 1991). The basic denitrification rate, applicable when all conditions are optimum, is set at 50% per day. This is reduced by multiplication by the product of the various controlling factors. The water factor increases linearly from zero at the drained upper limit to 1.0 at saturation; the carbon factor increases from zero when there is no humus present to 1.0 when there is 2.0% organic carbon present in stable organic matter; and the temperature factor increases exponentially from a value of 0.1 at 1°C to 0.7 at 40°C.

**NITRIFICATION.** Nitrification is calculated as a function of soil water, temperature, pH and NH<sub>4</sub><sup>+</sup> concentration, again following an approach similar to that used in Ceres (see Jones and Kiniry 1986; Godwin and Jones 1991). The maximum rate is determined from the NH<sub>4</sub><sup>+</sup> concentration in the soil layer using a Michaelis-Menten expression, with the concentration at which 50% is denitrified in one day being set at 90 g Mg<sup>-1</sup>. This rate is multiplied by the minimum of factors that reflect the impact of temperatures, soil water content, and pH. The temperature factor, which is determined from the soil temperatures of the layer using an exponential function, increases from zero at freezing to a maximum of 1.0 at 35°C, and remains at the maximum at high temperatures. The pH factor increases linearly from zero at pH 5.0 to a maximum of 1.0 at pH 8, and the soil water factor increases from zero at the lower limit to 1.0 at the drained upper limit, and then decreases at higher moisture contents to zero at saturation.

**LEACHING.** Water draining through a soil can bypass the main body of the soil and carry only a small proportion of the dissolved solute in any given layer (see Addiscott and Whitmore 1991). The degree to which intra-layer mixing of rapidly draining water and water already present in a layer approaches a steady-state is influenced by the aggregate size distribution of the soil (Addiscott et al. 1986). These effects are not simulated in detail, but accommodated with an empirical factor that reduces the nitrogen concentration in the drainage water below that in the layer at large.

**UPTAKE.** Nitrogen in the crop is modelled assuming that plant parts (leaf, stem, root) have an upper and a lower nitrogen concentration, expressed on a dry weight basis, and that these alter with phenological stage (see van Keulen and Seligman 1987). Leaves and stems have a wider concentration range than roots and have higher maximum and minimum concentrations for most phenological stages. Maximum leaf nitrogen concentration is set at 6.0% from emergence to initiation of the terminal spikelet, from which point it falls to a value of 0.5% by the end of grain filling. The minimum value for leaf nitrogen starts at 2.5%, then falls to 0.25% by end of grain filling. Equivalent values for root nitrogen are 2.5% falling to 1.0% for the maximum value, and 1.5% falling to 0.5% for the minimum. These values are based on those used by Groot (1987) and Porter (1993).

Crop nitrogen demand is calculated on the basis of the difference between the current nitrogen concentration of leaves, stems, and roots and their maximum value for the current developmental stage. This difference, multiplied by shoot or root dry weight gives total crop nitrogen demand for the day. Nitrogen uptake is calculated from the nitrogen demand, assuming that mineral nitrogen present in the rooted zone is available within a relatively short time period (van Keulen et al. 1975). A value of 30% availability for any day has been used, higher than the 10% suggested by Groot (1987).

Nitrogen uptake takes place in soil layers that have been penetrated by roots, and that have a moisture content above the lower limit. The potential rate of nitrogen uptake

from the total soil profile is obtained by adding the amounts of nitrogen in the soil layers in which water content is above the lower limit multiplied by the percentage that is assumed to be available on any day. Actual uptake is calculated downwards from the surface layer, a process that is continued until the required amount is obtained, or until the lowermost layer occupied by roots is reached.

### Crop Development

**VEGETATIVE.** Germination occurs at the maximum rate if there is more than 0.1 mm extractable water per mm depth in the seed zone, as in the Simtag model of Stapper (1984). Once in process, and assuming no further moisture stress, 2 d at the optimum temperature are required for germination of a seed with no dormancy, longer if the temperature is less than or greater than the optimum range. Soil temperatures may be most appropriate for these and some other calculations (see Hay and Wilson 1982), but as there is still some doubt as to the method used for computing soil temperatures, air temperatures are used. The temperature response has a base temperature set at 0°C, similar to the value of 0.4°C derived by Addae and Pearson (1992), but lower than the value of 2°C reported by Angus et al. (1981), and a lowermost optimum of 26°C. Dormancy effects are accounted for as an input describing the condition of the seed at planting time.

Elongation of the shoot (coleoptile) is set at 1.0 cm d<sup>-1</sup> at optimum temperatures [cf. 4.2 mm d<sup>-1</sup> reported by Addae and Pearson (1992)] so that time to emergence varies with sowing depth. The effect of adverse moisture contents in the seed zone during the emergence phase is quantified using the same procedure used for germination. The rate of elongation decreases linearly when the available water content falls below a threshold of 0.1 mm mm<sup>-1</sup>, and there is no elongation if extractable water in the seed zone drops below zero. The extension rate of the radicle is set at 4.0 cm d<sup>-1</sup> during the emergence phase (Addae and Pearson 1992), and is reduced by temperature and soil moisture deficit as for germination and shoot growth during emergence.

**REPRODUCTIVE.** The life-cycle of the plant is broken into eight phases with nine demarcating stages, as documented

in Table 1. The phases were chosen to ensure both general conformity with the widely used Zadoks scale (Zadoks et al. 1974), and its possible successor, the Bbch scale (Lancashire et al. 1991), and easy recognition of phase starting and end points. It is recognized, however, that some phase endings may have less fundamental significance than others (e.g. double ridges and spike emergence cf. terminal spikelet), and future model development will be directed to overcoming this limitation whilst maintaining a close relationship to field scales. In particular, attention will be placed on the double ridges stage, which appears to occur shortly (6–8 Bdays) after germination in many spring wheats (van Keulen and Seligman 1987) but much later (14–18 Bdays) in some winter wheats (Chapleau 1984; Porter et al. 1987).

The duration of the different phases is characterized in terms of Bd, chronological days at the optimum temperature and photoperiod, with no drought or nutrient stresses operative. Characteristic values, based on unpublished data and a general summary of the literature [in particular, Masoni et al. (1990) and McMaster et al. (1992)] are shown in Table 1. Some of these durations, as indicated in the table, are assumed to vary between cultivars, while others are regarded as being less variable among cultivars. In actuality, however, all may vary among cultivars, or among groups of cultivars, and scope for making appropriate changes is built into the model. Further, the end of the grain filling period may occur earlier than the potential date. The plant will cease filling kernels if the assimilate available on any day (reserves and current assimilation) falls to zero.

The increment in development (reproductive) age on any particular day is calculated as a function of the daily minimum and maximum temperatures (°C) and, when appropriate, the photoperiod and vernalization status. The effect of water status on rate of progression is not accounted for at present. Biological days are summed, and as soon as the characteristic number of Bd for any particular phase is reached, the succeeding phase is entered.

For the temperature function, a multiple point approach requiring as a minimum, four cardinal temperatures ( $T_{base}$ ,  $T_{opt}$ ,  $T_{oph}$ , and  $T_{high}$ ) has been used. These cardinal values summarize a temperature response curve in terms of (1) the

Table 1. Phases of reproductive development in Cropsim-Wheat

Phase	Characteristic durations (days with optimum conditions)	Environmental controls	Variability assumed
Germination to double ridges	6–20	Temperature (incl. vernalization), Photoperiod	Cultivar
Double ridges to terminal spikelet	2–6	Temperature (incl. vernalization), Photoperiod	Cultivar
Terminal spikelet to last leaf fully expanded	8–12	Temperature, Photoperiod	Cultivar
Last leaf fully expanded to spike emergence	3–7	Temperature, Photoperiod	Cultivar
Spike emergence to the start of anthesis	1–5	Temperature, Photoperiod	Sub-species
Start to end of anthesis	2–3	Temperature	Sub-species
End of anthesis to begin grain fill	2–4	Temperature	Sub-species
Begin grain fill to end of grain fill	13–20	Temperature (incl. base change)	Cultivar

temperature ( $T_{base}$ ) at which activity is zero but above which activity commences, (2) the lowest temperature ( $T_{optl}$ ) at which activity proceeds at a maximum rate, (3) the highest temperature ( $T_{opth}$ ) at which activity proceeds at a maximum rate, and (4) the temperature ( $T_{high}$ ) at which activity is zero but below which the process in question shows some activity. Fluctuating daily temperatures are accounted for by calculating hourly temperatures ( $T_h$ ) from a linear function between  $T_{min}$  and  $T_{max}$ , and then calculating IBT according to:

$$T_h \leq T_{base}, T_h \geq T_{high} : IBT = 0$$

$$T_h \geq T_{optl}, T_h \leq T_{opth} : IBT = 1.0$$

$$T_{base} < T_h < T_{optl} : IBT = (T_h - T_{base}) / (T_{optl} - T_{base})$$

$$T_{opth} < T_h < T_{high} : IBT = (T_{high} - T_h) / (T_{high} - T_{opth})$$

The increment in biological time for the day is calculated by summing the hourly increments and then dividing by the number of individual hourly values (13).

Linear interpolation between  $T_{max}$  and  $T_{min}$  was chosen so that outputs would coincide with those that could be derived from a simple  $(T_{max} + T_{min})/2$  approach when the daily extremes in temperature ( $T_{max}$  and  $T_{min}$ ) lie between the temperature base and the lowermost optimum, and to avoid problems of interpretation that arise when a sine curve or other function is used in contrasting seasons at latitudes where daylength changes markedly throughout the year.

For biological day computations, the base temperature for the phases from germination to anthesis is assigned a value of  $0^\circ\text{C}$ , from anthesis to the end of the grain filling period,  $8^\circ\text{C}$ . These values, which are easily changeable, were chosen to accord with reports in the literature. Gallagher (1979), for example, chose a base temperature of  $0^\circ\text{C}$  for a winter wheat, based on a regression analysis in which the residual variation increased rapidly with base temperatures greater than  $+3^\circ\text{C}$  and less than  $-3^\circ\text{C}$ . French et al. (1979) reported a base temperature of  $3^\circ\text{C}$  for spring wheats, while Angus et al. (1981) showed that the base temperature changes during the life cycle of the wheat plant. They derived a base temperature of  $2.6^\circ\text{C}$  for the period from sowing to emergence,  $3.5^\circ\text{C}$  from emergence to anthesis and  $8.9^\circ\text{C}$  from anthesis to maturity.

The effect of daylength is simulated using the curvilinear function used in Ceres (Ritchie 1991). The straight line function discussed by Major and Kiniry (1991):

$$DFDE = 1 - (DESP * (DETP - DAYL))$$

in which DFDE is the daylength factor and DAYL the photoperiodically effective daylength (i.e. including civil twilight) is also included in the code, along with the exponential function used by Angus et al. (1981) and derived from wheat development data from Australia, the Philippines and Sweden. Future work will be directed at determining which function is of the most general applicability. All functions are characterized by two parameters, the threshold photoperiod (DETP) and the photoperiod sensitivity (DESP). Changes in daylength at values greater (or less for the exponential) than the threshold have no impact on the development rate.

The photoperiod factor is used as an efficiency factor to reduce the development rate on any given day. It is used along with a vernalization factor, the minimum value of these two being used following the approach of Ritchie (1981). Photoperiod sensitivity is assumed through until the last leaf is fully expanded, but with scope for changed sensitivities at key developmental stages, while vernalization sensitivity is also assumed until last leaf, but with no change in the vernalization factor after terminal spikelet.

The VF is determined as a function of accumulated vernalization days:

$$VF = 1 - VRNR (VRNC - VRNA)$$

where VF is the vernalization factor, VRNR is the response to accumulated vernalization days, VRNC is the vernalization requirement of the cultivar (days), and VRNA is the vernalization "age" (i.e. accumulated vernalization days). The temperature response of the vernalization process is such that vernalization can occur between  $-1^\circ\text{C}$  and  $12^\circ\text{C}$ , with maximum effect in the range  $0^\circ\text{C}$  to  $8^\circ\text{C}$ . This response is based on the one used in Arcwheat1 (Weir et al. 1984) and one of the modifications suggested by Reinink et al. (1986). The vernalization effectiveness of any particular day is computed from hourly temperature means between the daily maximum and minimum temperature. Vernalization status is lost when temperatures exceed  $30^\circ\text{C}$ .

The vernalization process is ended at terminal spikelet, but the crop is assumed to respond to vernalization status until anthesis. The value of the vernalization factor at terminal spikelet is thus maintained until anthesis. Reinink et al. (1986) argued that the vernalization status should be fixed somewhat earlier than terminal spikelet, but this has not been incorporated in the current version. Further, no account was taken of reports that the rate of development of crops planted approximately one month or more before the shortest day of the year, or at latitudes less than  $30^\circ\text{C}$ , is lower than for earlier or later planted crops, or for those at higher latitudes (Stapper 1984). Further data will be required before this aspect can be verified and treated effectively.

### Crop Growth

Growth processes are modulated by both the water status and the nitrogen concentration of the plant. These effects are taken into account through the use of "deficit factors" that are calculated from water and nitrogen balance data and used as multipliers applied to the various growth processes. Prior to the computation of growth aspects, therefore, the various deficit factors are determined.

**DEFICIT FACTORS.** For water, the ratio of actual to potential transpiration is used as a descriptor of the general water status of the crop. Two deficit factors are calculated from the descriptor. The first, used currently to modulate the dry matter accumulation rate, is set equal to the actual to potential transpiration ratio when this is equal to or less than unity; it is not allowed to exceed unity. The second factor, used for leaf expansion and other growth processes, allows for a more severe impact of water stress and increases linearly



from zero when the actual to potential transpiration rate has a value of 0.5, to unity when the transpiration ratio is unity.

For nitrogen, the concentration of the leaves is used to set two deficit factors, one being more severe than the other. The factors are set equal to 1 when the leaf N concentration is above an upper bound, equal to zero when below a lower bound, and modulated linearly between 0 and 1 in the range between upper and lower bounds. Different limits are used for the two factors, and these are input as species characteristics.

**DRY MATTER ACCUMULATION.** The conservative relationship between potential crop growth rate and photosynthetically active radiation receipt, as expressed in terms of a radiation use efficiency, and as used in a number of previous models, is used to calculate potential dry matter accumulation. Radiation use efficiency, however, is assumed to be a function of daily photosynthetically active radiation receipt, to help accommodate the finding that radiation use efficiency generally increases along with the fraction of diffuse radiation, which in turn generally increases as the daily radiation receipt decreases. The function used is based on the calculations reported by Goudriaan and van Laar (1978) and is normalized to a photosynthetically active radiation receipt of  $10 \text{ MJ m}^{-2} \text{ d}^{-1}$ . Normalized values, which are used as multipliers to adjust a standard radiation use efficiency at  $10 \text{ MJ PAR m}^{-2} \text{ d}^{-1}$ , range from 2.8 at a PAR receipt of  $1 \text{ MJ m}^{-2} \text{ d}^{-1}$  to 0.9 at  $17 \text{ MJ m}^{-2} \text{ d}^{-1}$ . Further, because radiation use efficiency has been shown to vary between experiments for reasons not fully understood, it is regarded as a cultivar rather than species specific characteristic. Values of  $2.2\text{--}2.8 \text{ g MJ}^{-1}$  photosynthetically active radiation have often been computed from data obtained over an extended period of growth (Gallagher and Biscoe 1978; Hunt and Edgington 1981; Stapper 1984; Kiniry et al. 1989), and 2.5 is used as the standard until more precise information is obtained by experimentation for an individual genotype.

The potential dry matter accumulation rate for a given canopy area index (CAID lamina plus stem and spike area) is calculated by multiplying the radiation use efficiency by the amount of photosynthetically active radiation intercepted by the crop canopy. This latter is calculated from the CAID using the usual exponential equation:

$$\text{PARI} = \text{PARD} * (1. - \exp(\text{ECPC} \times \text{CAID})) \quad (5)$$

where PARI is intercepted PAR, PARD is the daily receipt of PAR and ECPC is the extinction coefficient for PAR (canopy area basis). This potential is adjusted by multiplying by a factor representing the effect of  $\text{CO}_2$  concentration, and the value so obtained converted to an actual dry matter accumulation rate by multiplying by the minimum of factors representing the effects of temperature, vapor pressure deficit, water shortage, and nitrogen shortage. The extinction coefficient for photosynthetically active radiation is currently set to a value of 0.65, a value reported earlier for a barley crop (see Monteith 1969), but this is input as a function of developmental stage so that changes during the life cycle can be accommodated.

The vapour pressure deficit factor, included because of the potential impact of this factor (Stockle and Kiniry 1990),

is calculated from input information that deals with a threshold vapour pressure deficit, above which there is no effect, and a sensitivity factor that is applicable at vapour pressure deficits greater than the threshold. The threshold is set to 2 kPa and the sensitivity to  $0.15 \text{ kPa}^{-1}$ . A mean daily vapour pressure is calculated from the minimum daily temperature, and an average vapour pressure deficit calculated from this and the saturated vapour pressure at the average day temperature. The method used to compute vapour pressure has been found to give good estimates in humid environments, but may be in error in arid environments (Bristow 1992). To accommodate this, information on the average difference between dew point at the minimum temperature and actual dew point can be read from the weather file if available, and used to adjust the minimum temperature prior to calculation of the daily vapour pressure.

**DRY MATTER DISTRIBUTION.** Dry matter is used first to satisfy aboveground growth, with roots essentially receiving from any surplus that may have accumulated in a general assimilate reserve. However, to ensure that the roots always receive some assimilates, the aboveground parts can only use up to a specified maximum fraction of the current days assimilation. This characteristic is input into the model as a function of stage of development. The maximum fraction that can be used by the aboveground parts increases from 0.3 at germination to 0.97 during grain filling. This is based on the review by Gregory et al. (1978), which showed that root growth generally ceased around anthesis, although roots at depth continued to grow after anthesis. Shoots will receive less than the maximum if leaf growth is reduced by water or nitrogen stress. In such a case, a general assimilate pool receives the excess, and root growth increases gradually as the size of the assimilate pool increases. The introduction of an assimilate pool was found necessary to avoid wide fluctuations in root and canopy growth when all assimilate remaining after the initial calculation of leaf, stem and root growth was moved to the roots. Assimilates do not move from the reserve pool to the roots, however, once leaf growth has ceased.

The method currently used to determine dry matter accumulation in the roots appears to result in inadequate below-ground growth with rapidly developing spring planted material, or excess accumulation with slowly developing fall planted material in a mild environment. To help overcome such problems, an allometric function (Troughton 1956) has been used to specify an upper limit to root growth.

The material allocated to the aboveground parts is distributed between leaf and stem in accordance with a specified parameter that is set to increase linearly from a value of 0.2 at the terminal spikelet stage to a final, cultivar specific value at the last leaf stage.

**LEAF GROWTH.** Expansion of leaves on the main stem is computed from the potential area of individual leaves and the rate of leaf appearance. Potential area, which is a function of apical dome size at the time of initiation (Kirby 1974), is correlated with the area of the previous leaf on the culm (see Stapper 1984). The potential increment from one leaf



to another is regarded as a cultivar characteristic and read from a file containing cultivar characteristics. Along with this leaf increment, potential size of the first leaf is also read from the file of cultivar characteristics. In earlier work, Stapper (1984) reported potential first leaf areas of 2.8, 2.0 and 1.8 cm<sup>2</sup> for cultivars Sonalika, Mexipak and Novi Sad respectively. In work with Cropsim, potential areas for different cultivars have varied from 1.0 to 6.0 cm<sup>2</sup>.

The potential increment in leaf area on the main stem is computed daily from the potential size of the expanding leaf and the ratio of daily phyllochron time to phyllochron interval. This daily increment, and hence the final leaf size, can be modified by water and nitrogen stresses. Both are characterized as indices and the minimum of these is used as a modifier of the potential. The daily increment of leaf area on tillers is derived from that of the main stem using arbitrary reduction factors of 0.8, 0.6 and 0.4 for tillers one, two and three or more, respectively.

Potential leaf dry matter accumulation is determined from the potential leaf expansion rate and specific leaf area. Typical specific leaf area values in wheat vary from 200 to 300 cm<sup>2</sup> g<sup>-1</sup>, depending on cultivar, temperature, light regime, water status, and crop age. Based on data obtained by Hotsonyame (1992), a standard value of 250 cm<sup>2</sup> g<sup>-1</sup> has been used, but this characteristic is input from a cultivar file and can thus be adjusted as required. The actual leaf dry matter accumulation is set equal to the potential when adequate assimilate is available from the seed, current assimilation and reserves, but is set equal to the total available assimilates when these are inadequate. In this case, leaf expansion is reduced to maintain specific leaf area at the specified value.

**LEAF SENESCENCE.** Potential leaf longevity appears to be cultivar specific in some species (e.g. cassava), but there is little information on this aspect in wheat, and potential leaf longevity has been set at 4 phyllochrons prior to the last leaf stage, considerably longer for subsequent stages. Environmental factors, however, have a distinct influence on the actual longevity of leaves. Extreme shading reduces longevity while low temperatures can also result in premature leaf death. To provide scope for handling accelerated senescence, a record is maintained of the age (temperature adjusted), dry weight, and area of the "cohort" of leaf material produced on any given day. The effect of shading is taken into account by accelerating the aging process. A critical value of leaf area index is assumed, and leaf material below the level at which this critical value is reached ages at an accelerated rate. An aging parameter represents the sensitivity of senescence to shading. Each day, the age of the cohort is adjusted, age is checked, and if the cohort is older than its life expectancy, it is removed, returning a fraction of its dry weight and nitrogen to the assimilate and nitrogen pool for that day.

The approach described above is designed for application throughout the life-cycle but is currently not used after the last leaf stage. Senescence after this stage is simulated by linear interpolation between empirical constants that specify how much of the original leaf area is lost by specific stages.

**LEAF DRY MATTER REDISTRIBUTION.** Redistribution of leaf dry matter occurs when leaves die, at which time a specified fraction of both the carbohydrates and nitrogen return to the main body for use elsewhere, and when nitrogen moves from leaf into the grain. It is assumed that nitrogen is not remobilized in an inorganic form, but as an organic molecule, so that any nitrogen redistribution is inevitably associated with dry matter redistribution.

**LEAF NUMBER.** There is a considerable amount of controversy in the literature concerning the environmental control of leaf appearance. Early work showed that the number of leaves on the main stem of wheat was a linear function of accumulated degree days after germination or emergence, implying that temperature is the main factor controlling the rate of emergence of new leaves (Gallagher 1979; Hunt and Chapleau 1986). More recent work has emphasized that the plotting of accumulated variables against each other could lead to erroneous conclusions (Demetriades-Shak et al. 1992), and that the phyllochron (the number of degree days elapsed between successive leaves on a culm) varies with planting date (Baker et al. 1980; Delecolle et al. 1985; Kirby et al. 1982; Kirby and Perry 1987). Baker et al. (1980) and Kirby et al. (1982) suggested that the phyllochron is fixed by the rate of change of daylength at emergence, but this hypothesis has not been supported with experimental evidence (e.g. Slafer et al. 1993). Cao and Moss (1989) reported that the rate of leaf appearance was a function of daylength with cultivars differing both in their sensitivity to daylength and in their rates of leaf appearance under long day conditions. For cultivars Yamhill, Stephens and Tres wheat, the maximum rate was in the region of 0.21 leaves d<sup>-1</sup> whereas for Nugaines it was approximately 0.22 leaves d<sup>-1</sup>. Sensitivity to photoperiod varied between approximately 1.7 and 2.5% h<sup>-1</sup>. This work has been criticised, however, because of low irradiance levels (Volk and Bughee 1991). Because of this, even though a number of vegetative aspects, particularly leaf length, can be affected by photoperiod (see Hay 1990), the rate of leaf appearance prior to terminal spikelet has been modelled as being independent of daylength, but dependent on temperature. Rate of leaf appearance, however, is considered a cultivar characteristic, based on the findings of Cao and Moss (1989) and other work in the literature (e.g. Syme 1974).

After terminal spikelet, the number of leaves yet to emerge appears fixed at three or four (Kirby and Appleyard 1984). The rate of leaf appearance has thus been modelled as a function of the rate of reproductive development, dependent on the basic duration of the terminal spikelet to last leaf phase and the photoperiodic sensitivity of development during this phase. During the phase after terminal spikelet, therefore, leaf appearance rate could be a function of photoperiod. Incorporation of such a response pattern helps achieve consistency with work that has shown photothermal time to be a superior predictor of leaf stage than thermal time (Masle et al. 1989; Mitchell et al. 1991), and final leaf number to increase when plants are grown in short daylength conditions, but to a lesser degree than the time taken to reach spike emergence (Allison and Daynard 1976; Hoogendoon 1985).

**ROOT EXTENSION AND DRY MATTER ACCUMULATION.** Rooting depth can increase at a rate of  $4.0 \text{ cm d}^{-1}$  (optimum conditions) to a maximum determined either by soil depth, by a specific species limit, or by soil physical conditions. Roots will only penetrate 10 cm into a saturated soil layer, will not extend into a layer in which the soil water content is at or below the lower limit, and will not extend more than one soil layer ahead of the lowest soil layer necessary to provide adequate water and nitrogen. The rate of root extension may be critical to performance in some moisture and/or nitrogen limited situations, and subsequent model development work will be directed to this aspect as appropriate datasets become available.

Root dry matter accumulation is determined by the amount of assimilate translocated from the aboveground parts, which is a function either of the general assimilate reserve pool, or of the stage specific minimum root fraction. The increment in total root length is calculated from the dry matter and the mean specific root length. A value of  $25\,000 \text{ cm g}^{-1}$  has been used for the specific root length, based on work summarized by Jones et al. (1991); the value chosen is not critical, however, because neither water nor nitrogen uptake is modelled as a function of root length. The root length increment is distributed in the soil profile using a similar procedure to that in the Ceres model (Ritchie and Otter 1984). The weighting function, however, is input as a species aspect rather than as a soil function, and this function is combined by multiplication with any soil specific limitations input along with other soil data.

**ROOT SENESCENCE.** A constant fraction of 0.5% of the roots present in each soil layer is assumed to die each day. Root weight and length are adjusted accordingly, and the fresh organic matter pool in the soil incremented.

**STEM AND SPIKE GROWTH.** Stem expansion is not currently simulated, but a stem and spike area is estimated from the stem dry weight by using a standard area:weight ratio factor of  $25 \text{ cm}^2 \text{ g}^{-1}$ . Stem (including spike) dry matter accumulation, prior to the last leaf stage, is computed from the ratio of stem to total aboveground dry matter increment, an input parameter mentioned earlier. Following the completion of expansion of the last leaf, all assimilates are devoted to the stem until it ceases growth. This occurs at an input specified stage, currently set to be at the end of anthesis. At this time, structural stem and spike growth is set to zero.

**STEM AND SPIKE SENESCENCE.** Active stem and spike area is assumed to decrease from the value reached at the onset of rapid grain fill to 5% of this value at physiological maturity. The final above-zero value reflects observations that the peduncle is often still green after the grain has reached maturity.

**GRAIN NUMBER.** Grain number is determined as a function of the difference between the aboveground dry matter at the end of anthesis and that at an earlier stage of development, currently set to be germination so that the dry matter factor is equal to the total aboveground dry weight at the end

of anthesis. A two-line relationship similar to the one described by Stapper (1984) is used, with an initial slope that is assumed constant for all cultivars, and a second slope that varies among cultivars and is used at dry matter accumulation values greater than a specified critical amount. This latter value varies among cultivars in a range from 0 to  $2.0 \text{ g}$  or greater.

**GRAIN DRY MATTER ACCUMULATION.** Potential daily grain dry matter accumulation is dependent on grain number and potential growth per individual grain. This latter is a cultivar specific aspect determined from input information on the maximum grain weight of the cultivar and the duration of the grain filling period, and simulated information on the grain number per plant. This latter is used to reduce the potential growth when grain number exceeds a critical value. Actual growth is less than the potential if the temperature falls outside an optimum range or if available assimilates (current plus reserves) are inadequate.

**GRAIN NITROGEN ACCUMULATION.** During grain filling, a pool of nitrogen is created jointly from leaves, stem, and roots. The size of this pool is calculated as the difference between the current nitrogen concentration of shoots or roots and their minima, multiplied by their current dry weights. The demand for nitrogen by the grain is computed from the grain growth rate and a cultivar specific target grain nitrogen concentration. It is influenced by temperature in accord with a response function input as a species characteristic.

**TILLER PRODUCTION.** Tillering is generally allowed to start when 2.5 leaves have appeared on the main stem, although this aspect is a characteristic that is defined in the species file and is thus one that could be changed to accommodate cultivars that produce tillers from the coleoptilar node. Once capable, a plant will produce tillers on each axis at a rate specified in the species file as long as assimilate is available in the reserve pool in sufficient quantity to be moving to the roots. All tillering, however, ceases after the last leaf stage.

**TILLER SENESCENCE.** Tiller senescence may commence at the terminal spikelet stage, with the number dying being dependent upon the average amount of assimilate available per stem and a cultivar specific critical assimilate amount. Senescent tillers return a fraction of their dry matter to the general reserve pool, and a fraction of their nitrogen to the stem. Leaf areas and weights and stem weight of senesced tillers are subtracted from the appropriate living variable sum.

### Critical Stress Effects

**SATURATION.** Saturated soil conditions readily kill young wheat seedlings, particularly prior to emergence. This aspect is simulated by assuming that 5 d with the seed in a saturated soil layer will result in complete plant death.

**LOW TEMPERATURE.** Low temperatures at the level of the crown can kill or severely damage wheat plants, with the degree of damage being related to the cultivar, to the

hardening that may have occurred prior to exposure, and to the conditions to which a hardened plant has been exposed. Hardening is modelled as occurring in two phases, as in Ceres. The first phase encompasses hardening at above zero temperatures, the second phase, at sub-zero temperatures. Hardening in the first phase occurs most rapidly at temperatures between 1°C and 8°C, and less rapidly as temperatures increase to 15°C. Ten days of full hardening conditions will harden the plant to a cultivar dependent maximum level of phase 1 cold tolerance. Hardening in the second phase, which is a drying phenomenon (Fowler, personal communication), occurs at temperatures below 0°C, with 12 d being required for complete hardening.

Plant death occurs when the temperature falls close to the hardened temperature. This latter is the temperature at which 50% of the plants would have died (LD<sub>50</sub>). The span of lethal temperature around the LD<sub>50</sub> is set at 8°C so that plant death commences at a temperature 4°C higher than the LD<sub>50</sub>, and reaches 100% at a temperature 4°C lower than the LD<sub>50</sub>.

No account is currently taken of the reduction in LD<sub>50</sub> that is often recorded as the winter progresses. The higher temperatures of spring, however, dehardens the plant, a process that commences when the daily maximum temperature exceeds 15°C.

Over and above the problem of plant death, low temperatures can have serious consequences when they occur in the period between spike emergence and anthesis. Frost in this

period can cause sterility in the spike. To account for this aspect, the number of days with a minimum temperature lower than 0°C is accumulated from spike emergence till the end of anthesis. Grain number is reduced in an arbitrarily set manner in direct proportion to the number of days of frost in the period; 5 days of frost is assumed to cause complete sterility. A warning message is written to the main output file when grain number is reduced because of frost around flowering.

### STRUCTURE OF CROPSIM-WHEAT

Cropsim-wheat is written in standard Fortran 77 with subroutines that correspond to the sections used for the model description, and these subroutines have subsections that correspond also to the subsections of the model description. This structure facilitates the upgrading of individual components as information on model performance relative to field data becomes available.

Each subroutine is called daily by the main program until the crop either fails or matures. Prior to the daily simulation loop, input files are read and variables initialized, while subsequent to the main loop, simulated variables are written to various standard (see Hunt et al. 1994) output files. To simplify evaluation of performance, the model reads files that contain crop performance data and writes some of this information along with the simulated data to model output files. The various subroutines are called in a set sequence, as indicated in the illustration of the main program in Table 2.

Table 2. Main program of the Cropsim-wheat simulation model

---

```

C CROPSIM MAIN PROGRAM
C L.A.HUNT, UNIVERSITY OF GUELPH, ONTARIO, CANADA
C CSWEND — A control switch that is set to 1 in subroutines
C 'develop' or 'growth' if the crop fails (dies!) or matures.

INCLUDE 'DEMGRDIS.INC'
INCLUDE 'IOMDGWNS.INC'
INCLUDE 'IPMOP .INC'

INCLUDE 'FNUM .INC'
CALL HEADER                ! Write screen heading
CALL INITIAL               ! Initialize variables
CALL INPUT                 ! Read inputs
CALL OUTPUT('H')          ! Write file headings and input echos

DO WHILE (CSWEND.NE.1)     ! Start simulation for day
  CALL WEATHER              ! Read weather; calculate soil temps
  CALL WATER                ! Calculate water balance components
  CALL NITROGEN              ! Calculate nitrogen pools, fluxes, etc.
  CALL DEVELOPMENT          ! Calculate developmental progress
  CALL GROWTH                ! Calculate growth components
  CALL STRESS                ! Calculate critical stress effects
  CALL DISEASE               ! Calculate disease progress
  CALL OUTPUT('T')          ! Write time-course outputs
END DO                     ! End simulation for day

CALL OUTPUT('E')           ! Write end of run outputs - yield, etc.

Close(11)                  ! Close weather file
DO L = 1,9                  ! Close output files
  Endfile(Fout(L))
  Close(Fout(L))
END DO

STOP ' '
END

```

---

The main input files used by Cropsim-wheat deal with crop management, soil, weather and genotype. There are two genotype files. One deals with characteristics that are generally known to vary among cultivars. It corresponds, in structure, closely to the files often maintained by plant breeders and germplasm curators, with details of the descriptors and performance summaries of particular arrays of cultivars. The second genotype file, the species file, deals with those characteristics that generally do not vary among cultivars, but that underlie the plants' response to environment and the overall level of performance. This file is structured such that the summary information used by the model is presented along with the information on which the summary was based, a reference to its source, and some background data that helps specify the material used in the original research.

The model will run when provided with a minimum of information on the command line at the time that the program is invoked. Required information encompasses the name of the file containing experimental details and simulation controls, and the number of the particular experimental treatment to be simulated. Such information does not have to be supplied manually, however, and generally would be supplied by a "driver" program that allows for a choice of experiments and treatments, and permits easy manipulation of input variables. A number of such "drivers" are available (e.g. the Ibsnat model driver: Hogenboom and Jones, 1994, personal communication). One specifically constructed for use with Cropsim is distributed along with the model. This driver is written in Basic and has scrolling menus for experiment and treatment selection, and a dedicated editor for data and simulation controls modification. It also provides access to a user provided editor for accessing the various input and output files, and a graphics package for viewing field and simulated data.

### DISCUSSION

The model described here has been used successfully to simulate the growth and development of crops from North America and European environments. Details of simulations completed with the model, and of the degree of matching between model performance and field data, will be provided in companion papers. The model however, has not been evaluated with datasets that encompass the full array of environments in which wheat is grown, nor the full range of genotypic variability in the species. It could thus be regarded as a model in development rather than one that is mature and fully evaluated. Such a view would reflect a reality that should underlie all model development — namely, that the process of model evaluation and development should be ongoing, and should be one that requires a continuing comparison of simulated and field data. Cropsim was built with this in mind, using file structures that facilitate the handling and storage of field information, and the easy comparison of field and simulated data. The model therefore, should be viewed as an initial 'capture' of current knowledge, and the description as a framework against which subsequent data comparisons and modifications can be referenced. With this context in mind, however, the model could be used as a tool to be applied in the analysis of field studies, to help

determine whether the data reflect current understanding or require new conceptual insights.

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- Addae, P. C. and Pearson, C. J. 1992. Thermal requirements for germination and seedling growth of wheat. *Aust. J. Agric. Res.* 43: 585–594.
- Addiscott, T. M., Heys, P. J. and Whitmore, A. P. 1986. Application of simple leaching models in heterogeneous soils. *Geoderma* 38: 185–194.
- Addiscott, T. M. and Whitmore, A. P. 1991. Simulation of solute leaching in soils of different permeabilities. *Soil Use Manage.* 7: 94–102.
- Allison, J. C. S. and Daynard, T. B. 1976. Effect of photoperiod on development and number of spikelets of a temperate and some low-latitude wheats. *Ann. Appl. Biol.* 83: 93–102.
- Amir, J. and Sinclair, T. R. 1991a. A model of the temperature and solar-radiation effects on spring wheat growth and yield. *Field Crops Res.* 28: 47–58.
- Amir, J. and Sinclair, T. R. 1991b. A model of water limitation on spring wheat growth and yield. *Field Crops Res.* 28: 59–69.
- Angus, J. F., Mackenzie, D. H., Morton, R. and Schafer, C. A. 1981. Phasic development in field crops. II. Thermal and photo-periodic responses of spring wheat. *Field Crops Res.* 4: 269–283.
- Baker, C. K., Gallagher, J. N. and Monteith, J. L. 1980. Day-length change and leaf appearance in winter wheat. *Plant, Cell and Environ.* 3: 285–287.
- Bristow, K. L. 1992. Prediction of daily mean vapour density from daily minimum air temperature. *Agric. For. Meteorol.* 59: 309–317.
- Cao, W. and Moss, D. N. 1989. Temperature effect on leaf emergence and phyllochron in wheat and barley. *Crop Sci.* 29: 1018–1021.
- Chapleau, A-M. 1984. Primordia and leaf production in relation to spikelet number of winter wheat and two related species. M.Sc. Thesis, University of Guelph, Guelph, ON. 73 pp.
- Delecolle, R., Couvreur, F., Pluchard, P. and Varlet-Granchet, C. 1985. About the leaf-daylength model under French conditions. Pages 25–31 in W. Day and R. K. Atkin, eds. *Wheat growth and modelling*. Plenum Press, New York, NY.
- Demetriades-Shah, T. H., Fuchs, M., Kanemasu, E. T. and Flitcroft, I. 1992. A note of caution concerning the relationship between cumulative intercepted solar radiation and crop growth. *Agric. For. Meteorol.* 31: 131–141.

- French, R. J., Schultz, J. E. and Rudd, C. L. 1979. Effect of time of sowing on wheat phenology in South Australia. *Aust. J. Exp. Agric. Anim. Husb.* 19: 89–96.
- Gallagher, J. N. 1979. Field studies of cereal leaf growth. 1. Initiation and expansion in relation to temperature and ontogeny. *J. Exp. Bot.* 30: 625–636.
- Gallagher, J. N. and Biscoe, P. V. 1978. Radiation, absorption, growth and yield of cereals. *J. Agric. Sci. (Camb.)* 91: 47–60.
- Godwin, D. C. and Jones, C. A. 1986. Nitrogen dynamics in soil-plant systems: The CERES model. Chapt. 14, Pages 101–106 in D. C. Godwin, C. A. Jones, J. T. Ritchie, P. L. G. Vlek, and L. G. Youndahl, eds. *The water and nitrogen components of the CERES models*. ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). Proc. Int. Symp. on Minimum Data Sets for Agrotechnology Transfer, March 21–26 1983. ICRISAT Center, India, Patancheru, A.P. 502 324, India.
- Godwin, D. C. and Jones, C. A. 1991. Nitrogen dynamics in soil-plant systems. Chapt. 13, Pages 287–321 in J. Hanks and J. T. Ritchie, eds. *Modeling plant and soil systems*. Agronomy Monograph No. 31. American Society of Agronomy, Madison, WI.
- Goudriaan, J. and van Laar, H. H. 1978. Calculation of daily totals of the gross CO<sub>2</sub> assimilation of leaf canopies. *Neth. J. Agric. Sci.* 26: 373–382.
- Gregory, P. J., McGowan, M., Biscoe, P. V. and Hunter, B. 1978. Water relations of winter wheat. 1. Growth of the root system. *J. Agric. Sci. (Camb.)* 91: 91–102.
- Groot, J. J. R. 1987. Simulation of nitrogen balance in a system of winter wheat and soil. Simulation Report CABO-TT, #13.
- Hay, R. K. M. 1990. Tansley Review No. 26: The influence of photoperiod on the dry-matter production of grasses and cereals. *New Phytol.* 116: 233–254.
- Hay, R. K. M. and Wilson, G. T. 1982. Leaf appearance and extension in field-grown winter wheat plants: the importance of soil temperature during vegetative growth. *J. Agric. Sci. (Camb.)* 99: 403–410.
- Hoogendoon, J. 1985. The physiology of variation in the time of ear emergence among wheat varieties from different regions of the world. *Euphytica* 34: 559–571.
- Hotsonyame, G. K. 1992. Factors controlling leaf area development of spring wheat, rye and triticale under field conditions in Ontario. M.Sc. Thesis, University of Guelph, Guelph, ON. 66 pp.
- Hunt, L. A. and Edgington, L. V. 1981. Dry matter accumulation and distribution in winter wheat grown in a humid continental climate. *Can. J. Bot.* 59: 415–420.
- Hunt, L. A. and Chapleau, A-M. 1986. Primordia and leaf production in winter wheat, triticale, and rye under field conditions. *Can. J. Bot.* 64: 1972–1976.
- Hunt, L. A., Pararajasingham, S., Jones, J. W., Hoogenboom, G., Imamura, D. T. and Oghoshi, R. M. 1993. GENCALC — Software to facilitate the use of crop models for analyzing field experiments. *Agron. J.* 85: 1090–1094.
- Hunt, L. A., Jones, J. W., Hoogenboom, G., Godwin, D. C., Singh, U., Pickering, N., Thornton, P. K., Boote, K. J. and Ritchie, J. T. 1994. General input and output file structures for crop simulation models. Pages 35–72 in *Application of modelling in the semi-arid tropics*. CoData, International Council of Scientific Unions.
- Jones, C. A. and Kiniry, J. R. (Eds.) 1986. CERES-Maize. Texas A & M University Press, College Station, TX. 194 pp.
- Jones, C. A., Bland, W. L., Ritchie, J. T. and Williams, J. R. 1991. Simulation of root growth. Chapt. 6, Pages 91–124 in J. Hanks and J. T. Ritchie, eds. *Modeling plant and soil systems*. Agronomy Monograph No. 31. American Society of Agronomy, Madison, WI.
- Kiniry, J. R., Jones, C. A., O'Toole, J. C., Blanchet, R., Cabelguenne, M. and Apanel, D. A. 1989. Radiation-use efficiency in biomass accumulation prior to grain-filling for five grain crop species. *Field Crops Res.* 20: 51–64.
- Kirby, E. J. M. and Appleyard, M. 1984. Cereal plant development and its relation to crop management. Pages 161–173 in E. J. Gallagher, ed. *Cereal production*. Butterworth, London, UK.
- Kirby, E. J. M. 1974. Ear development in spring wheat. *J. Agric. Sci. (Camb.)* 82: 437–447.
- Kirby, E. J. M., Appleyard, M. and Fellowes, G. 1982. Effect of sowing date on the temperature response of leaf emergence and leaf size in barley. *Plant, Cell Environ.* 5: 477–484.
- Kirby, E. J. M. and Perry, M. W. 1987. Leaf emergence rates of wheat in a Mediterranean environment. *Aust. J. Agric. Res.* 38: 455–464.
- Lancashire, P. D., Bleiholder, H., Van den boom, T., Langeluddeke, P., Strauss, R., Weber E. and Witzemberger, A. 1991. A uniform decimal code for growth stages of crops and weeds. *Ann. Appl. Biol.* 119: 561–601.
- Major, D. J. and Kiniry, J. R. 1991. Predicting daylength effects on phenological processes. Pages 15–28 in T. Hodges, ed. *Predicting crop phenology* CRC Press, Boca Raton, FL.
- Masle, J., Doussinault, G., Farquhar, G. D. and Sun, B. 1989. Foliar stage in wheat correlates better to photothermal time than to thermal time. *Plant, Cell Environ.* 12: 235–247.
- Masoni, A., Ercoli, L. and Massantini, F. 1990. Relationship between number of days, growing degree days and photothermal units and growth in wheat (*Triticum aestivum* L.) according to seeding time. *Agricoltura Mediterranea* 120: 41–51.
- Matthäus, E., Karschall, T., Frühauf, C., Grossman, S. and Wechsung, F. 1991. The agroecosystem model winter wheat DEMETER. Potsdam-Institute for Climate Impact Research, Natural Systems Department. Potsdam, Germany.
- McMaster, G. S., Wilhelm, W. W. and Morgan, J. A. 1992. Simulating winter wheat shoot apex phenology. *J. Agric. Sci.* 119: 1–12.
- McMaster, G. S. 1993. Existing wheat yield models. Distributed listing, USDA – ARS Crops Research Lab, Fort Collins, CO.
- Mitchell, R. W. A., White, E. and Sylvester-Bradley, R. 1991. Prediction of flag-leaf emergence in wheat crops. *Field Crops Res.* 27: 119–130.
- Monteith, J. L. 1969. Light interception and radiative exchange in crop stands. Pages 89–111 in J. D. Eastin, ed. *Physiological aspects of crop yield*. American Society of Agronomy, Madison, WI.
- Porter, J. R. 1984. A model of canopy development in winter wheat. *J. Agric. Sci. (Camb.)* 103: 383–392.
- Porter, J. R., Kirby, E. J. M., Day, W., Adam, J. S., Appleyard, M., Ayling, S., Baker, C. K., Beale, P., Belford, R. K., Biscoe, P. V., Chapman, A., Fuller, M. P., Hampson, J., Hay, R. K. M., Hough, M. N., Matthews, S., Thompson, W. J., Weir, A. W., Willington, V. B. A. and Wood, D. W. 1987. An analysis of morphological developmental stages in Avalon winter wheat crops with different sowing dates and at ten sites in England and Scotland. *J. Agric. Sci. (Camb.)* 109: 107–121.
- Porter, J. R. 1993. AFRCWHEAT2: A model of the growth and development of wheat incorporating responses to water and nitrogen. *Eur. J. Agron.* 2: 69–82.
- Priestley, C. H. B. and Taylor, R. J. 1972. On the assessment of surface heat flux and evaporation using large-scale parameters. *Mon. Weather Rev.* 100: 81–92.
- Reinink, K., Jorritsma, I. and Darwinkel, A. 1986. Adaptation of the AFRC wheat phenology model for Dutch conditions. *Neth. J. Agric. Sci.* 34: 1–13.

- Ritchie, J. T. 1972.** A model for predicting evaporation from a row crop with incomplete cover. *Water Resour. Res.* **8**: 1204–1213.
- Ritchie, J. T. 1981.** Water dynamics in the soil-plant-atmosphere system. *Plant Soil* **58**: 81–96.
- Ritchie, J. T. 1991.** Wheat phasic development. Pages 31–54 in J. Hanks and J. T. Ritchie, eds. *Modeling plant and soil systems*. American Society of Agronomy, Madison, WI.
- Ritchie, J. T. and Otter, S. 1984.** Description and performance of CERES-WHEAT: A user-oriented wheat yield model. USDA – ARS, Washington, DC.
- Sharpley, A. N. and Williams, Jr. (Eds.) 1990.** EPIC — Erosion/Productivity Impact Calculator: 1. Model Documentation. US Department of Agriculture Technical Bulletin No. 1768. 235 pp.
- Sinclair, T. R. and Amir, J. 1992.** A model to assess nitrogen limitations on the growth and yield of spring wheat. *Field Crops Res.* **30**: 63–78.
- Singels, A. and de Jager, J. M. 1991a.** Refinement and validation of the PUTU wheat crop growth model. 1. Phenology. *S. Afr. Tydskr. Plant Grond* **8**: 59–66.
- Singels, A. and de Jager, J. M. 1991b.** Refinement and validation of the PUTU wheat crop growth model. 2. Leaf area expansion. *S. Afr. Tydskr. Plant Grond* **8**: 67–72.
- Singels, A. and de Jager, J. M. 1991c.** Refinement and validation of the PUTU wheat crop growth model. 3. Grain growth. *S. Afr. Tydskr. Plant Grond* **8**: 73–77.
- Slafer, G. A., Halloran, G. M. and Connor, O. J. 1993.** Phyllochron was not affected by the rate of change in daylength. *Agronomy Abstracts*. American Society of Agronomy, Madison, WI. p. 124.
- Stapper, M. 1984.** Simtag: A simulation model of wheat genotypes. Model Documentation. International Center for Agricultural Research in the Dry Areas Publication. Aleppo, Syria.
- Stockle, C. O. and Kiniry, J. R. 1990.** Variability in crop radiation-use efficiency associated with vapor-pressure deficit. *Field Crops Res.* **25**: 171–181.
- Syme, J. R. 1974.** Leaf appearance rate and associated characters in some Mexican and Australian wheats. *Aust. J. Agric. Res.* **25**: 1–7.
- Troughton, A. 1956.** Studies on the growth of young grass plants with special reference to the relationship between the shoot and root systems. *J. Br. Grassl. Soc.* **11**: 56–65.
- van Keulen, H. 1975.** Simulation of water use and herbage growth in arid regions. *Simulation Monographs*, Pudoc, Wageningen, The Netherlands. 184 pp.
- van Keulen, H. and Seligman, N. G. 1987.** Simulation of water use, nitrogen nutrition and growth of a spring wheat crop. *Simulation Monographs*, Pudoc, Wageningen, The Netherlands. 310 pp.
- van Laar, H. H., Goudriaan, J., van Keulen, H. (Eds.) 1992.** Simulation of crop growth for potential and water-limited production situations (as applied to spring wheat). *Simulation Reports* 27, CABO-TT, 72 pp.
- Weir, A. H., Bragg, P. L., Porter, J. R. and Rayner, J. H. 1984.** A winter wheat crop simulation model without water or nutrient limitations. *J. Agric. Sci. (Camb.)* **103**: 371–382.
- Zadoks, J. C., Chang, T. T. and Konzak, C. F. 1974.** A decimal code for the growth stages of cereals. *Weed Res.* **14**: 415–421.