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A dynamic model of crop growth and partitioning of biomass

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Abstract

A model is presented of growth and partitioning to leaves, stems and roots in herbaceous, vegetative crops in response to atmospheric conditions and water supply. It comprises 12 state variables and 33 parameters (including four functional relationships), all of direct physiological significance. The important characteristic of the model is the simultaneous consideration of crop assimilate and water balances achieved by calculations made at short time steps (1 h or less) in order to capture the physiological responses of crop growth and water use as they respond to diurnal environmental patterns.

In the model, root-zone water content decreases with transpiration and soil evaporation, and increases with rainfall, irrigation and deepening of the root zone as the crop develops. Photosynthesis depends upon intercepted radiation and temperature and also on canopy conductance determined from crop water status. Respiration of organs is calculated as separate requirements for maintenance and growth. Transpiration proceeds with photosynthesis but in response to evaporative demand, reducing crop water content, which is in turn replenished from the root zone based on its water content and the root length that explores it. Partitioning of assimilate to leaves, stems, and roots depends upon diurnal oscillations in assimilate supply, temperature, and crop water content within limits set by phenological development. Phenological development, here the initiation and expansion of leaves and the maturity and senescence of canopy and root systems, is determined by temperature. Examples, and trends, of model performance are compared with measured physiological and agronomic responses of sunflower to strategies of irrigation. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction and background

Crop simulation modelling commenced with treatments of crop photosynthesis that combined geo-

metrical considerations of canopy structure with solar position to describe the consequent diurnal pattern of irradiance on, and photosynthetic response of, the component elements of foliage (de Wit, 1965; Duncan et al., 1967). Later, more comprehensive models, still concentrating on diurnal behaviour, were constructed to include transpiration (de Wit et al., 1970), water and nitrogen limitations (van Keulen and Seligman, 1987), and partitioning of assimilate between shoot and root

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(Brouwer and de Wit, 1969; de Wit et al., 1978; Huck and Hillel, 1983). That line of work continued, especially in the development of simulation models of individual crops of sugar beet (Fick et al., 1973), potato (Ng and Loomis, 1984; Pinto, 1988), and alfalfa (Denison and Loomis, 1989). During the same period, however, the bulk of crop modelling activity shifted to simpler 'summary' models operating on a daily rather than diurnal basis. Whereas the diurnal models have a major objective of testing research hypotheses concerning the interacting physiological processes that determine crop performance, the daily are more focussed on the solution of problems in crop management (e.g. IBSNAT, 1988; Muchow and Bellamy, 1991; van Keulen and Wolf, 1986). Passioura (1996) has subsequently referred to these as 'science' and 'engineering' models, respectively.

Most current crop models, and at least one exists for each major crop, operate on daily time steps. Models, at that level, can include functional treatments of phenological development, growth, water use, and nitrogen nutrition (e.g. O'Leary et al., 1981; Jones and Kiniry, 1986; van Keulen and Seligman, 1987; O'Leary and Connor, 1996; Villalobos et al., 1996) but the linkages between those component processes are weak. The marked diurnal patterns that characterise irradiance, temperature and evaporative demand produce interactions between assimilation and water use that are grossly simplified in daily models. Further, the responsiveness of these models is severely restricted by their reliance on empirically derived partitioning coefficients to distribute growth, or net assimilate, to the component organs of the crop and so adjust the system (update the state variables) at each time step. These partitioning coefficients are determined from observation of how the masses of component organs of crops change with phenological development and environmental conditions. In other words, a great weakness of these daily-time-step models, as simulations of crop behaviour, is that partitioning coefficients apply a good part of the answer of how crops grow rather than propose testable scientific hypotheses. It is through the testing of such underlying hypotheses that understanding can grow and models can improve.

There is great importance to furthering understanding of the growth dynamics of crops because increases in crop yield are largely being achieved by greater

partitioning to reproductive organs (i.e. greater harvest index) rather than by greater biological yield through increased radiation- or water-use efficiencies (Taylor et al., 1983; Loomis and Connor, 1992; Evans, 1993). One way to assist progress here is to propose, assemble and test hypotheses about the dynamics of assimilate partitioning in growing crops in the form of simulation models. Success in this venture may widen the applicability of crop simulation models in crop management but more especially would provide models suited to the search for optimum combinations of physiological and morphological characters (crop ideotypes) suited to specific environments and production systems. This would be especially important as genetic manipulation becomes easier and more rapid. Paltridge (1970) and Schulze et al. (1983) have made a start on these issues but there has been no further progress in recent years.

The concept of a dynamic balance between root and shoot activity as the basis for the partitioning of assimilate between those organs has been with us for sometime (as summarized by Brouwer, 1983). The acclimation and productivity of terrestrial plants requires the continual exchange of water, secured from the soil by roots, for CO₂ obtained from the atmosphere by leaves. In other words, water balance is central to the growth strategy of any crop, even in moist soil. As soil dries, the balance between growth and activity of roots and canopy becomes increasingly critical to growth and survival. This argument concerning shoot–root relationships might be extended to require concomitant consideration of the role of roots in the uptake of nutrients, especially nitrogen that is so important in many cell constituents. The argument for nutrients is less advanced than for water, however, and as a first step, it seems realistic to treat root–shoot balance in terms of water and assimilate.

Two limitations to the inclusion of functional treatments of root–shoot interactions in crop modelling stand out. The first is the daily time scale that, as explained above, has come to dominate crop modelling and which draws the prescription of productivity and growth away from that at which physiological processes operate. Of few models that have persisted with short time steps, the ALFALFA model (Denison and Loomis, 1989; Loomis et al., 1990) reveals how hourly calculations open the way for detailed physiological treatments. The second is the common tech-

nique of crop modelling which first establishes potential productivity based on radiation alone, and then, includes in successive steps, the limitations caused by water and nutrient stresses (Penning de Vries et al., 1989; Goudriaan and van Laar, 1994). While perhaps appropriate for daily models, this approach cannot integrate the dynamic response that plant growth exhibits diurnally.

A third limitation to the inclusion of more intensely functional treatments in crop models, the difficulty of access and/or cost of sufficient computing power, has long since been overcome. The current generation of desktop machines has adequate power for even the most complex crop simulation models.

The present study was undertaken to develop a model of biomass accumulation, partitioning, and water use in herbaceous annuals. The objective is to link physiological responses operating diurnally to long-term accumulation of biomass and its partition among component organs. Sunflower (*Helianthus annuus* L.) is chosen as a model crop for the development of the simulations and an assessment of model performance is made against data collected on the response of this crop to strategies of irrigation. Those experiments, involving 12 treatments over two years, combined diurnal and daily measurements of meteorological conditions with weekly measurements of crop water use and accumulation of biomass (Connor et al., 1985a), bi-weekly measurements of canopy development (Connor and Jones, 1985), diurnal measurements of leaf water potential and leaf conductance (Connor and Jones, 1985), and crop photosynthesis and transpiration (Connor et al., 1985b). Some of those data are used to establish parameter values for crop development so the output from the model is not independent of them. The objective of this comparison, however, is not to reproduce the measured responses but rather to demonstrate the ability to display the major observed features of diurnal and long-term crop behaviour with sufficient, and defined, points of control to investigate a number of issues in crop physiological research.

Such models can find two basic applications. First, they can explore principles of crop productivity, for example, the growth and adaptation strategies that have evolved in various (or at least idealised) species. Second, with appropriate modification and amplification, they can provide the cores of a new range of crop

models capable of simulating diurnal performance. One test of such models would be that partitioning coefficients to organs and other quantitative relationships between their sizes could be optional outputs from the model rather than essential inputs as in the present suite of daily models.

2. The model

2.1. General

A model was constructed to link a set of equations that describe crop development, photosynthesis, respiration, water uptake and transpiration through the maintenance of suitable internal conditions for continued assimilation and tissue expansion. For this, the model hypothesises balanced growth of canopy and root system in response to diurnal oscillations in crop water status that proceed in response to diurnal environmental conditions and longer-term changes in soil moisture content. The growth of stems is included, but no attempt is made to extend the model to the development of yield even though extensions to that end are obvious within the style presented. This latter step was avoided here because the model loses its generic character once variations are included to account for the wide range of flowering and yield formation strategies that characterise crop species. That is seen as a second-level task.

2.2. Model structure

The entire model, presented diagrammatically in Fig. 1 was built in the STELLA II Modelling Language (Anon., 1994) in three sectors denoted *Biomass*, *Development* and *Water*. Each sector, more generally called a submodel (e.g. Forrester, 1961), groups state variables that are linked by flows (the double lines) of a common material. While material flows are thus, by logic, restricted to individual sectors, information (the single lines) may also flow within and between sectors to define the feed-forward and feed-back controls that characterise biological systems.

As described in Table 1, the model has 12 state variables (rectangles), 29 parameters (circles) and is driven by three external weather variables. In Fig. 1, *model parameters* are distinguished by shading from

weather variables and *intermediate variables* (also circles). The latter are included to assist calculations or to describe aspects of model performance. Descriptive names are used throughout. To assist interpretation, the names of state variables are written in capital letters, material flows commence with a capital letter, and parameters are written entirely in lower case. The computer code for the three sectors is available on request.

2.3. Development sector

Phenological development rate (Dvr) depends on air temperature (temp) above a base (tbase) and is accumulated (as if a material flow) into PHENOSTAGE to determine thermal durations of leaf expansion (ttlfprod), calculated from maximum leaf number (nmax), phyllochron (phyl), and thermal time for leaf expansion (ttle), the subsequent transition to complete stem growth, and senescence of the canopy (ttll). In this way, intermediate variables for canopy (cangrw) and stem (stemgrw) growth (range 0 to 1), form one aspect of the partitioning of new biomass to canopy and stem, respectively. Thermal time (ttr), calculated from soil temperature, is used here to define the active life of new roots. The factors controlling the longevity of roots are poorly understood (Eissenstat, 1997)

although it is known there is substantial turnover (Huck and Hillel, 1983).

The vertical expansion of the root system is also included in the development sector. ROOTDEPTH increases at a rate (Rtexp) depending upon soil temperature (soilt) until the maximum available root depth (mxdpth) is reached. In this model, carbohydrate supply controls root mass and length but not root depth.

2.4. Water sector

Soil water is considered in two layers. ROOTZONE, which contains roots, and SUBSOIL, which does not. As roots grow, ROOTDEPTH increases and ROOTZONE gradually incorporates the water content of SUBSOIL. Transpiration (Transp) draws water from the crop (WCCROP), which in turn draws water (Uptake) from the ROOTZONE. Rainfall (Rain) and irrigation (Irrig) add water to ROOTZONE until the maximum available water-holding capacity (mxwhc1) is exceeded. Then, water infiltrates (Infilt) into SUBSOIL, and in the same way Drains from SUBSOIL when its water-holding capacity (mxwhc2) is exceeded.

Potential transpiration (ptr) depends upon crop cover (cover) and evaporative demand, which is cal-

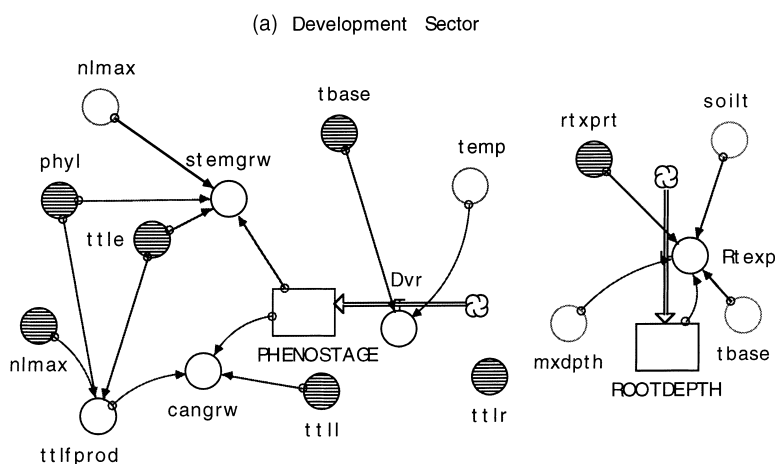


Fig. 1. Relational diagram of the model in three sectors corresponding to (a) Development, (b) Water, and (c) Biomass. State variables are rectangles connected by material flows drawn with double lines. The 'clouds' are sources and sinks of material to/from outside the model. Model parameters, defined in Table 1, are distinguished by shading from weather variables and intermediate variables. The intermediate variables are used either as steps in calculation or to record output to describe model performance. Information flows are shown by single lines connecting parameters and state variables to control symbols on material flows. State variables and parameters, defined in one sector, are 'ghosted', as necessary (less distinct outlines), within and into other sectors. This is done to simplify the presentation of information flow.

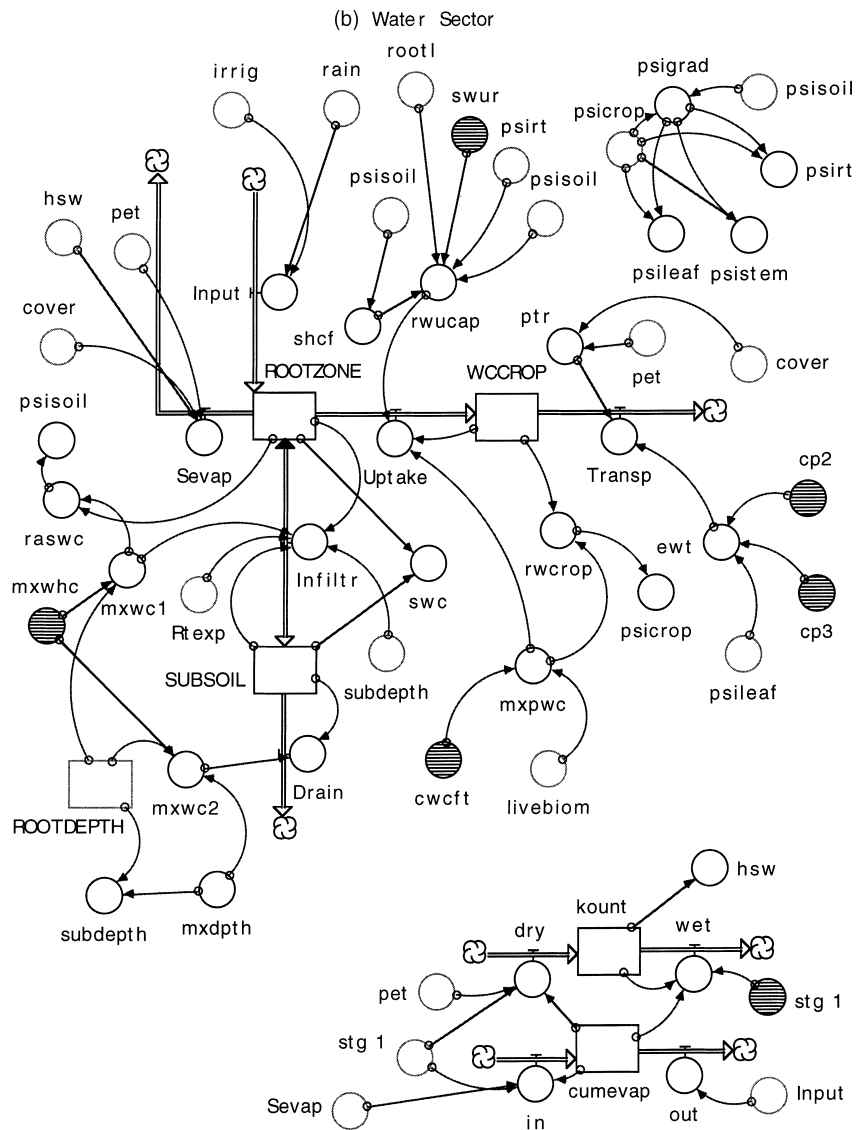


Fig. 1. (Continued)

culated as potential evapotranspiration (pet). Crop cover is calculated from leaf area index (lai) and the canopy extinction coefficient (k), the latter depending on leaf angle. Transient wilting affects k and thereby the interception of radiation at low leaf water potential (psileaf). Actual transpiration (Transp) may fall below ptr depending upon psileaf , the controlling variable for canopy conductance. Two control points (cp2 and cp3) define threshold water potentials

for the start of stomatal control and the point of complete closure, respectively. At complete closure, crop transpiration proceeds at 10% of the potential rate.

Maximum crop water content (mxwc) is calculated from total crop biomass (see next section) and the parameter cwcft , which defines crop water content at full turgor. WCCROP is replenished by Uptake of water from ROOTZONE at a rate that depends upon

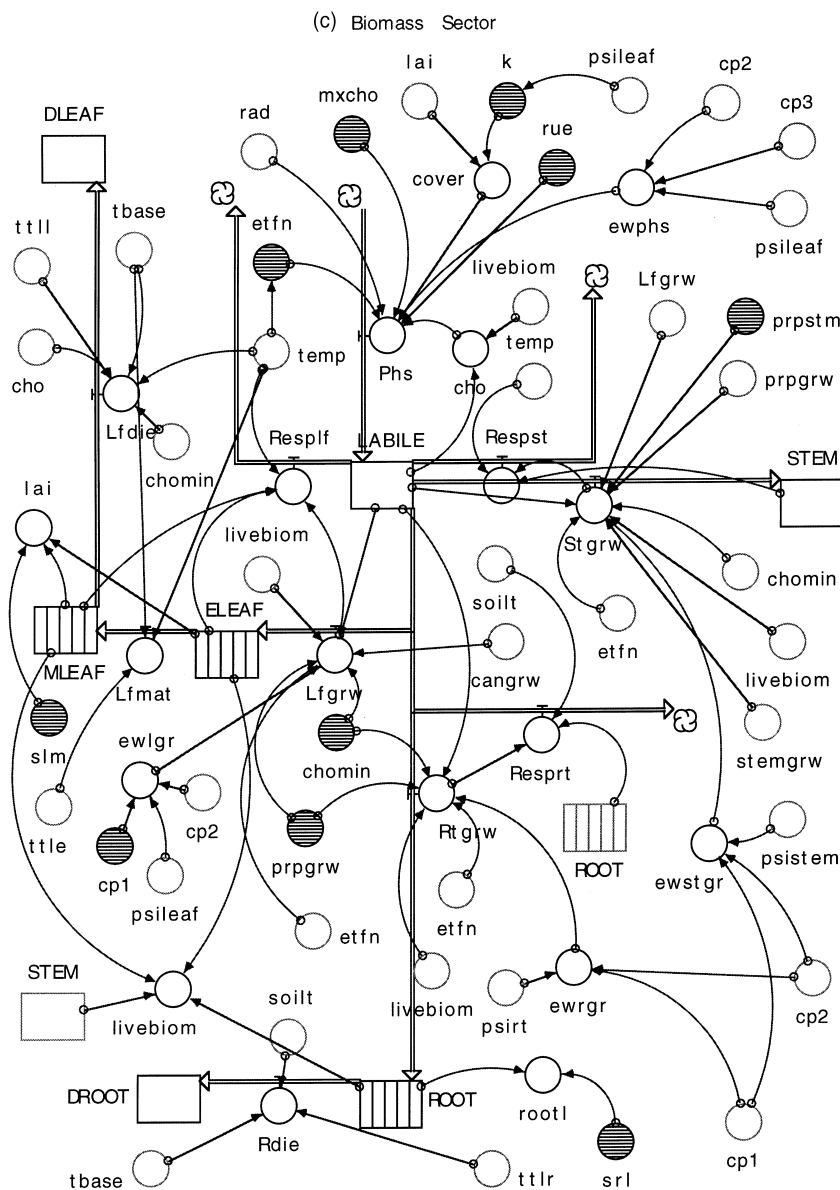


Fig. 1. (Continued)

root length (rootl), the specific water-uptake rate (swur) per unit water potential difference between root (psirt) and soil (psisoil), and soil hydraulic conductivity (shcf), a function of psisoil. Root length (rootl) is calculated as the product of ROOT biomass and specific root length (srl). Crop (psicrop, see later) and soil (psisoil) water potentials are calculated from their respective relative water contents (rwcrop,

raswc). Water potentials of leaf (psileaf), stem (psistem) and root (psirt) exhibit the diurnally varying gradient between psicrop and psisoil.

Evaporation (Sevap) is the direct loss of water from soil that is wet after rain or irrigation, at a rate that depends upon gap in the canopy (1-cover). Sevap is simulated following Ritchie (1972). Evaporation is energy-limited (stage 1) immediately following rain-

Table 1

Definition of driving variables, state variables and model parameters, with units and exemplary values

Name	Description	Unit	Parameter (example values)
<i>Driving variables</i>			
temp	dry bulb temperature (hourly)	°C	
rain (irrig.)	per hour	mm	
rad	shortwave radiation (hourly)	MJ m ⁻²	
<i>Development</i>			
State variable			
PHENOSTAGE	accumulated thermal time	°C h	
ROOTDEPTH	depth of roots	mm	
Parameters			
nlmax	maximum leaf number	—	25
phyl	interval between leaf prodn.	°C h	560
rtxprrt	rate of root depth increase	mm (°C h) ⁻¹	0.04
tbase	base temperature	°C	4
ttle	duration of expansion of a leaf	°C h	6000
ttll	duration of a mature leaf	°C h	12 000
ttlrr	duration of activity of a root	°C h	6000
<i>Water</i>			
State variables			
ROOTZONE	water content rootzone	mm	
SUBSOIL	water content sub soil	mm	
WCCROP	water content crop	mm	
Parameters			
cp2	middle threshold leaf water potential	MPa	−1.5
cp3	lower threshold of leaf water potential	MPa	−3.0
cwcft	ratio crop water at full turgor to crop dry mass (biomass)	g g ⁻¹	5
stg1	duration of energy-limited soil evap.	mm	4
mxdpth	explorable depth	mm	1500
mxwhc	volumetric range available water	—	0.2
swur	specific rate water uptake	cc m ⁻¹ MPa ⁻¹	0.0015
f(pscrop)	relation of pscrop to WCCROP		
f(psisoil)	relation of psisoil to ROOTZONE		
f(psigrad)	relation of psileaf, psistem, psirt to pscrop and psisoil		
<i>Biomass</i>			
State variables			
DLEAF	mass of dead leaf	g m ⁻²	
DROOT	mass of dead root	g m ⁻²	
ELEAF	mass of expanding leaf	g m ⁻²	
LABILE	mass of mobilizable assimilate	g m ⁻²	
MLEAF	mass of mature leaf	g m ⁻²	
ROOT	mass of active root	g m ⁻²	
STEM	mass of stem	g m ⁻²	
Parameters			
chomin	minimum proportion of labile assimilate for organ growth	—	0.06
cp1	upper threshold of leaf water potential	MPa	−0.6
crl ^a	constructional respiration proportion (CR) of leaf growth	g g ⁻¹	0.29
crr ^a	CR of root growth	g g ⁻¹	0.22
crs ^a	CR of stem growth	g g ⁻¹	0.22
k	canopy extinction coefficient	—	0.60

Table 1 (Continued)

Name	Description	Unit	Parameter (example values)
mxcho	max prop. CHO for photosynthesis	—	0.30
prpgrw	prop of labile pool available for growth	—	0.035
prpstm	stem growth as early prop of leaf	—	0.1
rue	radiation-use efficiency	g MJ^{-1}	3.50
slm	specific leaf mass	$\text{m}^2 \text{g}^{-1}$	50
smrl ^a	specific maintenance respiration (MR) of leaf mass at 20°C	$\text{g g}^{-1} \text{h}^{-1}$	0.0008
smrr ^a	specific MR of root mass at 20°C	$\text{g g}^{-1} \text{h}^{-1}$	0.0006
smrs ^a	specific MR of stem mass at 20°C	$\text{g g}^{-1} \text{h}^{-1}$	0.0004
srl	specific root length	m g^{-1}	100
f(tfnc)	effect of temp on phs, organ growth senescence		

^a Not shown on diagram. They are embedded in corresponding equations.

fall or irrigation until an amount (stg1), characteristic of soil type, is lost. Then, Sevap goes into a supply-limited phase (stage 2) falling rapidly with time (hsw). Two variables, kount and cumevap, seen in the lower right of the water sector (Fig. 1) are dummy state variables used to determine the transition from stage 1 to stage 2 evaporation and the time (hours) since wet (hsw). They are not included in Table 1.

2.5. Biomass sector

Photosynthesis (Phs) provides assimilate to a common pool of non-structural carbohydrate (LABILE) that exists within all (living) organs of the crop. Its rate depends upon intercepted radiation, calculated via crop cover from leaf area index (lai) and k , and the radiation-use efficiency (rue) for (gross) assimilate production. Leaf area index (lai) is itself calculated as the product of specific leaf mass (slm) and the sum of expanding (ELEAF) and mature leaf biomass (MLEAF). In addition to radiation, Phs responds to temperature (etfn) and psileaf, using the same stomatal control points cp2 and cp3 as for transpiration but with the difference that Phs is zero at cp3. If organ growth is reduced more than photosynthesis, the concentration of assimilate in the crop (cho) may rise above mxcho and inhibit photosynthesis.

ELEAF, MLEAF and ROOT are distinguished in the model from the other state variables. In STELLA terminology, these state variables are conveyers rather than the homogeneous reservoirs of the Forrester system. For conveyers, outflow is related to the time

sequence of inflow with transit times that can be fixed or variable. Here, flows from ELEAF, MLEAF and ROOT depend upon phenological development, calculated as thermal time. Leaves mature (Lfmat) and die (Lfdie), and roots die (Rtdie) at rates that depend upon temperature.

2.6. Distribution of the LABILE pool

Flows from LABILE provide materials for dry matter growth and for respiration.

Growth of ELEAF (Lfgrw), STEM (Stgrw), and (active) ROOT (Rtgrw) have access to a proportion (prpgrw) of the assimilate pool above a minimum concentration (chomin). Although all organs have access to the same proportion (prpgrw) of LABILE for growth, their actual use of it is modified in the long term by phenological development, explained previously, and instantaneously by organ water status. The model uses a common response of expansive growth of leaf, stem and root to temperature (etfn) and water potential. The control for water is linearly proportional between two values of water potential, $\text{cp2} < \text{cp1}$. Growth falls from a maximum rate at cp1 to zero at cp2. To apply this scheme to the expansion of component organs, their individual water potentials (psileaf, psistem, psirt) are calculated from the gradient of water potential (psigrad) from soil (psisoil) to crop (psicrop). Psigrad varies diurnally, reaching zero when psicrop equilibrates with psoil during the night period. This occurs daily except when psoil falls to very low levels or evaporative demand is high.

The respiration flows from LABILE for ELEAF, STEM, and ROOT (Respl, Respst, Resprt), each comprise two components. First, the temperature-independent growth respiration (with coefficients for leaves, stems, and roots, crl , crs and crt , respectively) and second, temperature-dependant ($Q_{10} = 2$) maintenance respiration with coefficients ($smrl$, $smrs$, $smrr$), using air and soil temperature as appropriate. MLEAF has the single component of maintenance respiration calculated using $smrl$. In contrast to growth, maintenance respiration may reduce LABILE below the threshold $chomin$. This arises when photosynthesis is greatly reduced for a prolonged period.

Thus, in this model the crop (as in reality) continues metabolism and has the opportunity for organ growth during the entire day according to the availability of water and assimilate.

In some crops, as in sunflower, stem growth is insignificant during early stages of the crop cycle but in others, formation and expansion of leaves is associated with growth of stems and petioles. In this model, the parameter ($prpstm$) specifies early (petiole and) stem growth ($Stmgrw$) as a proportion of leaf growth ($Lfgrw$), before the commencement of its phenologically controlled major growth phase.

In distinction to some daily models that also use development as a framework for assimilate or biomass distribution (e.g., Carberry et al., 1993; Villalobos et al., 1996), there is no attempt here to define maximum size as a boundary for plant or organ growth. Rather, it is assumed that at the densities at which crops are usually sown there is soon sufficient intraplant competition that growth of all vegetative organs (leaves, stems and roots) is restricted by assimilate supply. In this way, maximum organ size is less than what might be attained by isolated individuals and those values become irrelevant in simulations as in plant performance in commercial crops.

2.7. Time step for integration

The equations of the model are formed to define responses on an hourly basis but the model can be run, if necessary, on shorter time steps. An idea of the importance of time step can be obtained from a consideration of whether the dynamic adjustment of canopy conductance is able to maintain internal crop

water status within operational levels under usual conditions of water supply, as follows.

A herbaceous crop of 5 t/ha biomass contains (WCCROP) ca. 30 t/ha water at full turgor, equivalent to 3 mm of transpiration. For a crop of full cover ($lai > 3$), daily potential transpiration (ptr) of 6 mm corresponds to a maximum rate of transpiration in the middle of the day approaching 1.2 mm/h, or ca. 40% of crop water content at full turgor ($mxwc$). Calculations of crop water loss and uptake must be made sufficiently frequently to reproduce crop water deficits and physiological responses that are known to occur at relatively high crop water contents (WCCROP). Stomata, for example, commence closure at or above relative water contents ($rwcrop$) of 0.9. Under the conditions described above, a crop at full turgor could lose that much water (0.3 mm) at midday in 15 min. Similar changes in WCCROP would take longer as stomatal control intervenes and water is adsorbed by the root system. All simulations presented here were made with a time step of 0.5 h.

2.8. Sunflower experiments

Responses of sunflower crops to irrigation, involving 12 treatments over two years, combined diurnal and daily measurements of meteorological conditions with weekly measurements of crop water use and accumulation of biomass (Connor et al., 1985a), bi-weekly measurements of canopy development (Connor and Jones, 1985), diurnal measurements of leaf water potential and leaf conductance (Connor and Jones, 1985), and crop photosynthesis and transpiration (Connor et al., 1985b).

The experiments were carried out over two successive summers (December to March of 1980/1 and 1981/2) at the then Irrigation Research Institute, Tatura, Victoria Australia (lat. 36°S, 114 m asl). Rainfall during the two seasons was 121 and 92 mm, respectively. Maximum temperatures remained above 25°C over the season and approached 40°C on occasions. Minimum temperatures exceeded 10°C. Pan evaporation for the two growing seasons were 804 and 798 mm, with daily values mostly in the range 7 to 9 mm. The soil is duplex with sharp transition from a clay-loam surface to massive clay at 15 to 20 cm

Table 2

Summary of irrigation^a regimes applied to sunflower crops at Tatura, Australia, in relation to rainfall, evaporation, and crop development

Crop stage	Days after sowing	Rainfall (mm)	Pan evaporation (mm)	Irrigation applied (mm)					
				T1	T2	T3	T4	T5	T6
1980/1981									
Sowing	0								
		72	391	120	120	120	—	—	—
Budding	50	25	143	137	137	137	137	—	—
Anthesis	70	18	107	103	103	—	103	103	—
Mid-seed	84	6	163	90	37	—	90	90	—
Maturity	114								
1981/82				T7	T8	T9	T10	T11	T12
Sowing	0								
		8	397	180	190	—	—	—	—
Budding	50	5	180	90	90	90	90	90	—
Anthesis	73	0	91	140	45	45	95	—	—
Mid-seed	87	28	130	100	75	75	25	100	—
Maturity	114								

^a Individual irrigations, each ca. 45 mm, were applied weekly as appropriate.

(Skene and Poutsma, 1962). Its available water-holding capacity to 1500 mm soil depth is ca. 160 mm.

The plots were sown on 5 December in both years into a fully recharged profile and, after establishment, were thinned to 53 000 per ha in rows 0.75 m apart. Six irrigation treatments were applied in each year through drip lines centred on each row of the crops. Two similar treatments were maintained in each year. These were the boundary treatments of weekly irrigation (T1 and T7 in 1980 and 1981, respectively) and no irrigation (rainfed) (T6 and T12). In both years, the other four treatments investigated various strategies of irrigation. The treatments (T1 to T12) are summarised in Table 2.

3. Model performance

3.1. Diurnal behaviour

The experimental program at Tatura included measurements of crop CO₂ exchange and transpiration

made with field assimilation chambers on various days after sowing (das). The simulations presented in Figs. 2 and 3 reproduce the characteristic responses observed there.

In T7, on 50 and 51 das, trends of photosynthesis and transpiration are displayed relative to the driving variables of radiation and temperature (Fig. 2a). Photosynthesis declined in the afternoon, relative to radiation. This reflected increasing water stress under conditions of high temperature. This response is further evident in the slight hysteresis in the relationship between photosynthesis and radiation presented in Fig. 3(a). This response combines the effect of wilting on radiation interception with decreasing leaf conductance on radiation-use efficiency. Wilting was a feature of the behaviour of these crops at Tatura towards the end of their weekly irrigation cycle.

In the responses presented in Fig. 2(b) for T4 at 42 and 43 das, peak photosynthesis was achieved before solar noon and fell rapidly during the afternoon. In this simulation, wilting and stomatal closure contributed to the marked decline of photosynthesis in the afternoon

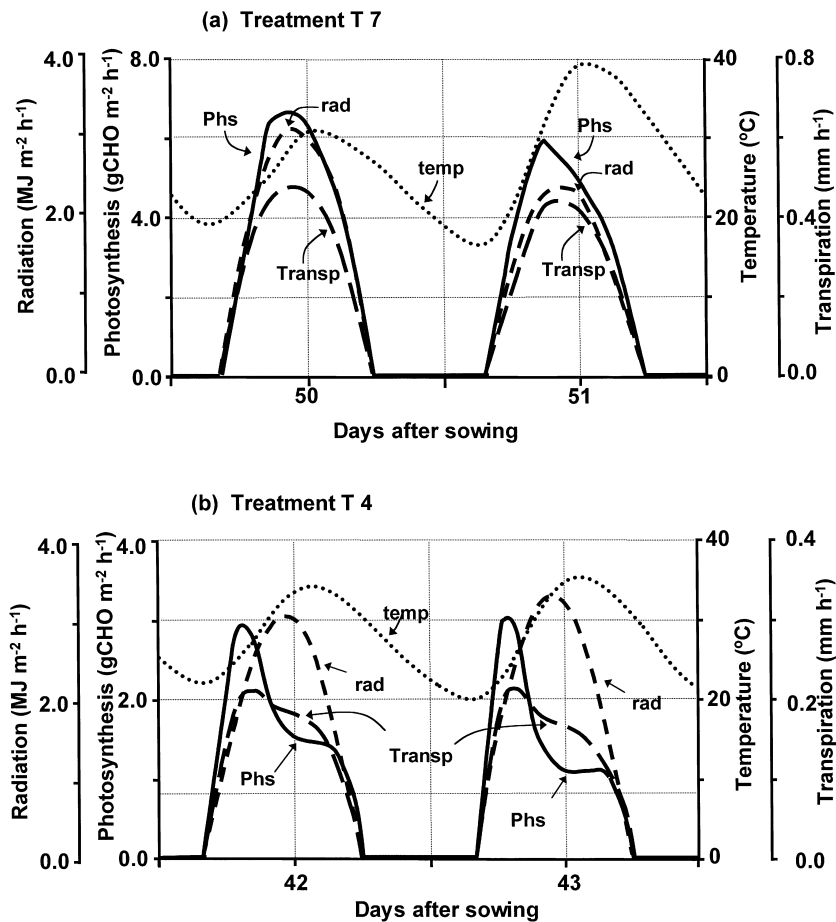


Fig. 2. Simulation of diurnal gross photosynthesis (Phs) and transpiration (Transp) of sunflower crops at Tatura, Australia in response to short-wave radiation (rad) and temperature (temp). (a) Days 50 and 51 after sowing for treatment T7. (b) Days 42 and 43 days after sowing for treatment T4.

and the consequent large hysteresis in the diurnal photosynthesis–radiation relationship displayed in Fig. 3(b).

3.2. Soil and crop water balance

Simulations of crop water potential over complete irrigation cycles together with corresponding simulated responses of leaf area index and crop (gross) photosynthesis and respiration, are presented in Fig. 4 for treatment T7 and in Fig. 5 for treatment T4.

No measurements of soil water potential were made in the experiments but the simulated limits of water potential correspond generally with those observed on

various occasions in the experiments, and with other observations on water relations of sunflower (e.g. Connor and Sadras, 1992; Sadras et al., 1993). Water potential in T7 (Fig. 4(a)) reveals a gradual adjustment to soil water availability as the season progresses, presumably reflecting in part the gradual decrease in potential evapotranspiration at this location (the summer solstice occurred 17 das) but also the dynamic adjustment of root length to leaf area in the model. This issue of balance of root length to leaf area is important to establishment and survival. More data are required to analyse this aspect of crop performance. In the experiments at Tatura, root lengths up to 7.8 km m⁻² were recovered at anthesis with great

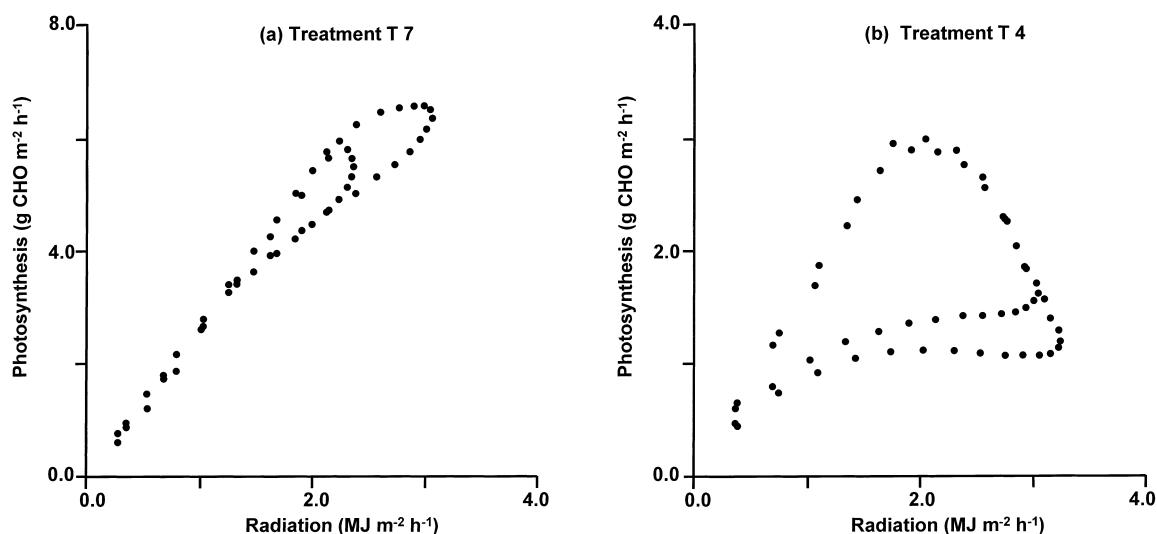


Fig. 3. Simulated relationship between gross photosynthesis and incident solar radiation of sunflower crops at Tatura, Australia. (a) Days 50 and 51 after sowing for treatment T7. (b) Days 42 and 43 after sowing for treatment T4.

difficulty, and potentially much loss, from the heavy clay soil. This is less than the ca. 20 km m^{-2} simulated for these experiments. Berengena (1977), however, recovered root lengths for sunflower crops ca. 20 km m^{-2} at Davis, California, as did Sadras et al. (1989) in Argentina.

The simulations of soil water potential in T4 (Fig. 5(a)) reveal periods of significant withdrawal and subsequent replenishment. The crop responded to rainfall of 22 mm on 35 das. The patterns of leaf water potential and of photosynthesis (Fig. 5(b)) offer evidence of stress and stomatal closure on the day before that rainfall. The greater minimum crop water potentials exhibited after that recovery then gradually decreased, once again with evidence of stress in the diurnal pattern of leaf water potential on the day before the subsequent irrigation (51 das).

Leaf area expansion also responded differentially in the two treatments. Expansion was significantly slower in T4 than T7 and in particular, Fig. 5(b) displays that simulated leaf expansion ceases in the two periods before the relief of water stress (see Fig. 5(a)).

3.3. Biomass and leaf area

A comparison is made in Fig. 6 between observed and simulated maximum leaf area index and biomass

at anthesis for the 12 treatments at Tatura (T1 to T12). The purpose here is to show a general level of coincidence and demonstrate that the diurnal responses in the balances of assimilation, respiration and the development of leaf area (Fig. 4(b), Fig. 5(b)) that lie at the core of this model accumulate consistently with the substantial differences in growth induced by the treatments in the experiments.

3.4. Partitioning and patterns of leaf expansion

The data presented previously emphasise that, in the model, the supply of assimilate varies diurnally in relation to external and internal conditions of the crop. Partitioning from the labile pool to the component organs depends only on internal conditions and is similarly diurnally variable.

Descriptions of the diurnal dynamics of leaf growth are presented in Fig. 7(a) for T7 on 50 and 51 das, and in Fig. 7(b) for T4 on 42 and 43 das. The model predicts cessation of leaf expansion during part of each day in both treatments, but with more prolonged effects and smaller growth rates in T4 (Fig. 7(b)) than in T7 (Fig. 7(a)). The model further proposes that leaf growth decreases during the early morning even while leaf water potential shows continuing recovery of water status. This response is controlled largely by

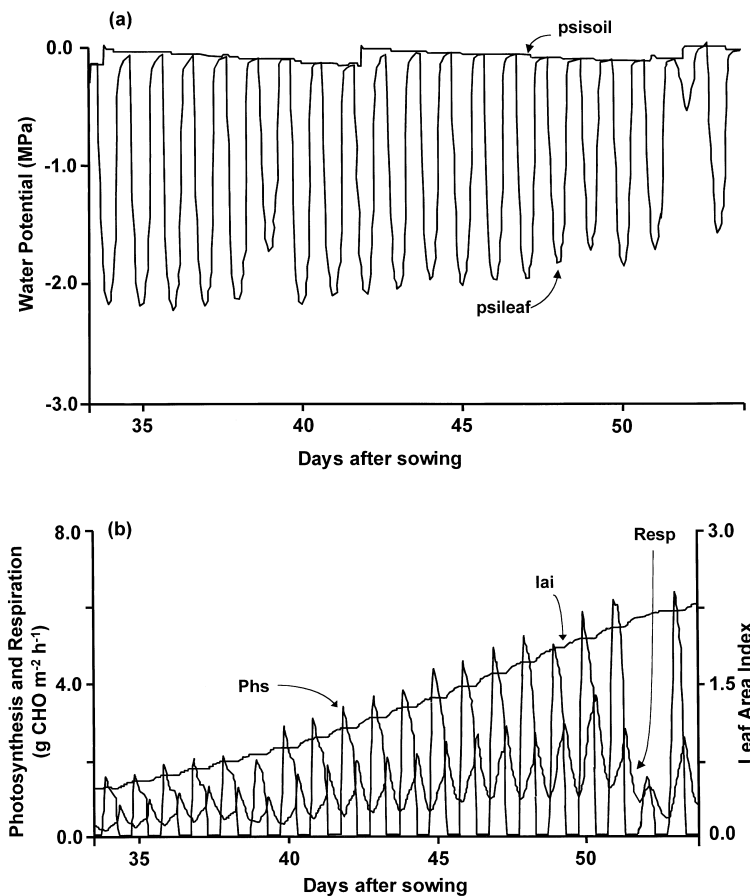


Fig. 4. Simulation for the period 34–53 days after sowing of the water relations and growth of sunflower treatment T7 at Tatura, Australia. (a) Rootzone (psisoil) and leaf (psileaf) water potentials, and (b) gross photosynthesis (Phs), respiration (Resp) and leaf area index (lai).

availability of assimilate, here shown to fall in both treatments during this period.

There were no diurnal measurements of leaf growth in this series of experiments, but the simulations correspond with observed patterns of diurnal leaf growth in other sunflower crops at Tatura (Palta, 1984) and at Davis (Berengena, 1977), under similar conditions.

3.5. Sensitivity analysis

A sensitivity analysis, using the weather and irrigation management conditions of treatment T4, investigated two issues. First, the response of the model in terms of maximum lai, biom at anthesis, and rlength) to changes of $\pm 20\%$ in nine model parameters (Table 3(a)), and second, the response to changes of

similar magnitude in three weather variables (temp, rad, and pet) (Table 3(b)). The effect of these changes is expressed as sensitivity coefficients (SC), which reveal the relative change in model output to the relative change in parameter input. Treatment 4 was chosen for the analysis because delayed irrigation ensured a wide range of water supply to the crop and consequent growth responses (Figs. 3 and 4).

The model displays significant responses to variation in model parameters with many SCs > 1 (Table 3(a)). The most responsive were rue, cp3, srl, swur, and mxcho, and the least responsive was chomin. The latter result may reflect a high value chosen for this parameter, but a major interaction with mxcho is inevitable. The dynamics of assimilate availability remains little understood and deserves continuing investigation.

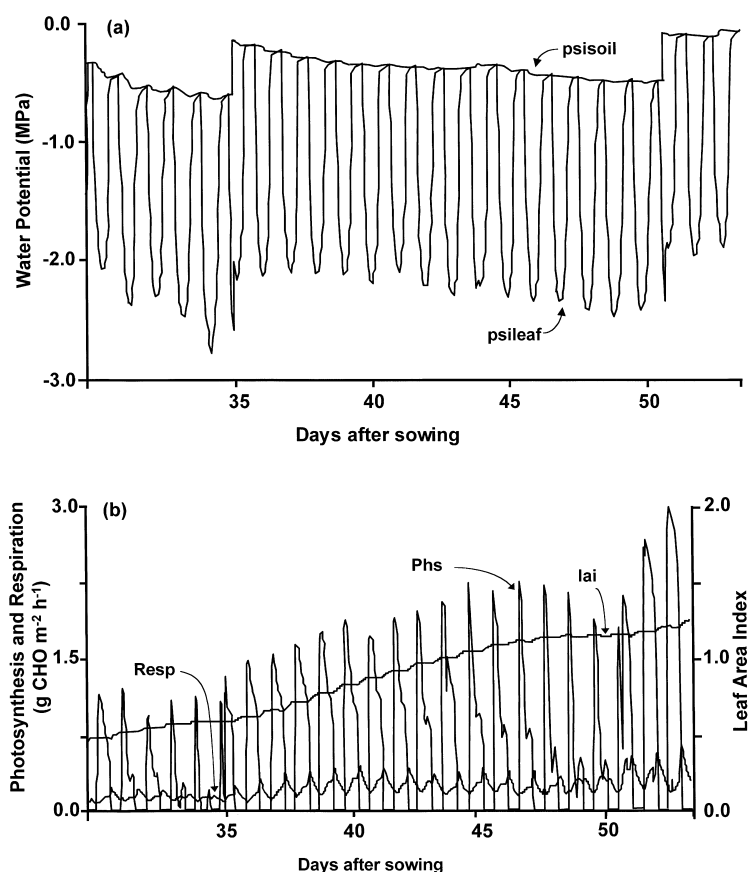


Fig. 5. Simulation for the period 30–53 days after sowing of the water relations and growth of sunflower in treatment T4 at Tatura, Australia. (a) Rootzone (psisoil) and leaf (psileaf) water potential, and (b) gross photosynthesis (Phs), respiration (Resp) and leaf area index (lai).

The analysis of the response to weather is more complex because changes in temp and rad also change pet. The sensitivity analysis of changing pet alone reveals how lowering pet in the high-evaporation environment chosen for the simulations (Table 2) has a positive effect on crop performance. Generally, responses to environmental variables are large, with many SC >2 (Table 3(b)). The analysis also investigated the effect of ignoring diurnal variation in temp and rad. In the case of rad, an average value was applied over daylight hours and for temp, either a simple mean or individual means for day and night (d/n) calculated from maximum and minimum temperatures relative to the durations of day and night. All these changes increased simulated growth, with the exception of rlength, which slightly decreased growth with mean rad. The relative effects for mean rad, mean

temp and d/n temp were for maximum lai, 10%, 33% and 29%, for biom at anthesis, 8%, 20% and 23%, and for rlength, -1%, 8%, 19%, respectively. This general response reflects the benefits to crop water status and production of lower temperatures and associated pet. Only with mean rad was there a sufficiently small advantage in biom to decrease the partitioning to rlength. None of the changes to temperature affected crop developmental rate (data not shown) because that response is assumed linear in this model and without feedback to crop growth.

4. Discussion

This model proposes a significant shift in emphasis from that which currently dominates crop modelling.

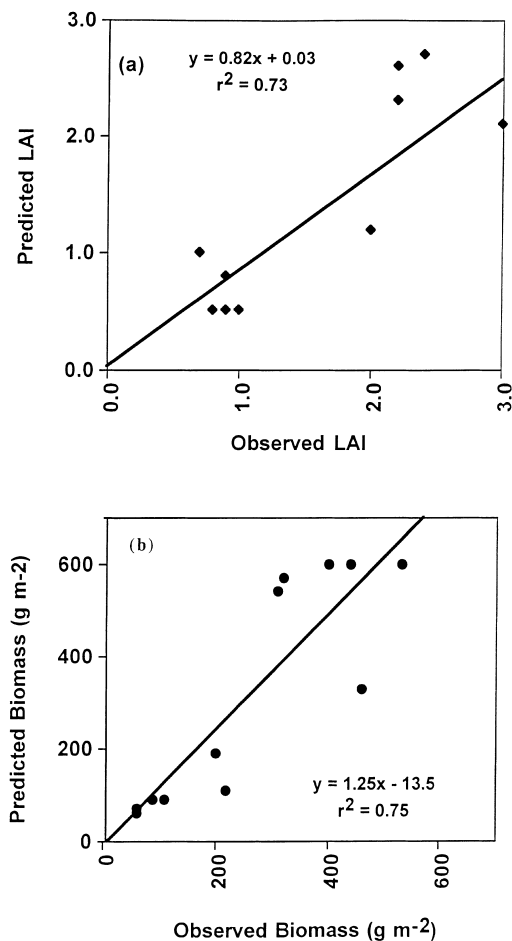


Fig. 6. Comparison of observed and simulated performance of sunflower under 12 irrigation treatments over two successive summers, 1980/1981 to 1981/1982, at Tatura, Australia. (a) Maximum leaf area index, and (b) aboveground biomass at anthesis.

It does have precedents, especially in the early work of de Wit et al. (1978) and Huck and Hillel (1983), and then in the more recent work of Ng and Loomis (1984), Norman (1989) and Denison and Loomis (1989). The model shares objectives with that early work and adds to it new approaches and modelling techniques. In contrast to daily time step models, this new model is able to relate long-term crop performance (week to week) to morphological changes that occur from day to day, and to the diurnal evolution of crop water status, assimilation and transpiration. Daily-time-step models are unable to accommodate

such detailed considerations of assimilation and partitioning to component organs and are therefore intrinsically limited in their capacity to explore the physiological bases of crop productivity and its response to short-term environmental fluctuations.

A determining decision in the present work was to describe the assimilate content of the crop and the water contents of crop and root zone with single state variables. An option, closer to internal physiological processes, would associate assimilate and water pools with each crop organ. That, however, would require many additional assumptions about distribution of assimilate and flow of water through the crop, for which there is considerable uncertainty in parameter values. Some limitations of using a single variable for crop water content were overcome by introducing dynamic gradients of water potential from soil to leaf. There are sufficient measurements of such gradients in crops to support that approach. However, it was felt that a reverse gradient of assimilate from the source in leaf to the most distal sink in root, although arguable, is not sufficiently well documented to justify inclusion. Instead, the relative isolation of roots from the source of assimilate is introduced indirectly by restricting the growth of roots at high crop water content when leaf and stem are in the better physiological condition and physical position to dominate the use of assimilate.

Although this model uses plant water potential for its control of assimilation and partitioning and does not invoke any explicit role for non-hydraulic signals in root–shoot interactions, its structure does include both source and sink limitations to growth. In this model, leaf water potential controls not just leaf conductance but leaf expansion also. The two scenarios outlined by Passioura (1996) for modelling the growth of drought-affected plants are not exclusive. There is no reason why individual models should not include both source and sink responses to water shortage or to claim that the CERES-based models (IBSNAT, 1988) that relate growth to soil water content support the sink-limited alternative. In the CERES-based models, soil water content is equally a surrogate for plant water potential. Models should include both source and sink responses if that is how plants operate (see Monteith, 1986). The experiments that underpin this work, and other studies (e.g. Sadras et al., 1993), have shown, that limitations on leaf expansion are

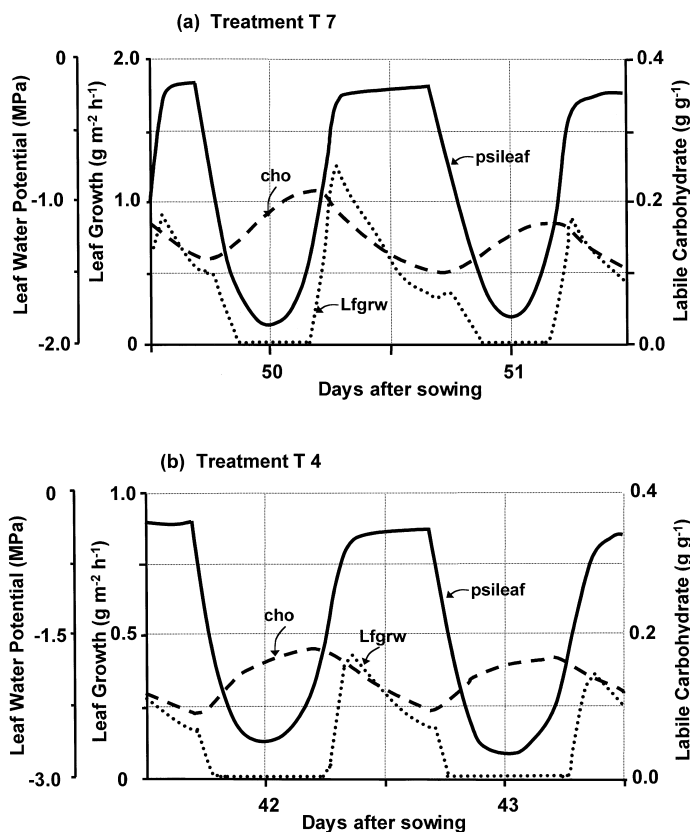


Fig. 7. Simulation of diurnal leaf water potential (*psileaf*), labile assimilate as a proportion of crop biomass (*cho*) and leaf growth (*Lfgrw*) of sunflower crops at Tatura, Australia. (a) Days 50 and 51 after sowing for treatment T7. (b) Days 42 and 43 days after sowing for treatment T4.

more important than stomatal closure in the control of internal leaf water status in sunflower under field conditions as in many other crops.

The use of a single state variable for root-zone water content introduces advantages and limitations. On the positive side, no assumptions are required about the relative growth and water-uptake activities of fractions of the root profiles, which generally decline exponentially with depth. On the other hand, expressions of water availability based upon average root-zone water content inevitably underestimate the importance of zones of wet soil, especially deep ones often critical in drought situations. These zones are formed as roots proliferate into wet soil and when light rain (or irrigation) wets surface layers. Despite these limitations, and the importance of accurate simulation of crop water status in the present work, we have shown (Figs. 4 and 5) that the model is able to perform well

over a wide range of water supply. Research will allow further development, but for the present, the model is re-emphasising the obvious—that accurate data on the length, distribution, and turnover of active and non-active roots are required to further our understanding of the water relations and performance of crops in response to environment and management.

The sunflower crops against which the model was compared varied greatly in growth due to an extreme range of irrigation treatments (Table 2). Despite inherent limitations arising from its simplicity described above, the model was shown to mimic important diurnal physiological responses of photosynthesis, water relations and transpiration (Figs. 2 and 3), and to integrate those responses over days and weeks to provide agronomically realistic responses of crop water use, biomass accumulation and partitioning to component organs (Fig. 6). The comparisons did,

Table 3

Sensitivity coefficients ^a for three model output responses to negative and positive changes of 20% in (a) nine model parameters, and (b) three weather variables

	Negative change			Positive change		
	lai (max)	biom (anth)	rtlength (anth)	lai (max)	biom (anth)	rtlength (anth)
(a) Model parameters						
rue	−2.14	−2.42	−2.29	2.62	2.30	1.98
cp1	−0.36	−0.33	−0.13	−0.12	−0.19	−0.40
cp2	0.71	0.54	0.25	−0.60	−0.68	−0.43
cp3	1.07	0.67	0.38	−1.90	−1.65	−1.33
srl	−0.95	−0.84	−1.46	0.83	0.50	1.36
prpgrw	−0.36	−0.32	−0.15	0.24	0.08	−0.05
swur	−1.19	−0.84	−0.55	0.71	0.50	0.30
mxcho	−1.31	−1.02	−0.80	0.29	0.12	0.10
chomin	0.12	0.11	0.15	−0.24	−0.13	−0.15
(b) Weather variables						
rad	−2.26	−2.42	−2.29	2.62	2.30	2.01
pet	1.43	2.12	1.21	−3.93	−4.50	−4.40
temp (T_{\max})	−2.98	−2.34	−2.19	−2.98	1.59	0.75
temp (T_{\min})	1.31	−0.60	0.10	−1.07	0.23	−0.58

Note: The analysis was made with the weather and irrigation management conditions of sunflower Treatment 4, Tatura, Australia, summer 1980/81 (Table 2), for the period up to anthesis. Model parameters as presented in Table 1.

^a Sensitivity coefficients are calculated as relative change in model output per relative change in input parameter/variable.

however, uncover some differences. For example, field data revealed a greater capacity for leaf area expansion in crops following water deficits than was predicted by the model's present considerations of water status and phenological development. If osmotic adjustment, known to be important in sunflower (see Connor and Sadras, 1992) played a role in that response, it could be included in the model as a dynamic adjustment in the relationship between crop relative water content and water potential, and perhaps also, in the values of the control points for stomatal closure and tissue expansion. That issue and others, e.g. diurnal and seasonal variation in extinction coefficient (k), and the effect on it of heliotropism, characteristic of sunflower canopies, await attention. The major issue here was to seek a framework directed at improving understanding of assimilate partitioning in response to water supply and that purpose does not require the inclusion of every process in detail.

It will be interesting to assess how expansion of the model with multi-layer canopy and multi-layer soil-root systems might improve performance. At the present time, complex models of individual physiological processes are available. The extensive treatise

of crop physiological modelling (Thornley and Johnson, 1990), for example, presents alternatives of varying complexity. It also reveals, however, how the development of treatments of carbon and water balance has largely continued over the past two decades in the absence of attempts to deal with their interactions that are the essence of crop growth and adaptation. The model presented here commences with simple treatments of individual processes in order to refocus attention on those interactions and thereby provide a framework for further expansion and development.

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