European Journal of Agronomy 14 (2001) 43–60

European Journal of Agronomy

www.elsevier.com/locate/eja

Simplifying Sirius: sensitivity analysis and development of a meta-model for wheat yield prediction

Roger J. Brooks [a], Mikhail A. Semenov [b,*], Peter D. Jamieson [c]

[a] *Department of Management Science, Management School, Lancaster University, Lancaster, LA1 4YX, UK*
[b] *IACR Long Ashton Research Station, Department of Agricultural Sciences, University of Bristol, Bristol BS41 9AF, UK*
[c] *New Zealand Institute for Crop & Food Research Ltd, Private Bag 4704, Christchurch, New Zealand*

Received 17 February 2000; received in revised form 19 June 2000; accepted 1 August 2000

Abstract

A sensitivity analysis and analysis of the structure of the Sirius wheat model has resulted in the development of a simpler meta-model, which produced very similar yield predictions to Sirius of potential and water-limited yields at two locations in the UK, Rothamsted and Edinburgh. This greatly increases the understanding of the nature and consequences of the relationships implicit within Sirius. The analysis showed that the response of wheat crops to climate could be explained using a few simple relationships. The meta-model aggregates the three main Sirius components, the calculation of leaf area index, the soil water balance model and the evapotranspiration calculations, into simpler equations. This results in a requirement for calibration of fewer model parameters and means that weather variables can be provided on a monthly rather than a daily time-step, because the meta-model can use cumulative values of weather variables. Consequently the meta-model is a valuable tool for regional impact assessments when detailed input data are usually not available. Because the meta-model was developed from the analysis of Sirius, rather than from statistical fitting of yield to weather data, it should perform well for other locations in Great Britain and with different management scenarios.

Keywords: Crop model; Model simplification; Meta-model; Mathematical modelling; Computer simulation

1. Introduction

Process-based models of varying complexity have been developed that can be used to estimate wheat yield at the site scale. These include Sirius (Jamieson et al., 1998c), AFRCWHEAT2 (Weir et al., 1984; Porter 1993), CERES-Wheat (Ritchie and Otter, 1985), and ECOSYS (Grant, 1998). Each of these is designed to simulate the growth and development of wheat in small, homogeneous areas. They require input data for weather, soil attributes and management practice (choice of cultivar, sowing date, nitrogen application and irrigation) at varying detail. They are able to supply output, on a daily basis, of variables such

* Corresponding author. Tel.: +44-1275-392181; fax: +44-1275-394007.

E-mail addresses: roger.brooks@lancaster.ac.uk (R.J. Brooks), mikhail.semenov@bbsrc.ac.uk (M.A. Semenov), jamiesonp@crop.cri.nz (P.D. Jamieson).

PII: S1161-0301(00)00089-7

as biomass, yield, soil water content, mainstem leaf number, leaf area and evapotranspiration. The complexity of the above models, measured as, for example, the number of model parameters, varies substantially. Consequently, the level of input detail also varies substantially. There is a common expectation that the more complex models, because they include explicit descriptions of many sub-processes, should produce more accurate results. This is not always so and, in practice, a simple model can predict crop yields as accurately as more complex ones (Jamieson et al., 1998b). For example, ECOSYS is a significantly more complex model than Sirius, and requires very detailed input information and high computer power to run, but its predictions of grain yield are not better than those from Sirius (Goudriaan, 1996).

Sirius is a mechanistic model of low to intermediate complexity, based around a detailed simulation of the phenological development of the plant (Jamieson et al., 1998c). The model calculates the final number of leaves using a daylength response mechanism (Brooking et al., 1995; Jamieson et al., 1995a) incorporating a simulation of vernalisation (Brooking, 1996; Robertson et al., 1996), with the number of leaves setting the thermal time to anthesis (Jamieson et al., 1998a). Biomass is accumulated according to the amount of light intercepted each day, at a light use efficiency that is constant unless reduced by water or nitrogen stress. The simulation of leaf area, which determines the amount of radiation intercepted, and therefore the amount of biomass accumulated, is calculated separately from the number of leaves, although progress after full canopy closure depends on phenological development (Jamieson et al., 1998c). Yield is calculated as the biomass accumulated during the grain fill plus up to 25% of the biomass at anthesis. Sirius also includes detailed modelling of the water and nitrogen processes in the soil as well as transpiration and surface soil evaporation. These are used to determine the amount of water or nitrogen deficit experienced by the plant which can result in reduced leaf area (hence light interception) and light use efficiency, combining to cause a reduction in the amount of biomass added each day. Importantly, Sirius has been able to mimic the performance of wheat crops in experiments in widely different environments over a several-fold yield range (Jamieson et al., 1998b,c, 2000).

In any modelling project, it is important to match the data requirements of the model with the available data and to tailor the process complexity to the project objectives (Brooks and Tobias, 1996). For example, excessive detail can lead to a model being inaccurate due to a mismatch of the model and available data. In many regional impact assessments detailed output from the crop models is not required. Instead, information about potential and water-limited yield is usually sufficient. The application of crop simulation models, such as Sirius, requires information on daily weather, soils, and management over a whole region at reasonably high spatial resolution. Such information is often unavailable. A possible solution would be a simplified meta-model with reduced input requirements, but which is able to reproduce the major responses of the original crop model.

There are a number of other potential advantages of developing a simplified model (Brooks and Tobias, 1999). The main advantage of a simpler model is often that it is easier to understand and consequently it is easier to interpret the results from the model. One aim of simulation modelling should always be to obtain a better understanding of the system being studied. Examination of the inner workings of the model can often be used to explain the model's results, such as the reasons for unusual or unexpected behaviour, rather than just treating the model as a predictive black box. This is particularly the case when, as with Sirius, the model is mechanistic, constructed by combining representations of the important processes thought to be taking place in the system. The process of simplifying an existing model can also give valuable insights into the system. Additional expected advantages of a simpler model include it being quicker to build, test and run. Consequently, common modelling advice is to use the simplest model that meets the modelling objectives (Brooks and Tobias, 1996). The main danger with using a simple model is that important aspects of the system may be omitted, so that the model is unrealistic. However, simplification of an existing model can give confidence in the simplified model by cross-validation against the original more complex model.

The overall aim of the work described here was to develop a simplified meta-model of Sirius. The development of the meta-model was carried out in two main stages. Firstly, a detailed sensitivity analysis was carried out as described in Section 2. This, in itself, gives a better understanding of the responses of Sirius to the input variables and parameters used in the model. Secondly, in order to explain the sensitivity results, the mechanisms of the processes represented in Sirius were analysed and this analysis is described in Section 3. The meta-model was then based on the simplified relationships derived from the analysis of Sirius. The general form of the meta-model is set out in Section 4 along with its specific implementation and the results obtained. Finally, Section 5 discusses the implications of the work.

2. Sensitivity analysis

The ability to be able to aggregate relationships into a meta-model depends on the characteristics and interactions among the variables in the system being investigated. Therefore, the initial stage of the meta-model methodology was to investigate the relationships between the inputs and outputs of the Sirius model through sensitivity analysis. The sensitivity analysis is described in this section. A more detailed description is given in Brooks and Semenov (1998).

The aim of the sensitivity analysis was to use Sirius to identify which parameters are most important in determining yield. Sensitivity analysis can also act as a verification test by highlighting unusual behaviour, which could be due to errors, as well as additional validation in that the relationships observed can be compared with experimental results.

The sensitivity analysis used data for Rothamsted in the UK, a site where Sirius has been validated (Jamieson and Semenov, 2000) and where reliable soil data and a long series of weather data were available. Each of the simulations was of winter wheat, and, for ease of discussion, the years refer to the year of harvest so that, for example, 1989 refers to wheat sown in autumn 1988 and harvested in summer 1989. The runs were performed in two stages as follows:

1. All of the 20 main Sirius input parameters (Table 1), and the four weather parameters (minimum temperature, maximum temperature, precipitation and radiation) were varied one at a time, in most cases for 51 values over the range $\pm 50\%$. This was done for 2 years; 1989, which is a year with little or no predicted water stress, and a fairly high simulated yield, and 1976, which had extreme summer conditions (very hot and dry) resulting in very low simulated yield. Each year was run with nitrogen limitation turned off, e.g. the nitrogen processes are simulated but the effects of any deficit on the plant are not.
2. In addition to the above scenarios, the weather parameters were varied for each of the years 1961–1990 over a more limited range, with nitrogen limitation off, and the results averaged in order to obtain an average response to changes in climate.

The base values of the parameters were chosen as typical values for the Rothamsted region or for the UK as a whole. In particular, the sowing date was chosen as 15 October, the cultivar was Avalon, the radiation use efficiency was set at 2.5 g MJ^{-1}, the extinction coefficient was 0.445 and no irrigation was applied. The summary output variables from Sirius are the dates of the phenological stages (sowing, emergence, floral commitment, anthesis, beginning of grain fill, end of grain fill, and maturity), the final number of leaves, the biomass at anthesis, the biomass at maturity, the grain yield, and these were all produced by the sensitivity runs and graphs generated for each. The daily outputs of variables such as the water deficit and leaf area index were not recorded, except for some extra runs where particular choices of parameters were made in order to analyse model behaviour further.

Table 1
SIRIUS model parameters used for sensitivity tests

Parameter Name	SIRIUS variable name	Values used at Rothamsted	Sensitivity test range
Soil parameters			
Saturation soil moisture	Qs	44%	±25%
Reservoir percolation constant	Kq	0.3	±50%
Initial water deficit	DEF	0	0–300
Available and unavailable water capacities	AWC[6] and UWC[6], values specified for each 25 cm of depth.	For AWC: 160; UWC: 80 for the top 25 cm and then 60 for the rest	±50%
Maximum root depth	MaxD	1.5	±50%
Vernalisation parameters			
Vernalisation rate response to temperature	VAI	0.0012	±50%
Vernalisation rate at 0°C	VBEE	0.015	±50%
Thermal time parameters			
Thermal time from sowing to emergence	TTSOWEM	150	±50%
Thermal time from anthesis to beginning grain fill	TTANBGF	100	±50%
Thermal time from beginning to end of grain fill	TTBGEG	650	±50%
Phyllochron	PHYLL	90	±50%
Cultivar parameters			
Intercept of LAI equation	CEPT	2.76	±50%
Slope of LAI equation	SLOPE	0.00616	±50%
Minimum possible leaf no.	AMNLFNO	8.5	±50%
Maximum possible leaf no.	AMXLFNO	24	±50%
Leaf number daylight response rate	SLDL	0.6	±50%
Extinction coefficient (extinction of PAR by LAI)	EXTINC	0.445	±50%
Radiation use efficiency	EFFIC	2.5	±50%
Soil and cultivar type			
Soil type	Soil	7	Types 0–5
Cultivar type	VARIETY	AVALON	14 types

2.1. Summary of sensitivity results

2.1.1. Model parameters

Sensitivity analysis using different scenarios may give different results but, based on the runs carried out, the important parameters (in some cases only over certain ranges) out of the 20 input parameters investigated are the initial soil water deficit, the soil depth and available water content, the thermal time parameters for the phyllochron and the grain fill period, the minimum leaf number and the radiation use efficiency (Table 1). Fig. 1 shows the effect of some parameters on simulated grain yield for 1989. The base value of the initial water deficit was zero and this was increased up to 300 mm in the sensitivity analysis. The other parameters in Fig. 1 were all varied over the range ±50%.

The final number of leaves, which sets the thermal time to anthesis, is often set in the model by the vernalisation process. However, for these scenarios, the minimum leaf number was high which resulted in it being used directly in the calculation of the final number of leaves with the vernalisation process having no effect. With a lower value, the two vernalisation parameters would probably be important rather than the minimum leaf number. Yield was not sensitive to

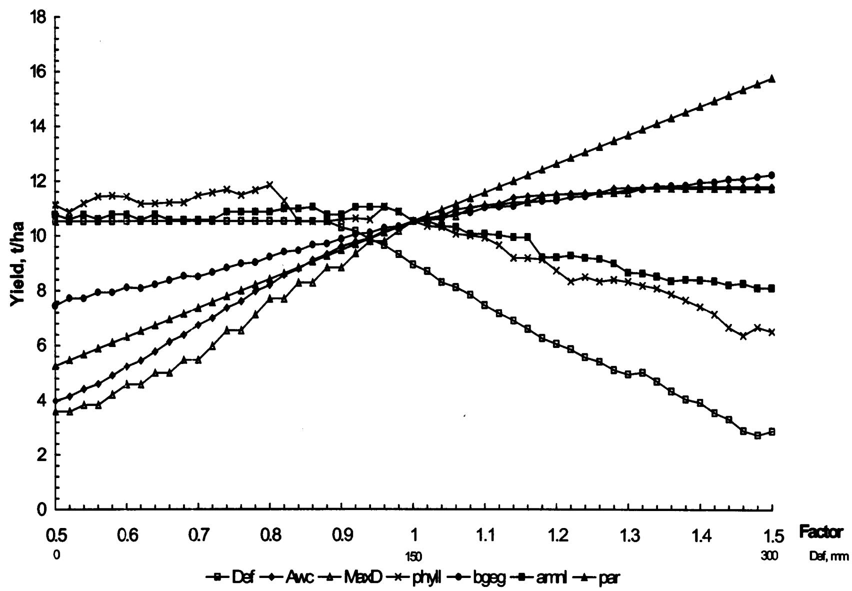

Fig. 1. Sensitivity analysis showing the effect of the most important parameters on yield for Rothamsted 1989 with unlimited nitrogen. The parameters are the initial water deficit (Def), the available water content of the soil layers (Awc), the soil depth (MaxD), the phyllochron (phyll), the grain fill thermal time (bgeg), the minimum leaf number (amnl) and the light use efficiency (par).

parameters determining the growth of the leaf area, those affecting excess water or those that had only a small effect on the anthesis date.

The light use efficiency is a scaling parameter that has the same effect on yield in any scenario, since yield is exactly proportional to the light use efficiency parameter. This parameter is therefore irrelevant in comparing the relative yields between different scenarios such as different soils, cultivars, sites or climates. To an extent, the thermal duration of the grain fill has a similar effect by scaling the length of the grain fill. The results showed that yield was approximately linearly related to the length of the grain fill period and so it will also often be unimportant in making a comparison of yields. For the Rothamsted climate, the initial water deficit has to be quite large to have any effect. Therefore, in this situation, the only important parameters are the soil depth and available water holding capacity per unit depth for each soil layer (their product across the soil layers is the total soil available water holding capacity, AWC), the phyllochron, and either the minimum leaf number or vernalisation parameters (depending on the choice of cultivar).

The available water content is specified as a soil input parameter in Sirius for each soil layer. The AWC sensitivity factor was applied to the values for all layers. This has a similar effect to applying the same sensitivity factor to the soil depth since, in both cases, the total AWC of the soil will be multiplied by the sensitivity factor (although the water is only available to the plant to the depth of the roots). Yield was found to be approximately linearly related to both factors (and hence to the total soil AWC) in water stressed conditions. For high values of AWC or soil depth, changes in these parameters have less effect because the plant only suffers water stress for part of the period. In 1989, there was sufficient precipitation, for very high values of AWC or soil depth, so that potential yield was reached. At very large soil depths, the roots do not reach the bottom of the soil and so yield is not affected by further increases in soil depth.

The phyllochron has a significant effect on the anthesis date with an increase delaying anthesis. Within a certain range, a large delay in anthesis tends to significantly reduce yield. In 1989, this

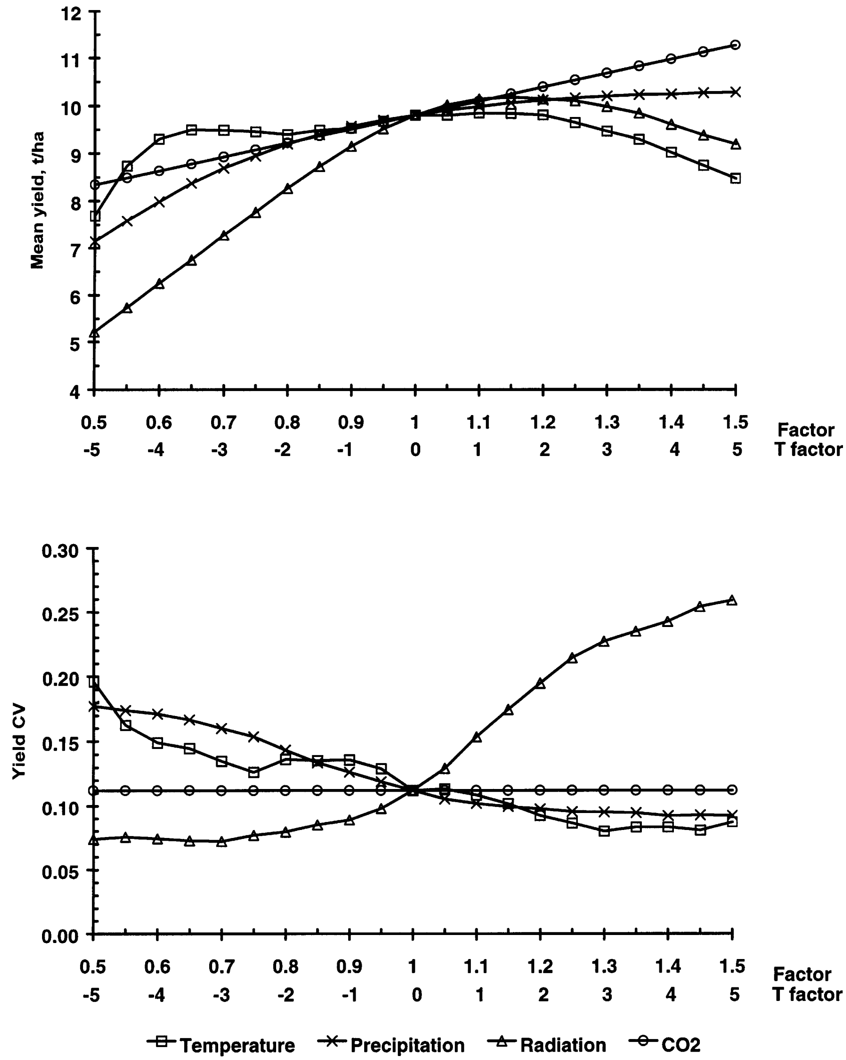

Fig. 2. Sensitivity of mean grain yield (a) and its CV (b) simulated by Sirius for 1960–1990 at Rothamsted, UK, to changes in temperature, rainfall, radiation and CO_2. Precipitation, radiation and CO_2 were changing by multiplying their values by Factor and temperature was changing by adding T-factor.

applies to anthesis dates later than the base value (12th June). Consequently, increases in the phyllochron in 1989 above the base value tended to decrease yield, with changes in the phyllochron below the base value causing little trend in yield although with some irregular variation. In 1976, the increases in the phyllochron increased yield when the sensitivity factor was less than 1.16.

The minimum leaf number also affects the anthesis date by setting the final number of leaves although the effect on the anthesis date is less than for the phyllochron. Therefore, the pattern of changes in yield is similar to that for the phyllochron, but of smaller magnitude.

2.1.2. Weather variables

Although the weather variables provide separate input values for each simulated day, they were varied in the sensitivity analysis by applying constant sensitivity factors throughout the period. Fig. 2 shows the mean and coefficient of variance of yield for the 30 sensitivity runs for Rothamsted 1961–1990.

The response of yield is the most irregular for temperature. The main effect of temperature is to set the phenological dates and so changes in temperature affect both the timing and duration of the main growth periods in which most of the biomass is accumulated and during which the water deficit tends to increase. In the runs for both 1976 and 1989, the trend of yield against temperature has maximums at temperature factor values of about -4 and $+4$ and a minimum in between at about -2°C. The curve of the average values for 1961–1990 (Fig. 2a) also has the same pattern, although much less pronounced, and between -2°C and $+2$°C there is very little change in yield. The sensitivity analysis considers a wide range of temperature variation and the fall in simulated yields for low temperature factors occurs because the simulation ceases by default 1 year after the sowing date. In reality, crops maturing in October would be at risk from disease. The coefficient of variation for the 1961–1990 yields tends to decrease as temperature increases because the earlier maturity means that there are fewer years with a water deficit sufficient to significantly reduce yield (Fig. 2b). If many years experience a water deficit, differences in precipitation mean that the severity of the water deficit varies considerably between years. The difference in yields is therefore much greater than if most years experience no water deficit yield loss.

Changing the precipitation affects the amount of water in the soil and hence the yield loss due to the water deficit. At high precipitation levels, there is sufficient water for the crop and so changes in precipitation have no effect. As with most crop models, there is no disease effect in Sirius and so no penalty for excess water. As precipitation reduces, both the length and severity of the water deficit increase and so each reduction in precipitation causes a progressively larger drop in yield. At very low values, the soil would run out of water during the growing period so that further reductions in precipitation would have less effect. Differences in the water deficit between different years mean that the coefficient of variation also tends to increase as precipitation reduces.

For the lowest values of solar radiation, no water stress is experienced and average yields for 1961–1990 initially increase linearly as solar radiation is increased. Increased solar radiation increases transpiration and, for each year there is a point after which further radiation increases cause a water stress yield loss. The increasing water deficit results in the average yield reaching a maximum at a radiation factor of about 1.2. The differing water stresses experienced in different years cause the coefficient of variation to increase as radiation increases.

It is assumed that the only effect of an increase in the CO_2 concentration is to improve the efficiency of plant photosynthesis. This is implemented in Sirius by changing the radiation use efficiency parameter, r, linearly with the increase in CO_2 above the baseline value of 353 p.p.m. Therefore yield is linearly related to CO_2, and the coefficient of variation is constant.

2.2. Random noise

One of the findings of the sensitivity analysis was that a slight change in some of the parameters could change the yield by as much as 500 kg ha^{-1}. Any model of this system will inevitably contain uncertainty as to the most appropriate values of the parameter. Often, there are difficulties in practice of measuring many of the soil and cultivar parameters. In addition, the soil parameters are likely to vary considerably at the field scale and so, even when some measurements are available, the measurements will just be a sample from this variation in values. The modelling usually aims to represent conditions at the field scale or larger and so, strictly, some average of the parameters over this scale is required. A further problem is that weather data will usually be measured at a different location from the field being simulated. The variation in simulated yields that occurs over the range of uncertainty of the parameters represents a fundamental limit to the accuracy that models can achieve. In particular, there are likely to be no benefits for yield predic-

Table 2
The mean and standard deviation of the yield values (in t ha^{-1}) for 1000 sets of parameter values chosen randomly from the uniform distribution over the given ranges

Range of noise	0	±0.5%	±1%	±2%	±3%	±4%	±5%
Input parameters							
Mean	10.52	10.41	10.40	10.41	10.40	10.36	10.32
Standard deviation	0	0.19	0.21	0.28	0.36	0.46	0.57
Weather parameters							
Mean	10.52	10.57	10.57	10.57	10.51	10.42	10.32
Standard deviation	0	0.78	0.13	0.22	0.26	0.34	0.39

tion by including excessive detail in crop models. This type of variation is also likely to be present in reality, with yield varying at the field scale due to variations in the quality of both plants and the soil.

The sensitivity of Sirius to small random perturbations of the input parameters (Table 1) was investigated by running the model for 1989 using random values of the sensitivity factors for each parameter. The factors were obtained by sampling from the uniform distribution over six set ranges from ±0.5% up to ±5%. Two sets of experiments were carried out with the first altering just the input parameters and the second altering just the weather parameters. Each of the weather parameters was varied by applying one factor throughout the period, as before. This represents the effect of a small systematic difference in the values across the whole year, perhaps due to consistent measurement errors or due to the weather site having a slightly different altitude from the field being simulated. The same temperature factor was applied to both minimum and maximum temperature and the range of noise for temperature was based on a typical mean temperature value in the growing period of 15°C. For example, for noise of the range ±1%, the temperature factor had the range ±0.15°C. For each scenario, the model was run with 1000 sets of parameter values. Table 2 shows the means and standard deviations of yield for each experiment.

The results confirm that yield predictions vary significantly for even a small variation in the values of the parameters. The distribution of yield for the input parameter scenarios follows the normal distribution closely (based on normal scores plots), except for the ±0.5% scenario where there are three distinct distributions resulting from the existence of just three different lengths of grain fill periods. The increase in the variance as the input parameter range increases is approximately exponential. For the weather scenarios, the distribution of yield is slightly negatively skewed. The actual yield value for the base parameter values (10 521 kg/ha^{-1}) is just a single point and the mean values for small random noise in the parameters ($\approx$10 400 kg/ha^{-1}) would therefore be a more appropriate result for this scenario.

The variation in yields for small changes in the parameters sets a limit on the match with observed yields that is possible with such a simulation model. Because similar random variations are likely to be present in the observed values, a perfect match between observed and simulated yields should not be expected. Tests of models should therefore use yields over a wide range so that the differences in yields are mainly due to differences in conditions for each scenario rather than local random variation (Jamieson et al., 1999).

3. Simplifying Sirius equations

The next stage of the study was to analyse the mechanisms within Sirius. This section explains how these can be combined to produce an equation for yield, which helps to explain the sensitivity results and also forms the basis of the meta-model.

3.1. Yield equation

The biomass added each day by Sirius throughout the simulated growth of the plant is given in gm^{-2} by

$$\text{biomass added in one day} = 0.48Srb(1 - e^{-xl}) \quad (1)$$

where S is the global solar radiation for the day ($MJ\ m^{-2}$), 0.48 is a transfer coefficient between global radiation and photosynthetically active radiation (PAR), r is the light (or radiation) use efficiency ($g\ MJ^{-1}$), $b(0 \leq b \leq 1)$ is the reduction factor for the light use efficiency due to drought, x is the extinction coefficient and l is the leaf area index (LAI). The term $0.48S(1-e^{-xl})$ represents the amount of PAR intercepted by the plant. As l increases, the radiation intercepted, and hence the biomass, increasess but the rate of increase becomes less due to the fact that new leaves will tend to overlap existing leaves. In particular, unless the leaf area is small, the biomass added is not sensitive to changes in the leaf area index.

In the grain fill period (GFP) all the biomass accumulated is allocated to the grain. The leaf area is reduced proportionally to the square of accumulated thermal time, although the daily thermal time value used is multiplied by a water deficit factor, $k(1 \leq k \leq 1.5)$. The equation for leaf area, l, during grain fill is

$$l = L\left(1 - \frac{(kT_{acc})^2}{T_{GFP}^2}\right) \quad (2)$$

where L is the LAI at the start of grain fill, T_{acc} is the accumulated thermal time to date in grain fill and T_{GFP} is grain fill period thermal time. The grain fill period ends when the leaf area reduces to zero. In the absence of a water deficit the thermal time of grain fill will therefore be T_{GFP}, but the thermal time will be reduced if such a deficit causes k to be greater than one. At anthesis the LAI will be at a value of 8.5 (a fixed Sirius parameter), unless a water deficit before anthesis reduces this value (although a severe deficit is required for a significant reduction). The LAI will reduce slightly in the few days between anthesis and the start of grain fill so that L will usually be between 8 and 8.5.

In the analysis, constant values for b, k, S and the daily thermal time T will be assumed during the grain fill period. Then, by substituting Eq. (2) for the reducing leaf area index into Eq. (1) and integrating over the grain fill period, the biomass added during the grain fill period is given by

$$\text{GFP biomass} = \int_0^{\frac{T_{GFP}}{k}} \frac{0.48Srb}{T} \times \left(1 - e^{-xL\left(1-\frac{k^2t^2}{T_{GFP}^2}\right)}\right) dt \quad (3)$$

The division by T converts the daily biomass of Eq. (1) into biomass per unit thermal time. This is then integrated over the grain fill period thermal time. Strictly, this relationship is modelled in Sirius just at the daily time step rather than continuously. In addition, a drought deficit during the few days between anthesis and the beginning of grain fill slightly reduces the length of the grain fill period in Sirius, although this effect is small and has been ignored in Eq. (3).

The integral can be evaluated by expanding the Taylor series for the exponential function and then integrating term by term (Ferrar, 1980 p114 Theorem 46) to give

$$\text{GFP biomass} = \frac{0.48SrbT_{GFP}}{kT} \times \left(1 - e^{-xL}\left(1 + \sum_{i=1}^{\infty} \frac{(xL)^i}{i!(2i+1)}\right)\right) \quad (4)$$

The term T_{GFP}/kT is the length of the grain fill period in days. The term within the outer brackets is the average proportion of radiation intercepted over the grain fill period. We will denote this by $f(x,L)$. This term can be evaluated easily but a good approximation (over the range of usual x values) is also given by $1 - e^{-xL\left(\frac{2}{3}-\frac{xL}{20}\right)}$. The possible values of $f(x,L)$ are between 0 and 1 but, unless L is very small, the value will be close to 1. As for the daily biomass equation, $f(x,L)$ is not particularly sensitive to the value of L unless L is small. For example, here $x = 0.445$ and L values of 6, 7 and 8 give $f(x,L)$ values of 0.76, 0.80 and 0.83 respectively.

In Eq. (4), r, T_{GFP} and x are cultivar parameters input by the user. As explained above, the LAI at the start of grain fill, L, will usually be about 8 and, in any case, the GFP biomass is not sensitive to this value. GFP biomass therefore mainly depends on the photothermal quotient S/T during grain fill and the water deficit variables b and k. The photothermal quotient will be determined by the weather pattern in the particular year and the specific timing of the grain fill period.

The final yield is the sum of the biomass added in the grain fill period and a proportion (up to a maximum of 0.25) of the anthesis biomass, A. The anthesis biomass is added to the yield over the grain fill period with the amount added each day being $0.25A \times T/T_{\mathrm{GFP}}$. However, since the number of days of the grain fill period is T_{GFP}/kT, the total anthesis biomass included in the yield will be $0.25A/k$. Again, the slight reduction in the length of the grain fill period due to a drought between anthesis and the start of grain fill has been ignored. Therefore, the yield is given in gm^{-2} by

$$\text{yield} = \frac{1}{k}\left(0.25A + \frac{4.8SrbT_{\mathrm{GFP}}}{T} f(x,L)\right) \qquad (5)$$

The anthesis biomass consists of the accumulation of biomass from the emergence of the plant until anthesis. The biomass added each day is given by Eq. (1). The total biomass accumulated therefore depends on the length of this period, which is set in thermal time, as a number of phyllochrons, by the calculation of the final number of leaves (which uses vernalisation and input cultivar leaf parameters). The phyllochron is also a cultivar parameter input by the user. After emergence the LAI increases from zero as a function of thermal time, although the initial increase is rapid and so the biomass added soon becomes insensitive to the precise LAI value. For a given thermal time period from emergence to anthesis, the total biomass accumulated depends on the rate of increase of biomass per unit of thermal time. The biomass added is proportional to solar radiation, S, and so, as for GFP biomass, anthesis biomass depends on the weather through the values of the photothermal quotient. The values during the initial part of the period when LAI is small are the least important.

As for the grain fill period, a water deficit prior to anthesis can reduce the biomass through a light use efficiency factor and can reduce the LAI. However, the deficit has to be very large for a direct reduction of biomass to occur, which is very unlikely in the UK. As already discussed, reductions in the LAI have little effect on the biomass added unless the LAI becomes very small which again is unlikely in the UK. Any effect is further reduced by the fact that at most one quarter of the anthesis biomass is included in yield. In Sirius, a drought deficit prior to anthesis has no effect on the timing of phenological events. Therefore, no effect of a water deficit prior to anthesis has been included in the yield equation.

The effect of the water deficit factor can be seen by denoting the potential grain fill biomass by G, where

$$G = \frac{4.8SrT_{\mathrm{GFP}}}{T} f(x,L). \qquad (6)$$

Therefore, the potential yield is $0.25A + G$ compared to the actual yield of $(0.25A + bG)/k$. The maximum value of k in Sirius is 1.5 and so it can reduce yield by up to one third. The light use drought factor, b, takes values between 0 and 1. Interestingly, this linear model of grain yield reduction in drought is conceptually similar to the Penman (1971) drought response model, tested successfully for wheat and other crops by Jamieson et al. (1995b).

The next sub-section explains the water balance and the calculation of the water deficit factors in Sirius.

3.2. Water balance and deficit

Flows of water within the soil are simulated in Sirius by dividing the soil into 5 cm layers. Water from precipitation is added to the top layers of the soil and percolates down if the layers are full. Water is removed from the soil by the plant for transpiration and, in addition, water is evaporated from the top layers although the amount evaporated is small when the leaf area is high. Water can also be lost if it percolates out of the bottom layers. The main changes in the amount of water in the soil are therefore the addition of precipitation and the removal of the amount transpired by the plant. This latter amount is given by,

$$\text{amount transpired} = \text{PTAY} \times W_{\text{SF}} \times (1 - e^{-xl}) \text{ mm day}^{-1} \quad (7)$$

where W_{SF} is a water deficit stress factor and PTAY is the Priestley–Taylor function (Priestley and Taylor, 1972), given by

$$\text{PTAY} = 1.5\frac{H}{H + 0.66}(0.241S - 0.1) \text{ mm day}^{-1} \quad (8)$$

where H is the slope of the saturated vapour pressure temperature curve (hPa °C^{-1}). Based on typical values of H in the summer months at Rothamsted,

$$\text{PTAY} \approx 0.19S \text{ mm day}^{-1}. \quad (9)$$

During most of the growth period the leaf area is not small and so $1 - e^{-xl} \approx 1$. Therefore, during this period,

$$\text{amount transpired} \approx 0.19 \times S \times W_{\text{SF}} \text{ mm day}^{-1}. \quad (10)$$

During the winter months the only effect is the addition of precipitation to the soil. In the UK climate this often leaves the soil fully saturated. A water deficit will therefore only accumulate during the main growth period once the amount transpired starts to exceed the average precipitation level. The daily amount of water removed from the soil will then be given by

$$\text{water removed} \approx 0.19 \times S \times W_{\text{SF}} - P \text{ mm day}^{-1} \quad (11)$$

where P is the precipitation in mm that day. The water deficit, D, experienced by the plant therefore mainly depends on the values of solar radiation and precipitation in the growth period.

If the useable water in the root zone of the plant is at least half the available water capacity, the water stress factor, W_{SF}, equals one (i.e. no effect). Otherwise the water stress factor is twice the useable water divided by the available water capacity, AWC. Since the useable water is the AWC − water deficit, the water stress factor is

$$W_{\text{SF}} = \min\left(\frac{2(\text{AWC} - D)}{\text{AWC}}, 1\right) \quad (12)$$

Therefore, the water deficit on day t, D_t, can be estimated by the recurrence relation

$$D_t = \max\left(D_{t-1} + 0.19 \times S_t \times \min\left(\frac{2(\text{AWC} - D_{t-1})}{\text{AWC}}, 1\right) - P_t, 0\right) \quad (13)$$

where S_t and P_t are the solar radiation and precipitation on day t. This relationship was found to model the water deficit well whether using actual daily values for the weather variables or using the average values for the month.

A water deficit can affect the biomass or LAI in Sirius through water deficit factors. In addition to the grain fill factors b and k explained above, there are also LAI and biomass factors prior to anthesis. These factors are all linear functions of W_{SF} within certain ranges of W_{SF}. For example $k = 1$ for $W_{SF} \geq 0.7$, $k = 1.5$ for $W_{SF} \leq 0.4$ and $k = 2^1/_6 - 5W_{SF}/3$ for $0.4 \leq W_{SF} \leq 0.7$. In particular, for a given water deficit, the Sirius water deficit factors can be calculated easily. Since W_{SF} is also linearly related to the water deficit, D, the factors are also linearly related to the water deficit. The light use factor, b, is given by $b = \min(2W_{SF}, 1)$ and so only has an effect when $W_{SF} < 0.5$, i.e. when the useable water is less than 1/4 AWC.

3.3. Explanation of the sensitivity results

The sensitivity results can be explained using the analysis of the model already set out. A full explanation is given in Brooks and Semenov (1998). For unlimited nitrogen, the analysis indicates that yield should be approximately given by Eq. (5) with the drought factors depending on the water balance as given above. For example, in the sensitivity analysis, yield was exactly proportional to the light use efficiency, r. This is because both the grain fill period and anthesis biomass are proportional to r, and r has no effect on the water balance. In the sensitivity results, yield is not very sensitive to the extinction coefficient, x, although the relationship does approximately follow a 1 − negative exponential relationship and these are both consistent with Eq. (5).

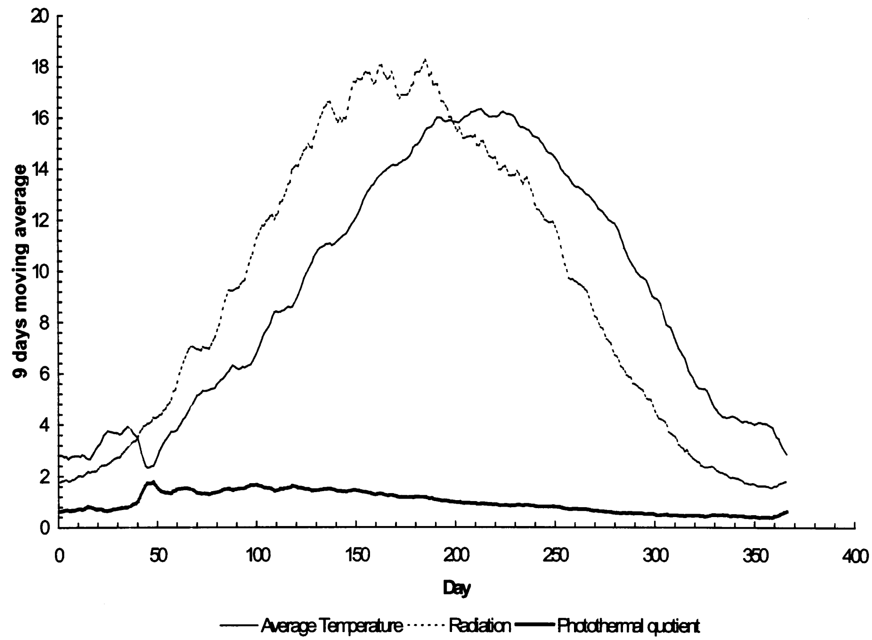

Fig. 3. Nine days moving average of temperature, radiation and photothermal quotient at Rothamsted for average 1961–1990 weather data.

Several parameters in the model affect the anthesis date. Changing the anthesis date alters the anthesis biomass by changing the timing and length of the growing period up to anthesis and, just as important, alters the timing of the grain fill period. A change in timing will also alter the water deficit experienced during the grain fill period. A change in anthesis date by a few days will alter the yield in an irregular manner depending mainly on differences in weather on the days that are added or removed from the grain fill period. A large change in anthesis date is likely to cause an overall trend in yield in addition to the irregular changes.

Anthesis date is mainly determined in Sirius by the number of leaves and the phyllochron, which determine the length of the thermal time period from emergence to anthesis. Extending this period will increase the anthesis biomass. The resulting change in the timing of the grain fill period also changes the grain fill biomass due to different values for the water deficit and the photothermal quotient, S/T, during the grain fill period. For the dry year of 1976, a delay in anthesis date tends to reduce the yield because the water deficit builds up over a longer period and the greater yield loss due to the increased water deficit has more effect on yield than the increase in anthesis biomass. Yield does increase again for a large delay because the grain fill period is moved into the middle of July when there were a couple of weeks with a significant amount of precipitation. A delay in the anthesis date for 1989 from the base value also tends to decrease yield for the same reason (Fig. 1). Using the base parameter values, the anthesis dates in 1976 and 1989 were 15th and 12th June, respectively. In both years, the photothermal quotient tends to reach a maximum towards the end of April and decline thereafter and so a delay in the anthesis date also tends to reduce the potential grain fill period biomass.

The analysis of Sirius also explains the sensitivity results for the weather parameters (Brooks and Semenov, 1998). Fig. 3 shows the average weather values for Rothamsted for 1961–1990 together with the photothermal quotient, S/T. The temperature sensitivity factor has two main effects. An increase in temperature will reduce S/T throughout the year but it will also make the phenological dates earlier (in particular the anthesis date and the grain fill period), since the phenological periods are specified in thermal time. The reduction in S/T reduces the potential anthesis biomass. However, an earlier grain fill period means that S/T is closer to its maximum value during the grain fill period (Fig. 3) and so there is much less change in the value of S/T during the grain fill period and, hence, in the potential grain fill period biomass. An earlier grain fill period also reduces the water deficit during the grain fill since the deficit builds up over a shorter period of time. The interaction of these factors produces the complex response of yield, together with the limit of 1 year for the simulated period explained in Section 2.1. In particular, yield is roughly constant within the range ± 2°C.

Changes in radiation and precipitation, on the other hand, have a negligible effect on key development dates. An increase in radiation increases the rate of accumulation of biomass throughout the year and increases the water deficit through greater transpiration by the plant. For low values of solar radiation, the water deficit is small enough that the potential yield is obtained. Both potential anthesis biomass and potential grain fill biomass are proportional to solar radiation and so the yield is also proportional. Apart from the feedback effect of the stress factor, the water deficit is also linearly related to radiation (Eq. (13)), and the deficit factors b and k are linearly related to the deficit. As a water deficit increases, at first the yield is reduced by the effect of k and then, for a more severe deficit, by the effect of b. Initially, increases in a deficit both reduce k and increase the proportion of the grain fill period it affects. This results in the curve in the high solar radiation values in Fig. 1. Precipitation affects only the water deficit and its values are similarly curved. The results for 1976 and 1989 show that, for low water values, k ceases to have any further effect (if $W_{SF} < 0.4$) and so the curve would tend to flatten out. Below this yield is approximately linearly related to precipitation through the effect of b.

4. Meta-model

4.1. Conceptual model

Based on the analysis described above, a simplified meta-model was developed assuming unlimited nitrogen. The meta-model is based on the yield Eq. (5) and the simplified water balance given by Eq. (13). Eq. (5) also requires the anthesis date and the anthesis biomass.

The meta-model consists of seven steps, but these can be implemented at several different levels of detail. The steps together with the alternative methods that could be used for each step are as follows:

Step 1. Calculate the final leaf number. The full Sirius mechanisms of vernalisation and the leaf number calculation, using thermal time and daylength could be used for this step. However, for similar conditions such as different years at the same site, it appears that final leaf number is approximately linearly related to mean temperature over the winter period and so a regression equation fitted to Sirius output could be used.

Step 2. Calculate the anthesis date. The total thermal time from sowing to anthesis is fixed once the leaf number is known. Sirius assumes 0.75 phyllochrons for each of the first two leaves, one phyllochron for each of the next six leaves and 1.3 phyllochrons for each additional leaf. The anthesis date can be calculated using temperature data as the date at which the thermal time to anthesis is reached.

Step 3. Calculate the potential anthesis biomass A (which equals actual anthesis biomass since anthesis biomass is affected very little by water stress). This depends mainly on the photothermal quotient, S/T, in the main growing period up to anthesis (typically, in the UK, about 3 months). The analysis indicates that an approximately linear relationship should exist between yield and the average value of S/T for the period before the anthesis date for UK conditions. This should enable a regression equation to be fitted to Sirius output.

Step 4. Calculate the potential grain filling period biomass, G. This is given by Eq. (6) using the average value of S/T for the grain fill period. In most circumstances, a value of about eight will be suitable for the leaf area at the start of the grain fill, L. The grain fill period can be identified using temperature data to accumulate thermal time, and using the input thermal time values from anthesis to the start of the grain fill and from the start to the end of the grain fill. If preferred, the last few days of the grain fill period can be ignored in calculating the average since these are the least important for accumulating biomass.

Step 5. Calculate the potential yield as $0.25A + G$.

Step 6. Calculate the water deficit during the grain fill period by accumulating the deficit using Eq. (13) and values of solar radiation and precipitation. Alternatively, it may be possible to fit a regression equation to Sirius output relating the water deficit to the accumulated value of $0.19S - P$ over the period from when this starts to take positive values until the middle of the grain fill period.

Step 7. Calculate the average of the water stress factors b and k during the grain fill period. These are simple linear functions of the water deficit. The simplest way to do this is to use the water deficit calculated for the middle of the grain fill period. A more precise method is to calculate daily values for the factors during the grain fill using the water deficit from step 6 and then take an average. If the water deficit is very high, the grain fill period will be shortened to a length of T_{GFP}/k, and so a revised grain fill period can be calculated using an average k value. Then the average of the drought factors can be calculated just over the revised period. If necessary, a revised value of G can also be calculated using this revised period (step 4).

Step 8. Calculate the final yield as $\frac{1}{k}(0.25A + bG)$.

Where weather data is used, either daily data or disaggregated monthly data (where the average value for the month is assigned to each day) could be used. The fact that yield can be related to cumulative values indicates that using monthly weather data should give similar results to using daily weather data.

Whichever way the meta-model is implemented, the main differences from Sirius are the absence of three of the principal Sirius model components, namely the model of leaf area index, the soil water balance model, and the evapotranspiration calculations. In addition, the growth of the plant is not simulated on a daily basis but, rather, biomass is related to the accumulated weather variables. Indeed, the only daily calculations are the adding up of the weather variables. An important characteristic of the meta-model is that it contains very little interaction between the components. Once the anthesis date and leaf number are known, the anthesis biomass, the GFP potential biomass and the water stress yield loss are all calculated separately. The meta-model also calculates both potential and water limited yield in one run.

The meta-model does not require the leaf area to be simulated but, instead, just uses average values of the photothermal quotient, S/T. The relationship between biomass and S/T exists because the pattern of change in leaf area will tend to be similar across different scenarios and because, in the UK, the biomass added is not sensitive to changes in leaf area.

The important variable for water stress is the water deficit during grain fill. This can be modelled well using Eq. (13) rather than with a detailed model of the soil in layers and the detailed evapotranspiration calculations.

4.2. Meta-model implementation and results

A meta-model was coded in Borland C++ Builder for Windows $9\times$/NT/2000 following the conceptual model[1]. Where there was a choice of methods to use, the model was constructed so as to be generally applicable for a wide range of circumstances.

The calculation of final leaf number uses the full Sirius daylength response mechanism so that it can be used for different varieties, latitudes and sowing dates. The ratio of total radiation for the 90 days prior to anthesis divided by total thermal time for that 90 days is used to calculate the

[1] Meta-model is available from www.lars.bbsrc.ac.uk/model/metamodel.html

anthesis biomass using a regression relationship fitted to the Sirius Rothamsted output data for Rothamsted for 1961–1990 with precipitation multiplied by 0.5 (to make all yields water limited). The regression relationship had a coefficient of determination R^2 value of 0.83.

The same ratio is calculated for the grain fill period (with the period being determined by accumulating thermal time after anthesis) and the grain fill period biomass calculated using the Eq. (2). The potential yield is then given by the grain fill period biomass plus one quarter of the anthesis biomass.

The meta-model was run for Rothamsted 1961–1990 with 50% precipitation and for Edinburgh with a poor soil and the results compared with those from Sirius. Daily weather data was used in both cases. The scenarios were chosen to give a wide range of yields mainly due to variations in water stress. Fig. 4 shows meta-model yield versus Sirius yield for (a) potential production and (b) water limited production at Rothamsted. Fig. 5 shows the meta-model yield versus the Sirius yield for water limited production at Edinburgh. In both cases the meta-model performed well giving a root mean square error (RMSE) of 682 and 831 kg/ha^{-1} respectively (compared to the standard deviations in Sirius yields of 1267 and 2176 kg/ha^{-1}) and correlation coefficients of 0.92 and 0.95. The leaf number tended to be too low for Rothamsted by about 0.4 leaves due to Sirius using soil temperature and correcting this by adding 0.4 leaves reduced the RMSE value for Rothamsted to 457.

4.3. Implications of the meta-model results

The good match of the meta-model yield values with those of Sirius indicates that the meta-model does contain the important aspects of Sirius and, in particular, that there are no other Sirius mechanisms substantially affecting the yield. Because the meta-model is based on analysis of the Sirius model, rather than just on its output, it should be able to match the Sirius output well for most scenarios in Britain (e.g., different sowing dates or cultivars) and probably for many other climates without serious modifications. The approximation of the Priestley–Taylor function PTAY in Eq. (9) will probably need an adjustment for a dry and hot climate. An effect of pre-anthesis drought may also need to be included in such circumstances.

The fact that the meta-model can reproduce the Sirius yield well does not necessarily mean that it should be used instead of Sirius. Sirius is a generic, mechanistic model with a detailed simulated phenology and, certainly where detailed in-

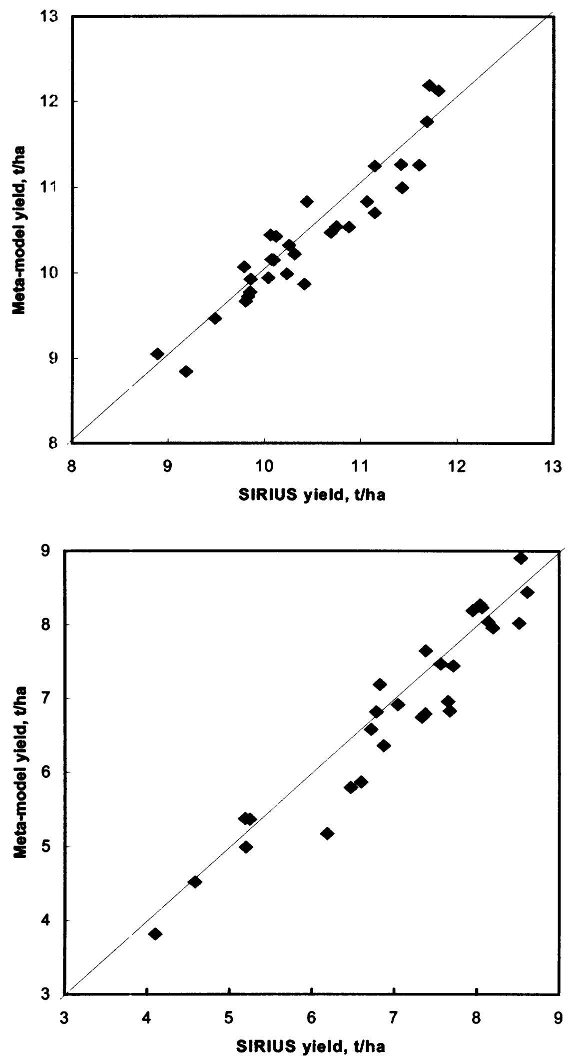

Fig. 4. Yield simulated by the meta-model versus yield simulated by Sirius at Rothamsted for 1960–1990 for potential production (a) and water-limited production (b).

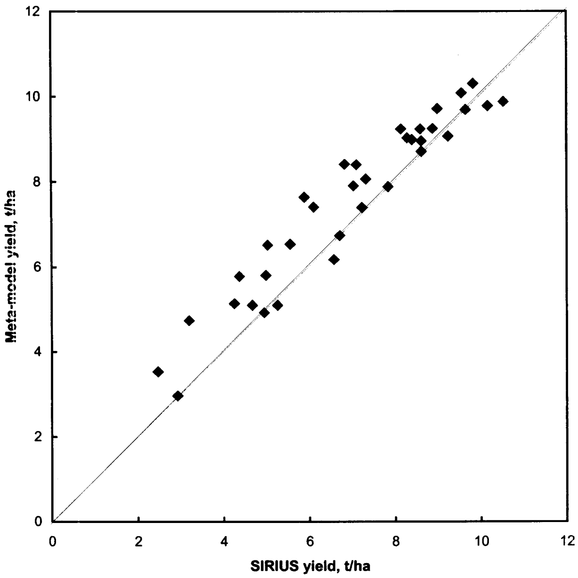

Fig. 5. Yield simulated by the meta-model versus yield simulated by Sirius at Edinburgh for 1960–1990 and poor soil (0.5 m) for water-limited production.

put data is available, it is likely to give more accurate results than the meta-model. Sirius provides detailed output data including daily values of a variety of variables. Rather, the benefits of the meta-model should be to greatly help in the analysis and understanding of Sirius results since it identifies the main factors affecting yield. In particular, it highlights the interaction of the anthesis date and the pattern of the photothermal quotient as well as the relationship between a water deficit and the water stress yield loss. Although Sirius only requires a short run time, the run time of the meta-model is shorter and so it could be used in situations where a large number of runs are required, such as comprehensive sensitivity analysis, detailed regional analysis of a large number of sites over many years, or searches for optimal performance such as the best sowing date.

The parameters and data used by the meta-model are the ones that need to be determined accurately for the meta-model or Sirius to perform well. As already discussed for the sensitivity results, those factors that significantly alter the anthesis date are important (particularly the phyllochron). Solar radiation affects not only potential yield but also the water deficit. However, this variable is often not directly measured but must be estimated from some other variable such as sunshine hours, for example. This makes its value uncertain and it is therefore important that sensitivity analysis is carried out on this variable.

The meta-model uses average or accumulated values of the weather variables and is able to perform well just with monthly weather data. It was run at Rothamsted with 50% precipitation and at Edinburgh for the soil with low AWC (80 mm), using daily weather data and 30-day moving average weather data. RMSE for the anthesis day and water-limited yield are 1 day and 147 kg/ha^{-1}, and 1.7 days and 470 kg/ha^{-1} for Rothamsted and Edinburgh, respectively. This indicates that replacing daily data with disaggregated monthly data in Sirius is unlikely to change the output significantly.

The meta-model identifies a further way of comparing Sirius with experimental data since the derived relationships should be present in the experimental data if Sirius is performing well. Parts of the model could also form the basis for further model development. Perhaps the photothermal quotient could have significance in terms of the physical processes of the plant but a more likely path would be to use the relationship of yield loss to $0.19S - P$ as a basis for simpler modelling of water stress.

5. Summary and conclusions

The sensitivity analysis and the further analysis of Sirius identified the parameters and variables that are the most important for model calibration and performance. For example, the total available water capacity is the most important soil parameter. This allows different soil types to be grouped together for regional impact assessments (Brooks and Semenov, 2000). The interesting responses of the simulated grain yield to mean temperature changes at Rothamsted have potential implications for climate change studies. When the mean temperature increases, the photothermal quotient decreases resulting in a decrease in total biomass and grain yield (Wolf et al., 1996), except where crop growth is limited by water stress. Then the shortening of the growth period reduces the exposure to water stress. The compensating effect of these factors means that, at Rothamsted, simulated grain yield shows little variation between temperature changes -2°C and 2°C.

The sensitivity analysis also found pseudorandom variations in simulated grain yield (up to 500 kg ha^{-1}) as a result of slight changes (up to 5%) in some model parameters and input variables. These cannot be determined precisely, which sets a limit to the accuracy of the yield prediction. This needs to be accounted for when comparing simulated and observed yield.

The development of a relatively simple meta-model greatly increases the understanding of the consequences of the relationships implicit within Sirius and shows, in particular, that the response to climate can be explained using a few simple relationships. Aspects of Sirius left out of the meta-model are the calculation of the leaf area index, the soil water balance model and the evapotranspiration calculations. The meta-model essentially uses cumulative values of weather variables, indicating that disaggregated monthly values should produce similar results in Sirius to those using daily weather data. The faster run time of the meta-model and the ability to analyse its results more easily may make it a valuable tool for regional impact assessments when many runs are required. Its level of detail may also be more appropriate in such circumstances since detailed high-resolution input data are usually not available.

The meta-model has mimicked well potential and water–limited yields simulated by Sirius at two locations, Rothamsted and Edinburgh. Since the meta-model was developed from the analysis of Sirius, rather then from statistical fitting of output data, it should perform well for other locations in Britain and different management scenarios. It is likely that the meta-model will match Sirius yield well for diverse environments and climates without serious modifications, but this hypothesis needs further testing.

Acknowledgements

Weather datasets were supplied by the UK Meteorological Office through the Climate Impacts LINK project and the ARCMET database. The work of R.J.B. was supported by the European Commission's Environment Programme under Contract Number ENV4-CT95-0154. IACR Long Ashton receives grant-aided support from the Biotechnology and Biological Sciences Research Council of the United Kingdom.

References

Brooking, I.R., 1996. The temperature response of vernalization in wheat-a developmental analysis. Ann. Bot. 78, 507–512.

Brooking, I.R., Jamieson, P.D., Porter, J.R., 1995. The influence of daylength on the final leaf number in spring wheat. Field Crops Res. 41, 155–165.

Brooks, R.J. and Semenov, M.A. 1998. Sensitivity analysis of the Sirius wheat model, Technical Report, IACR Long Ashton Research Station.

Brooks, R.J., Semenov, M.A., 2000. Modelling climate change impacts on wheat in central England. In: Climate Change, Climatic Variability and Agriculture in Europe. An Integrated Assessment. Downing, T.E., Harrison, P.A., Butterfield, R.E., Lonsdale, K.G. (Eds.), Research Report No. 21, Environmental Change Unit, University of Oxford, Oxford, pp. 157–178.

Brooks, R.J., Tobias, A.M., 1996. Choosing the best model: Level of detail, complexity and model performance. Math. Comp. Modelling 24 (4), 1–14.

Brooks, R.J., Tobias, A.M., 1999. Methods and benefits of simplification in simulation. In: Al-Dabass, D., Cheng, R.C.H. (Eds.), UKSim 99 Fourth National Conference of the U.K. Simulation Society, 7–9 April 1999. UK Simulation Society, St Catharines College, Cambridge, pp. 88–92.

Ferrar, W.L., 1980. A Textbook of Convergence. Oxford University Press, Oxford.

Goudriaan, J., 1996. Predicting crop yields under climate change. In: Walker, B.H., Steffen, W. (Eds.), Global Change and Terrestrial Ecosystems. Cambridge University Press, Cambridge, pp. 260–274.

Grant, R.F., 1998. Mathematical modelling of root growth under different nitrogen and irrigation treatments: the ecosys approach. Ecol. Modelling 107, 237–264.

Jamieson, P.D., Brooking, I.R., Porter, J.R., Wilson, D.R., 1995a. Prediction of leaf appearance in wheat: a question of temperature. Field Crops Res. 41, 35–44.

Jamieson, P.D., Martin, R.J., Francis, G.S., 1995b. Drought influences on grain yield of barley, wheat and maize. N.Z. J. Crop Hort. Sci. 23, 55–66.

Jamieson, P.D., Brooking, I.R., Semenov, M.A., Porter, J.R., 1998a. Making sense of wheat development: a critique of methodology. Field Crops Res. 55, 117–127.

Jamieson, P.D., Porter, J.R., Goudriaan, J., Ritchie, J.T., Keulen, H., van Stol, W., 1998b. A comparison of the models AFRCWHEAT2, CERES-Wheat, Sirius, SUCROS2 and SWHEAT with measurements from wheat grown under drought. Field Crops Res. 55, 23–44.

Jamieson, P.D., Semenov, M.A., Brooking, I.R., Francis, G.S., 1998c. Sirius: a mechanistic model of wheat response to environmental variation. Eur. J. Agron. 8, 161–179.

Jamieson, P.D., Porter, J.R., Semenov, M.A., Brooks, R.J., Ewert, F., Ritchie, J.T., 1999. Comments on "Testing winter wheat simulation models' predictions against observed UK grain yields" by S. Landau et al (1998). Agric. For. Meteorol. 96, 157–161.

Jamieson, P.D.; Berntsen, J.; Ewert, F.; Kimball, B.A.; Olesen, J.E.; Pinter, P.J.; Jr, Porter, J.R.; Semenov, M.A.; 2000. Modelling CO_2 effects on wheat with varying nitrogen supplies, Agro-Ecosystems and Environment (in press)

Jamieson, P.D., Semenov, M.A.; 2000. Modelling nitrogen uptake and redistribution in wheat, Field Crops Res. (in press)

Penman, H.L., 1971. Irrigation at Woburn VII. Report Rothamsted Experimental Station for 1970 2, 147–170.

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., Taylor, R.J., 1972. On the assessment of surface heat flux and evaporation using large scale parameters. Monthly Weather Review 100, 81–92.

Ritchie, J.T., Otter, S., 1985. Description and performance of CERES-Wheat: A user-oriented wheat yield model. In: Willis, W.O. (Ed.), ARS Wheat Yield Project, Department of Agriculture, Agricultural Research Service, ARS 38, pp. 159–175.

Robertson, M.J., Brooking, I.R., Ritchie, J.T., 1996. The temperature response of vernalization in wheat: modelling the effect on the final number of mainstem leaves. Ann. Bot. 78, 371–381.

Weir, A.H., Bragg, P.L., Porter, J.R., Rayner, J.H., 1984. A winter wheat crop simulation model without water or nutrient limitations. J. Agric. Sci. Camb. 102, 371–382.

Wolf, J., Evans, L.G., Semenov, M.A., Eckersten, H., Iglesias, A., 1996. Comparison of wheat simulation models under climate change. I. Model calibration and sensitivity analyses. Climate Res. 7 (3), 253–270.