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Development and evaluation of a CERES-type model for winter oilseed rape

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Abstract

Because of its large N fertiliser requirements and long growth cycle, winter oilseed rape (*Brassica napus* L.) is considered to expose its environment to substantial risks of N losses. Soil–crop models provide unique tools to analyse such impacts, with an accuracy that primarily relies on the simulation of crop C and N budgets. Here, we describe a model simulating the growth and development of oilseed rape that was adapted from CERES-N Maize and a previously existing rape model. In addition to its soil components, the model, called CERES-Rape, has modules for crop phenology, net photosynthesis, leaf area development and grain filling, as influenced by crop N status. A new feature compared to previous rape models is the ability to predict the crop's C and N budgets throughout its growth cycle, including losses from leaves by senescence. It also contains a mechanistic description of N translocation from vegetative parts to pods and grains after the onset of flowering. The model has been calibrated on a one-year experiment with three fertiliser N levels conducted in France, and subsequently tested on a similar experiment from Denmark for which no parameters were adjusted. In the vegetative phase, the time course of biomass and N accumulations in the various plant compartments was well simulated, with predicted values falling within one or two standard deviations from the mean in the measurements, except for the low-N treatments for which the high rates of leaf senescence could not be mimicked. After the onset of flowering, some bias appeared in the simulation of crop N uptake which impaired the predictions of final grain N yields. Simulated grain dry matter yields matched observations within ±15% for the calibration data set, but were over-estimated by a factor of 2 for the other data set. Despite the above shortcomings, the simulation of fertiliser effects on the dynamics of crop N uptake and dry matter was judged sufficiently satisfactory to allow an investigation of N losses from rapeseed–cropped soils with the CERES-Rape model. © 1998 Elsevier Science B.V.

Keywords: Oilseed rape; Soil–crop model; Dry matter; N partitioning

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1. Introduction

In temperate regions where its cycle lasts nearly one year, the growth of winter oilseed rape (*Brassica napus* L.) is subjected to climatic hazards that

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may exert an important influence on yield, notwithstanding damage by pests. In addition, oilseed rape has high fertiliser requirements, as compared to other winter crops such as winter wheat (*Triticum aestivum* L.), which enhance the risk of N loss from the soil–crop system to the environment, whether by nitrate leaching, ammonia volatilisation or denitrification. In the context of the reformed European Common Agricultural Policy of 1992, which promoted in Europe the cultivation of rape as a bio-fuel crop, it seemed relevant to study the effects of soil and climate variability on both the final yield and the environmental impacts of this crop. As a consequence of their dynamic nature, these effects may only be studied by means of a model simulating the relevant crop processes as related to soil and weather conditions.

A few rapeseed models exist in the literature (Habekotté, 1996; Backx et al., 1984; Petersen et al., 1995), but they are incomplete as regards the above objectives. The first two models do not simulate the autumn and winter phases, whereas the third one (DAISY) accounts neither for the loss of leaves due to senescence, nor for the partitioning of dry matter between pods and vegetative parts after flowering.

On the other hand, the CERES models constitute a coherent, widely used framework for developing and testing soil–crop models embedded in a simulation software shell made available through an international network (IBSNAT, 1990). Here we adapted the CERES-N Maize model (Jones and Kiniry, 1986) to rapeseed by modifying the routines for net canopy photosynthesis, root growth and distribution within the soil profile, N uptake and partitioning of C and N assimilates between crop compartments (roots, leaves, stems, pods, and grain). The resulting model, called CERES-Rape, is described and tested against experimental data in this paper. Its submodel for leaf and pod area indices has, however, already been calibrated and tested in a companion paper (Gabrielle et al., 1998).

The modified routines are based on standard concepts underlying other CERES models (e.g., Villalobos et al., 1996), with attempt to maintain a balance between mechanistic and empirical approaches. A constant radiation-use efficiency (RUE) is used for net canopy photosynthesis in the vegetative phase (Gosse et al., 1986), and is altered in the reproductive phase when pods photosynthesize. The partitioning of dry matter (DM) between stems and leaves depends on development with thermal time, and source–sink relationships are introduced for the translocation of N from vegetative parts to the growing pods after flowering. Effects of N stresses due to low soil availability are taken into account as regards net photosynthesis and leaf or pod elongation.

All the routines mentioned have been calibrated on a data set from a one-year experiment in Northeastern France involving cv. Goéland and three fertiliser N treatments. Using the same parameter set, the model was further evaluated on a 1-yr experiment from Denmark featuring another cultivar (Ceres) and similar N treatments.

2. Materials and methods

2.1. Experimental data

The basic features of the two data sets used in the model tests are summarised in Table 1. The Châlons set was used for the calibration of the model's equations for leaf and pod area (Gabrielle et al., 1998), root growth, N uptake, and assimilate partitioning, whereas the Jyndevad data served for critically evaluating the model predictions of crop DM and N content obtained with the parameter set derived in Châlons. Experimental details are given in Leviel et al. (1998) for Châlons and in Petersen et al. (1995) and Andersen et al. (1996) for Jyndevad.

In all experiments, crops were fully irrigated and weed- and pest-protected, so that associated stresses were negligible. Daily climatic data (global radiation, minimum and maximum air temperatures, precipitation and potential evapotranspiration) were measured at a local weather station located within 1 km from the experimental fields.

In Châlons, three replicate 30 m × 30 m blocks arranged in a split-plot design with N treatment as main plot and sampling date as subplot were drilled in 0.29-m rows in late summer. At that time, soil inorganic nitrogen storage down to 120 cm was ca. 100 kg N ha^{-1}. Every two weeks (four weeks in winter), in each block, three subsamples of 0.45-m^2 were collected, yielding a surface of 1.3-m^2 per replicate. In Jyndevad, three autumn-sown (0.12-m rows) N treatments were established in 15.2-m^2 plots

Table 1
Selected characteristics of the two experiments used for the calibration and evaluation of the CERES-Rape model

Name and location	Soil	N treatments		Cultivar	Sowing and harvest dates
		Name	Fertiliser N doses (kg N ha^{-1})		
Châlons; 4.1°N, 6.7°E	Grey rendzina on chalk (Typic Udorthent; depth = 40 cm)	N0	0	Goéland	8/9/1994
		N1	135		11/7/1995
		N2	272		
Jyndevad; 54.3°N, 12.3°E	Coarse sand (Orthic Haplohumod; depth = 60 cm)	N0	48	Ceres	20/8/1991
		N1	155		15/7/1992
		N2	261		

arranged in a randomised block design, with four replicates. Every 10 days in spring, 0.5-m^2 samples were taken in each plot.

In all experiments, the collected plants were separated into leaves (with senescent and green fractions), stems, roots (although only the tap root was sampled), and pods. The subsamples were then weighed after drying for 48 h at 80°C, and analysed for carbon and nitrogen content using the Dumas method. To quantify the biomass and N losses from the crop, dead leaves were collected weekly on plastic mesh placed on the soil surface below the canopy.

For the in situ analysis of root growth, 4-m wide and 2.5-m deep trenches were dug once a month perpendicular to the rows, in which a vertical face was prepared using knives, brushes and small bellows to make the roots visible. The presence or absence of roots was then mapped through a 20-mm grid mesh fixed on the face. This yielded the crops' maximum rooting depth for each treatment, but not directly the root length density (RLD, cm roots cm^{-3} soil) which was also of interest in the N uptake part of the model. However, we assumed the distribution of this variable to parallel that of the frequency of occupation we had measured over the profile, with an occupation of 100% corresponding to a maximum RLD value of 5 cm roots cm^{-3} soil, as measured by Petersen et al. (1995) on winter rape.

2.2. Model description

From daily weather data (rain, air temperature, and solar radiation), the CERES-Rape model computes the variables related to crop growth and development and to the soil water and N balances. Its soil components have been tested and adapted for the prediction of soil water flow, nitrate leaching and N mineralisation (Gabrielle et al., 1995; Gabrielle and Kengni, 1996) from the original CERES-N Maize routines, and will not be described here.

The following paragraphs detail the CERES-Rape modules for crop phenology, photosynthesis and leaf and root development, and their interactions with N availability in soil. For these functions, a potential rate linked to air temperature and solar radiation is first calculated and then multiplied by stress factors between zero and unity accounting for possible limitations of N. Lastly, some of the equations and coefficients presented were derived from the Châlons data set.

2.2.1. Crop phenology

Crop emergence occurs after 120 growing degree-days with a base temperature of 0°C (GDD$_0$) from sowing, as modulated by soil moisture content (Leterme, 1988). The phenology module of CERES-Rape then considers one vegetative stage, from crop emergence to the onset of flowering, and subsequently three reproductive stages:

(i) from the onset of flowering to mid-flowering
(ii) from mid-flowering to the end of flowering
(iii) from the end of flowering to crop maturation.

The four boundary dates associated with the above stages depend on sowing date, on GDD from emergence with a base temperature of 0, and on mean day length until (i) starts. This part of CERES-Rape is discussed in detail by Husson and Leterme (1998), who found prediction errors of 7 to 9 days for the flowering dates in a cross-validation study involving eight cultivars and over 10 locations in France. Since we focused on the analysis of crop growth processes, we did not deal with the validation of this phenology module, given in addition the limited climatic range of our experimental data. The boundary dates of the reproductive stages were then set to their observed values.

Leaf expansion stops after (ii), when pods become a sink for N and induce translocation of N from leaves and stems. This does not stop photosynthesis in the vegetative parts, but reduces its efficiency and accelerates senescence for lack of N (Sinclair and de Wit, 1975). In addition to the depressive effect of the decreasing leaf N content, the radiation available to the leaves is reduced because of shading by the overlying pods (reflection by flowers is not considered yet). After (i), the N taken up by shoots is partitioned to pods. Pods start elongating after (ii), and progressively increase photosynthesis.

2.2.2. Leaf and pod area

The modelling of the crop leaf and pod area indices (LAI and PAI, respectively) has been described and tested in a companion paper (Gabrielle et al., 1998), and will not be discussed further. In short, the daily increase in LAI or PAI is a function of degree-days with a base temperature of 4.5°C. The potential LAI growth rate is modulated by leaf N content if N is limiting for leaf expansion. Senescence from N deficiencies or mutual shading within the canopy is also included.

2.2.3. Root growth

In the Châlons experiment, the root tip extended downwards with a constant rate in thermal time (base 0°C) of approximately 0.08 cm $°C^{-1}$, whatever the N treatment (Fig. 1). However, this rate appeared to be reduced by about 40% below the topsoil (0–40 cm layer) in zones of compact chalk that comprised most of the subsoil. In these zones, the potential value of 0.08 cm $°C^{-1}$ still held for the few monitored plants growing over veins where chalk provided mechanical constraint to root elongation (Fig. 1). In the model, the potential rate was diminished by the empirical coefficient of 40% below the topsoil. The maximum rooting depth observed was 120 cm, so root penetration was not allowed to exceed that depth.

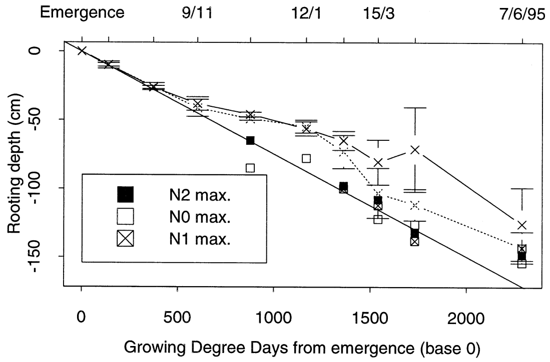

Fig. 1. Dynamics of rooting depth observed in Châlons for the three N treatments. The cross symbols associated with lines represent the average (±1 s.d.) rooting depths for N0 (· · ·) and N2 (———), whereas the square symbols represent the maximum rooting depths observed in veins of altered chalk, where mechanical stresses were negligible. The straight line illustrates the regression of those points against thermal time ($R^2 = 0.98$, $df = 15$), the slope of which is the root maximum penetration rate (see text).

The daily increase in root length density (RLD, cm roots cm^{-3} soil) was considered proportional to the rate of root vertical elongation. In each soil layer L that had been colonised, (with L varying from 1 at the surface to N at the bottom) the variation of RLD was thus:

$$\Delta \mathrm{RLD}(L) = \mathrm{RLD}_{\max} v_{\mathrm{RLD}}(L) \Delta Z_r \qquad (1)$$

where Z_r is the rooting depth (cm), $\mathrm{RLD}_{\max}$ is the maximum RLD (set at 5 cm roots cm^{-3} soil, after Petersen et al. (1995)), and v_{RLD} is the relative lateral extension rate (cm^{-1}).

Such approximation allowed us to derive values of v_{RLD} for each soil layer, based on the Châlons data for all treatments. Due to the same mechanical stresses as for the root vertical extension, v_{RLD} was diminished in the chalky layers (varying from 1.33 in the topsoil layer to 0.25 underneath).

2.2.4. Photosynthesis

In the vegetative phase, the daily increase in crop dry matter (ΔDM, t ha^{-1} day^{-1}) resulting from net canopy photosynthesis by the leaves is calculated from incoming solar photosynthetically active radiation (PAR, MJ m^{-2} day^{-1}) as:

$$\Delta DM = RUE \times PAR(1 - a)(1 - \exp[-k LAI]) \quad (2)$$

where RUE is the efficiency of the conversion of intercepted PAR (PAR_i) into dry matter (g DM MJ^{-1} m^{-2}). The last two terms in Eq. (2) represent (i) the fraction of PAR that is not reflected by the canopy, calculated as $(1-a)$, where a is the canopy reflectivity for PAR and (ii) the fraction intercepted by the canopy, which is based on a Beer–Lambert attenuation law, with a factor proportional to the leaf area index involving an extinction coefficient k. Canopy reflectivity was taken as 0.05, while k has been shown to be in the range 0.7–1.0 for rape by Andersen et al. (1996), and was here set to 0.75 which is typical for crops with relatively flat leaves, and as derived from Gosse et al. (1983).

Eq. (2) has been successfully used for modeling the dry matter growth of a series of crops, including spring and winter rape (Gosse et al., 1986; Morrison et al., 1995; Andersen et al., 1996), from which studies a median RUE value of 2.4 g DM MJ^{-1} m^{-2} intercepted PAR was selected.

After the start of elongation, pods are said to be autotrophic for C, although translocations from leaves have been reported in their early growth (Leterme, 1985). Pod growth lasts 1000 GDD_0 (Leterme, 1988) with a constant radiation-use efficiency of 2.0 g DM MJ^{-1} PAR during the first 500 GDD_0, linearly decreasing to 0.1 g DM MJ^{-1} PAR because of oil production in grains and pod senescence (Leterme, 1985). The extinction coefficient for pods is set at 0.5 according to measurements by Andersen et al., 1996. The PAI increases from mid-flowering on, and is subject to N stress.

2.2.5. Dry matter partitioning

Throughout the growth cycle, leaf photosynthate is distributed among the root, stem, and leaf compartments. Until stem growth becomes a significant sink in late winter, leaves have priority for dry matter. After a time interval of 1000 GDD_0 from emergence, corresponding to the onset of stem elongation, stems have priority over leaves. New leaves are generated with a specific weight that depends on leaf number (Gabrielle et al., 1998). The fraction of total net photosynthesis (ΔDM, g DM m^{-2} day^{-1}) partitioned to the stems is then dependent on thermal time (base 0°C), and calculated as:

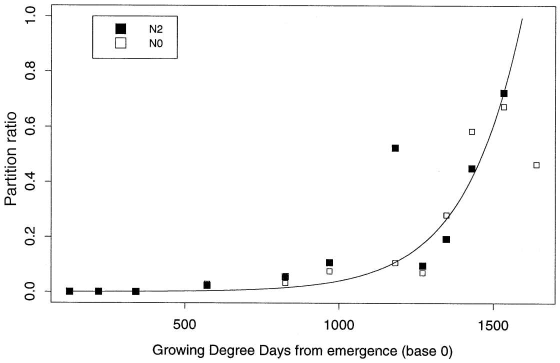

Fig. 2. Fraction of daily dry matter increase that is partitioned to the stems, for two treatments in Châlons (symbols) as a function of thermal time. The solid line is an exponential regression (see text; RMSE = 0.0188, $df = 7$).

$$\frac{\Delta DM_{stems}}{\Delta DM} = \exp\left[5.85 \times 10^{-3}(GDD_0 - 1500)\right] \quad (3)$$

where ΔDM_{stems} is the dry matter partitioned to the stems. Eq. (3) was established by regression on the data corresponding to the N0 and N2 treatments in Châlons, and its coefficients did not seem to be affected by crop N status (Fig. 2). For $GDD_0 > 1500$, the right-hand side of Eq. (3) is set at 1. Throughout the growth cycle, the photosynthate remaining after partitions to leaves and stems is stored in the roots.

In reproductive stage (ii), pod photosynthate is partitioned to pod walls, after which priority is given to the grain. The average size of both pods and grains, as calculated by the phenology module, may limit the intake of dry matter by these compartments on the basis of allometric relationships (Vardon, 1994).

2.2.6. N uptake

N uptake from the soil is based on a supply-and-demand scheme, with the demand being driven only by the vegetative parts (leaves, stems and roots). Crop demand is controlled by a critical N concentration in shoots that represent an optimum for crop biomass production. This concentration decreases with increasing dry matter, following a relationship relatively similar for all C_3 crops (Greenwood et al., 1990). A particular form of this equation has recently been established for rapeseed by Colnenne et al. (1998), and validated for shoot biomass up to 650 g DM m^{-2}. This critical shoot N concentration is:

$$N_c = 4.48(\mathrm{DM}/100)^{-0.25} \text{ if } \mathrm{DM} \geq 90, \quad \text{otherwise } N_c = 4.60 \tag{4}$$

where DM is the shoot dry matter (g m^{-2}), and N_c is the critical N concentration (%). Shoots tend to generate new tissue with the critical concentration N_c, and to attain it in the rest of the dry matter where the actual concentration is noted N_a. However, critical N levels may be exceeded by more than 60% for wheat (Justes et al., 1994) and 43% for rapeseed (Colnenne et al., 1998), which corresponds to the maximum shoot N concentrations obtained in field crops. We then allowed an arbitrary 40% margin above N_c for the shoots, which was restricted to the leaves because it appeared that the measured N concentrations in the stems never exceeded the critical shoot concentration. Lastly, the root N demand was taken from CERES-N Maize (Jones and Kiniry, 1986) based on the following N dilution equation:

$$N_{ro} = 4.0(\mathrm{DM}/100)^{-0.3} \text{ if } \mathrm{DM} \geq 100, \quad \text{otherwise } N_{ro} = 4.00 \tag{5}$$

where DM is the root dry matter (g m^{-2}) and N_{ro} is a N concentration (%) that represents an average level of N in roots for a given level of root biomass under nonstress conditions.

The daily demand (N_{dem}) for each compartment thus reads:

$$\begin{aligned} N_{dem} &= 10^{-2}[\mathrm{DM} \times (1.4N_c - N_a) + \Delta\mathrm{DM} \times 1.4N_c] && \text{for leaves and roots} \\ N_{dem} &= 10^{-2}[\mathrm{DM} \times (N_c - N_a) + \Delta\mathrm{DM} \times N_c] && \text{for stems} \\ N_{dem} &= 10^{-2}[\mathrm{DM} \times (1.4N_{ro} - N_a) + \Delta\mathrm{DM} \times 1.4N_{ro}] && \text{for roots} \end{aligned} \tag{6}$$

with DM referring the compartment of the corresponding dry matter (g m^{-2}), and N_a to the N concentration (%). The unit of N_{dem} is then g N m^{-2}. Because of a systematic underestimation of root N concentration by the model, a 40% margin above the reference level N_{ro} was also allowed for this compartment, as for the leaves.

N supply by the soil depends on the availability of nutrients and on the absorption capacity of the roots in each soil layer. In preliminary tests, when using the original equation of CERES-N Maize for N supply from soil, it appeared that this term was never limiting. Even after calibrating this equation, the simulated dynamics of N supply seemed unlikely, because it was insensitive to low nitrate concentration. Actually, the supply equation was developed for maize undergoing severe water stress, where diffusion of nitrate was limited by dry soil conditions, contrary to our mostly nitrate-limited conditions for winter rape. We then proposed an equation based on a steady-state diffusive transport of NO_3^- to the roots, after Watts and Hanks (1978). The daily supply of N (N_{Sup}, kg N ha^{-1}) from each soil layer in the root zone reads:

$$N_{Sup} = D \times \mathrm{RLD}^{1.5} \frac{([\mathrm{NO_3}] - 0.5)Z}{\theta} \tag{7}$$

where Z is the layer thickness (cm), θ the volumetric moisture content, and $[NO_3]$ is the nitrate concentration in mg N kg^{-1} soil. If $[NO_3] \leq 0.5$ mg N kg^{-1}, there is no absorption, because this residual nitrate is assumed unavailable to the roots. D is analogous to a diffusion coefficient per unit area of root (cm day^{-1}), and was calibrated at 2×10^{-3} cm day^{-1} against absorption data for the N2 treatment. Eq. (7) implies roots are zero-sinks (i.e., the NO_3^- concentration is nil at the root surface), although plants can regulate it by adjusting NO_3^- concentration in xylem (de Willigen and van Nordwijk, 1987). For lack of definite evidence, Eq. (7) does not include the possible effect of the low temperature experienced by the shoots and roots in winter on the absorption of N. Although a temporary depressing effect was exhibited on potted rapeseed plants abruptly subjected to a temperature of 7°C (Laine et al., 1996), this temperature stress was alleviated within a few days as the uptake tended to respond essentially to the crop demand, which had accordingly diminished due to the low temperature (Bigot and Boucaud, 1996). In our model, the indirect effect of low temperatures on crop absorption of N is thus found in the decrease of net photosynthesis; hence, N demand.

2.2.7. N partitioning

In the vegetative parts, the partitioning of N between shoots and roots is in proportion to their respective demands for N. For shoots, N concentration is not identical in leaves and stems, because N demand obeys different equations for either organ.

In the reproductive phase, we modelled the N translocations from roots, stems and leaves to pods after the scheme of Sinclair and Muchow (1995) for maize. Two pools of N available from these organs are calculated at mid-flowering by assuming residual N contents of 0.8 g N m^{-2} for leaves, 0.8 g N g^{-1} DM for stems, and 0.6 g N g^{-1} DM for roots, according to the mean values measured at harvest in Châlons. The N translocation pools are noted TRNLF, TRNST and TRNRO for leaves stems and roots, respectively, and computed (in g N m^{-2}) as:

$$\begin{aligned} &\mathrm{TRNLF} = \mathrm{LAI}(N_a - N_r) && \text{for the leaves} \\ &\mathrm{TRNST} = \mathrm{DM}_{\mathrm{stem}}(N_a - N_r) && \text{for the stems} \\ &\mathrm{TRNRO} = \mathrm{DM}_{\mathrm{root}}(N_a - N_r) && \text{for the roots} \end{aligned} \qquad (8)$$

where a and r denote the actual and residual contents, respectively.

Afterwards, in stages (ii) and (iii), the daily flow of N to the pods from the leaves (or stems) corresponds to the daily GDD (base 0°C) divided by the total duration of pod growth, set at 600 GDD_0, times the pool size. In stage (iii), the N uptake by vegetative components stops. In stage (ii), the translocated N is stored in the pod walls, after which it is partitioned to the growing seeds. In grains and pods, a maximum N concentration of 5% (w/w) is imposed, resulting in either a lower N intake by the pods or a temporary storage in the pod walls if seed demand is limiting.

As a result of translocation, a fraction of leaf area becomes senescent (Gabrielle et al., 1998). Stem biomass is also reduced by assuming that 1 g of translocated N corresponds to 6.25 g of DM.

2.2.8. Water and N stresses

As in CERES-N Maize, environmental stresses are summarised as multiplicative 0–1 factors appearing in the equations for net photosynthesis and leaf and pod elongation.

The water factor is taken here as unity throughout the growing season, since crops were irrigated to prevent water stress. The N stress factors for organ elongation are based on the Nitrogen Nutrition Index (NNI; see e.g., Lemaire et al., 1989), expressed as the ratio of actual to critical N content in a given compartment (leaves or pod walls). NNI is moreover bounded between zero and unity. Eq. (4) was used for calculating critical levels in leaves, whereas a specific curve for N dilution in the pod walls had to be introduced (Gabrielle, 1996).

In CERES-N Maize, a factor similar to the NNI is used to account for N stress on leaf photosynthesis. Here, however, we based this response function on data by Gammelvind et al. (1996), who measured the net CO_2 assimilation rates of winter rape leaves and pods in relation to their specific N content (SLN, g N m^{-2}). A similar relationship was also derived by Sinclair and Amir (1992), both at the leaf and at the canopy level. The 0–1 factor for leaf photosynthesis thus reads:

$$N_{\mathrm{leaf}} = (-4.7\mathrm{SLN}^2 + 28.2\mathrm{SLN} - 8.5)/33.8 \qquad (9)$$

In addition, N_{leaf} was maintained above 0.2, corresponding to the range of response investigated by Gammelvind et al. (1996). In a similar manner, the N factor for pod photosynthesis reads:

$$N_{\mathrm{pods}} = (-1.3\mathrm{SPN}^2 + 8.6\mathrm{SPN} - 2.3)/10.63 \qquad (10)$$

where SPN is the specific nitrogen content of pod walls (g N m^{-2}).

2.2.9. Yield components

The yield components (mean number of pods per plant, and of seeds per pod) are calculated at the end of flowering as a function of the amount of radiation intercepted and of the extent of predicted water stress during stage (iii) (Vardon, 1994). From that day onwards, grains start to develop and accumulate C from pod photosynthesis and N from translocation. Oil concentration (O_c, % w/w) in seeds at harvest is calculated from N concentration (N_g, % w/w), and seed weight (SW, g DM $seed^{-1}$) after Andersen et al. (1996):

$$O_c = 63.3 - 7.37N_g + 1.31\mathrm{SW} \qquad (11)$$

2.3. Model calibration

In Section 2.2, the equations described were parametrised from the literature or from regressions on the Châlons data. Thus, as a general rule, these parameter values were not obtained from an adjustment of the CERES-Rape model to observed data. However, systematic discrepancies had to be addressed by such direct curve-fitting in the phenology and N uptake modules. For the former, an underestimate of the grain to pod dry matter ratio led us to increase the potential for DM intake by the grains, as compared to that originally obtained by Leterme (1985) on cv. Jet Neuf.

In Jyndevad, none of the crop parameters obtained in Châlons were calibrated, although the cultivar employed (Ceres) was different. We hypothesized that genotype parameters had little influence, except for the phenological development that was not fully simulated since the actual flowering date was input to the model.

In both sites, the simulated soil water and N dynamics were checked against measurements of soil moisture and N content, and the corresponding parameters were adjusted to provide realistic predictions (Gabrielle, 1996). However, the model was not forced with the observed data of soil water and inorganic N content. Lastly, a freezing event in early January 1995 in Châlons induced losses of green leaf area that were not taken into account by the model; therefore, the simulated values of green LAI, leaf DM and N contents were re-initialised after the freeze.

3. Results and discussion

The major variables relevant to crop growth, as output by CERES-Rape, are compared to field obser-

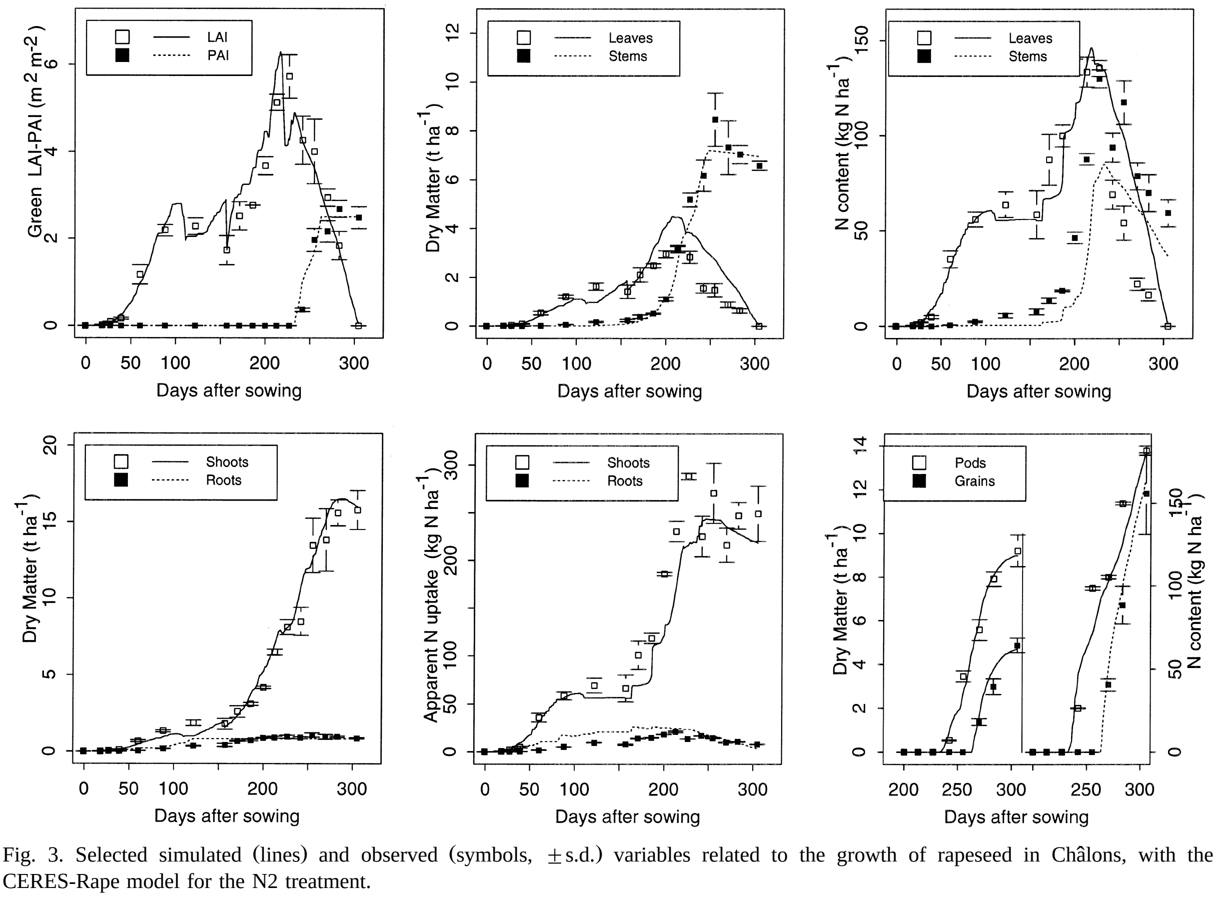

Fig. 3. Selected simulated (lines) and observed (symbols, ±s.d.) variables related to the growth of rapeseed in Châlons, with the CERES-Rape model for the N2 treatment.

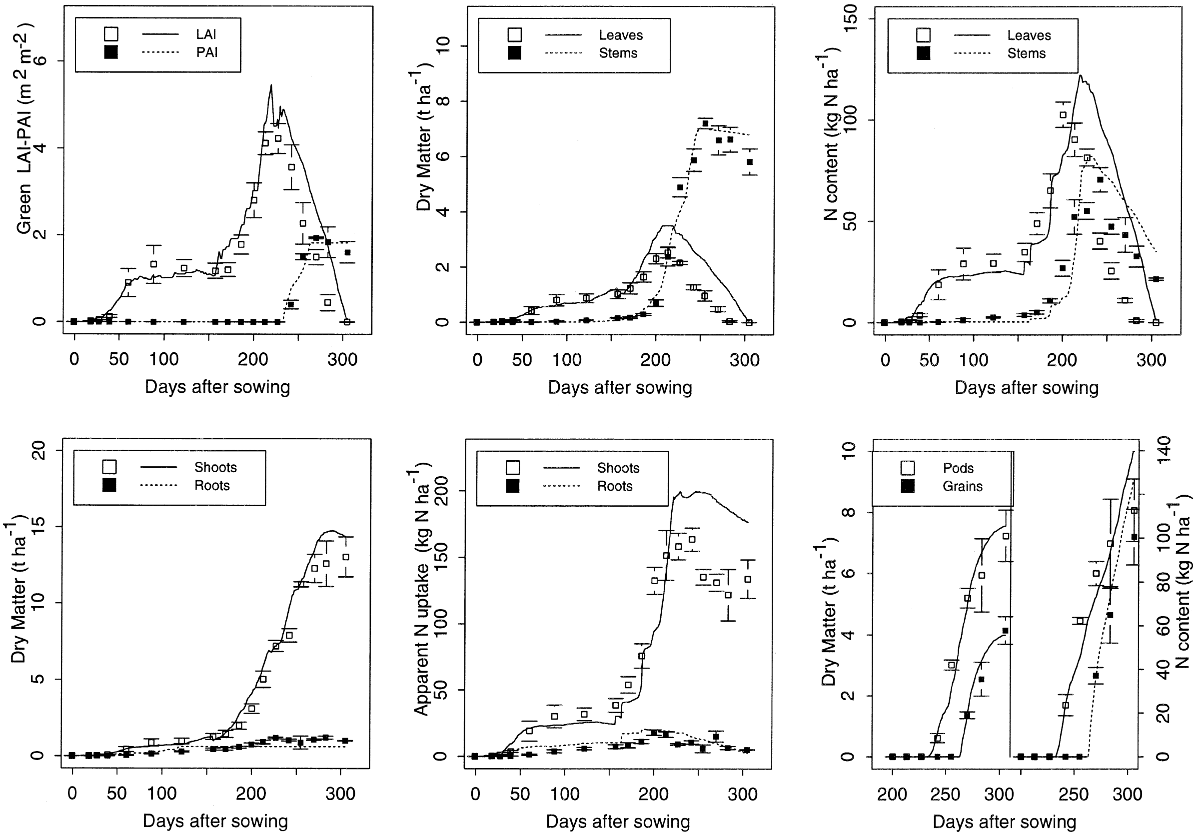

Fig. 4. Selected simulated (lines) and observed (symbols, ± s.d.) variables related to the growth of rapeseed in Châlons, with the CERES-Rape model for the N1 treatment.

vations on Figs. 3–5 for Châlons and on Figs. 6–8 for Jyndevad, for treatments N2, N1 and N0, respectively.

3.1. Vegetative growth

In both locations, the time course of plant total dry matter was well simulated for the high-N treatments (N2 and N1), but tended to be overestimated for the other treatment (N0) from spring onwards. The prediction of potential net photosynthesis was then correct, with the N stress factor being possibly biased. Actually, DM overestimation seemed correlated with an overprediction of green LAI, as was notably the case for the N0 crop in Jyndevad. This emphasizes the sensitivity of DM production to LAI, especially in the low range, as encountered in the N0 treatments. However, since in those cases LAI is limited mostly because of a high turnover of leaves, senescence and green LAI are difficult to predict accurately. As expressed in the model, leaf senescence is driven by threshold parameters, which are relatively sensitive, making it difficult to find the right balance between leaf C–N contents and area at the canopy level.

This difficulty explains why the observed plateau of LAI for the N0 crop in Châlons could not be reproduced by the model from the end of winter onwards, which resulted in an overestimation of crop total DM. In Jyndevad, the model simulated a LAI plateau until spring that must have been too high when compared to actual LAI at its end, and this induced a constant overestimation of crop DM.

Simulation of plant apparent N absorption proved more problematic than dry matter, especially in the spring–summer phases during which different pat-

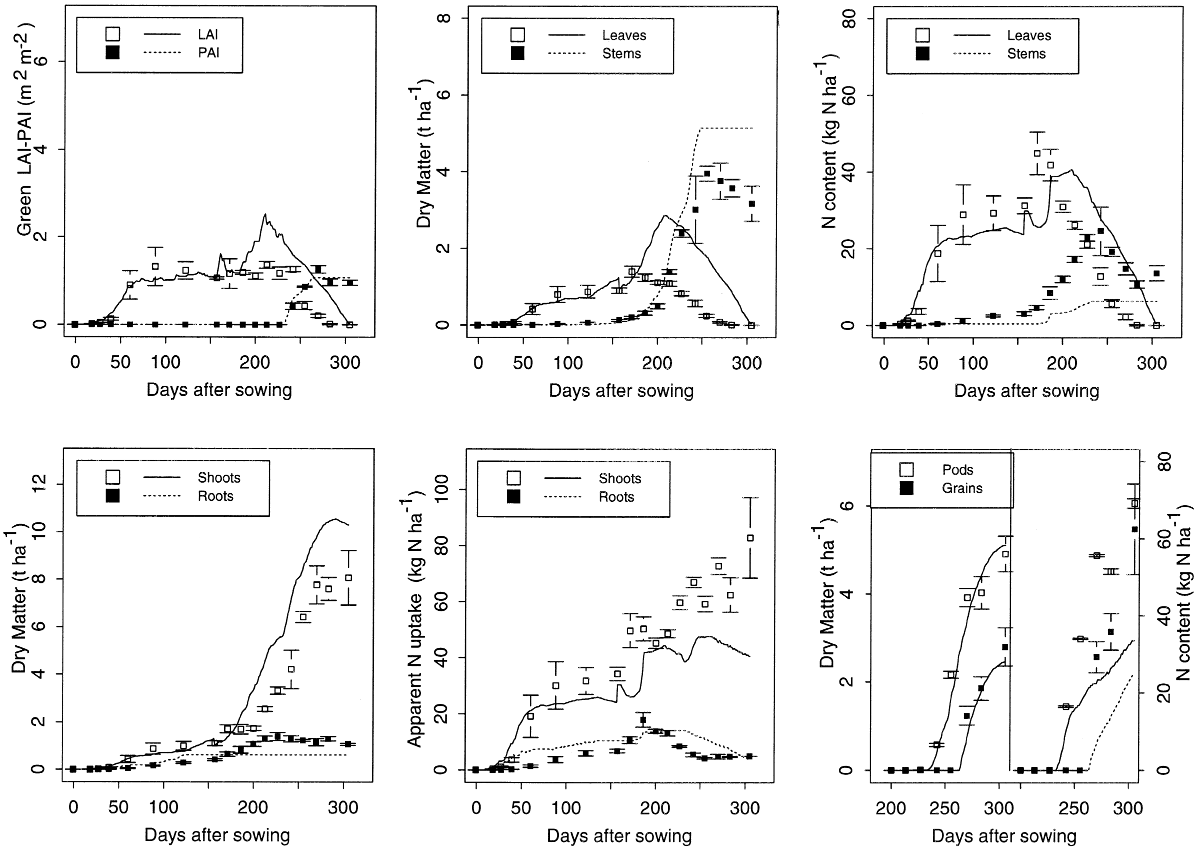

Fig. 5. Selected simulated (lines) and observed (symbols, ±s.d.) variables related to the growth of rapeseed in Châlons, with the CERES-Rape model for the N0 treatment.

terns were observed. Until early spring, crop N was reasonably well simulated, sometimes reflecting small errors in crop DM, with the exception of the N0 treatment in Jyndevad, for which N was markedly underpredicted despite overpredicted DM. This indicates that the N limitation on photosynthesis was not strong enough in the low range of specific leaf N, and also that soil supply may have been underestimated. This is not apparent in the Châlons N0 simulation, but the comparison cannot be made because it involved twofold higher levels of DM.

After flowering, the accumulation of total crop N was strikingly different between the N1–N2 and N0 treatments: crop N stabilised, or even decreased (N1, Châlons) in the former case, whereas it increased by 15–20% in the latter. Such a pattern has also been reported by Schjoerring et al. (1995), but could not be fully explained by CERES-Rape. For the N0 treatments, the model simulated a slight decrease in crop N after flowering because N uptake stopped, and structural N was lost in falling leaves, instead of the observed increase in crop N. This resulted in a marked underestimation of pod N in Châlons. Enabling uptake of N by stems and further translocation to grains after flowering removed this bias (data not shown), but appears to be in disagreement with the hypothesis that stems senesce during that period, as evidenced by their decreasing DM. In addition, this uptake scheme induced an overestimation of crop N for the N1–N2 treatments.

Another factor accounting for bias in Châlons is the strong increase in leaf N concentration observed for all treatments upon regrowth in spring. It corresponded to a storage by the crops of soil N made

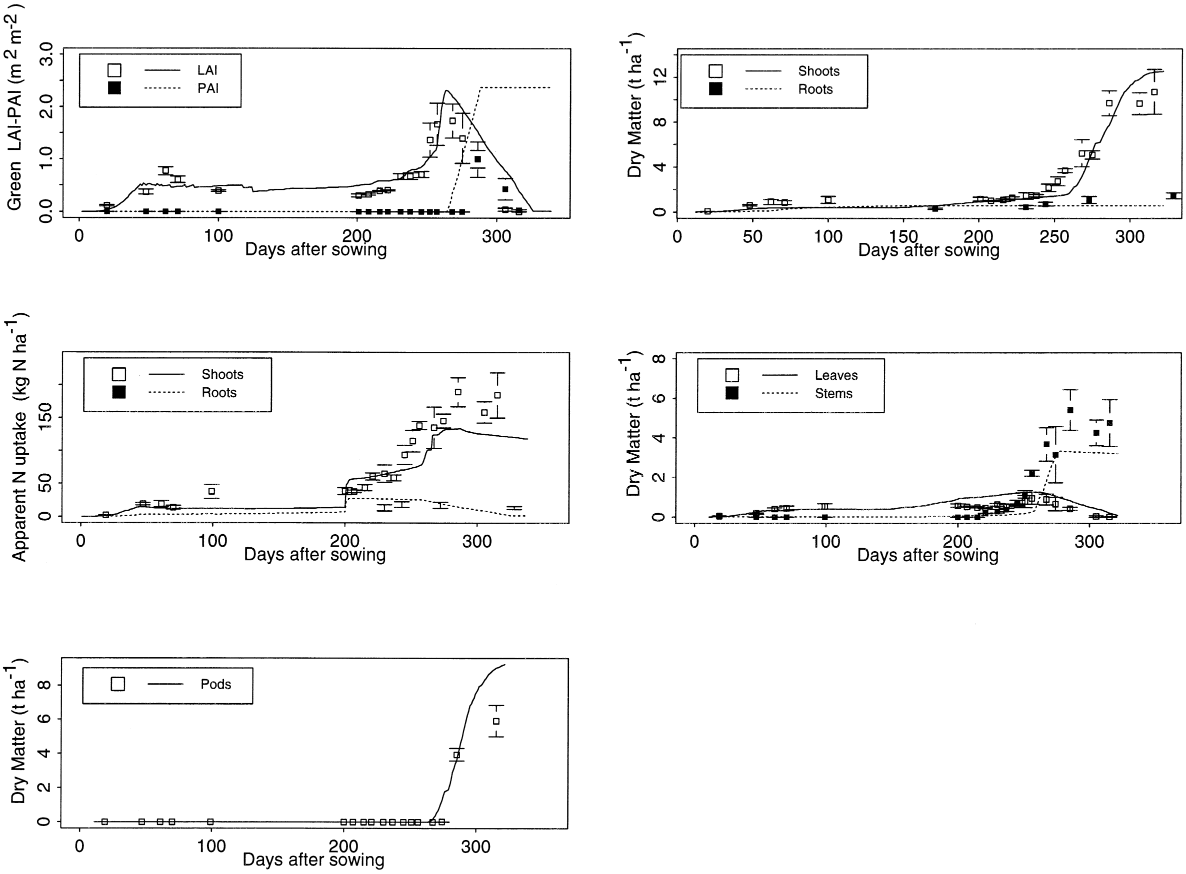

Fig. 6. Selected simulated (lines) and observed (symbols, ±s.d.) variables related to the growth of rapeseed in Jyndevad, with the CERES-Rape model for the N2 treatment.

available through mineralisation and fertiliser application, but could not be explained by the concept of critical N content, since it was also associated with an increasing biomass. This discrepancy underlines a structural weakness of the supply and demand scheme for computing N uptake, relying on the assumption that it is essentially regulated by crop biomass. In cases of high soil N availability, this assumption is indeed likely to be violated, and alternative concepts for N uptake should be worth considering, such as the use of a Michaelis–Menten absorption model with respect to soil NO_3^- concentration that circumvents the use of a plant demand term.

The partitioning of DM between stems and leaves seemed correct for all treatments in Châlons, which would be expected because the regression of Eq. (3) was obtained at the same location. In Jyndevad, except for the N0 treatment for which total DM was biased, the DM of leaves and stems were also correct, which supports the use of a leaf DM demand term to regulate DM allocation in the model. Leaf demand is calculated from the increase in LAI by use of a specific leaf weight (SLW, g DM m^{-2}). SLW was parametrised from measurements on individual leaves in Châlons according to leaf number, and although this parameterisation may vary according to the rape cultivar, it seemed to apply in Jyndevad to some extent. To assume a fixed time course for SLW, regardless of crop N status or cultivar, could be regarded as a weak point in the model. However, this method of driving leaf biomass demand is probably as successful as the common alter-

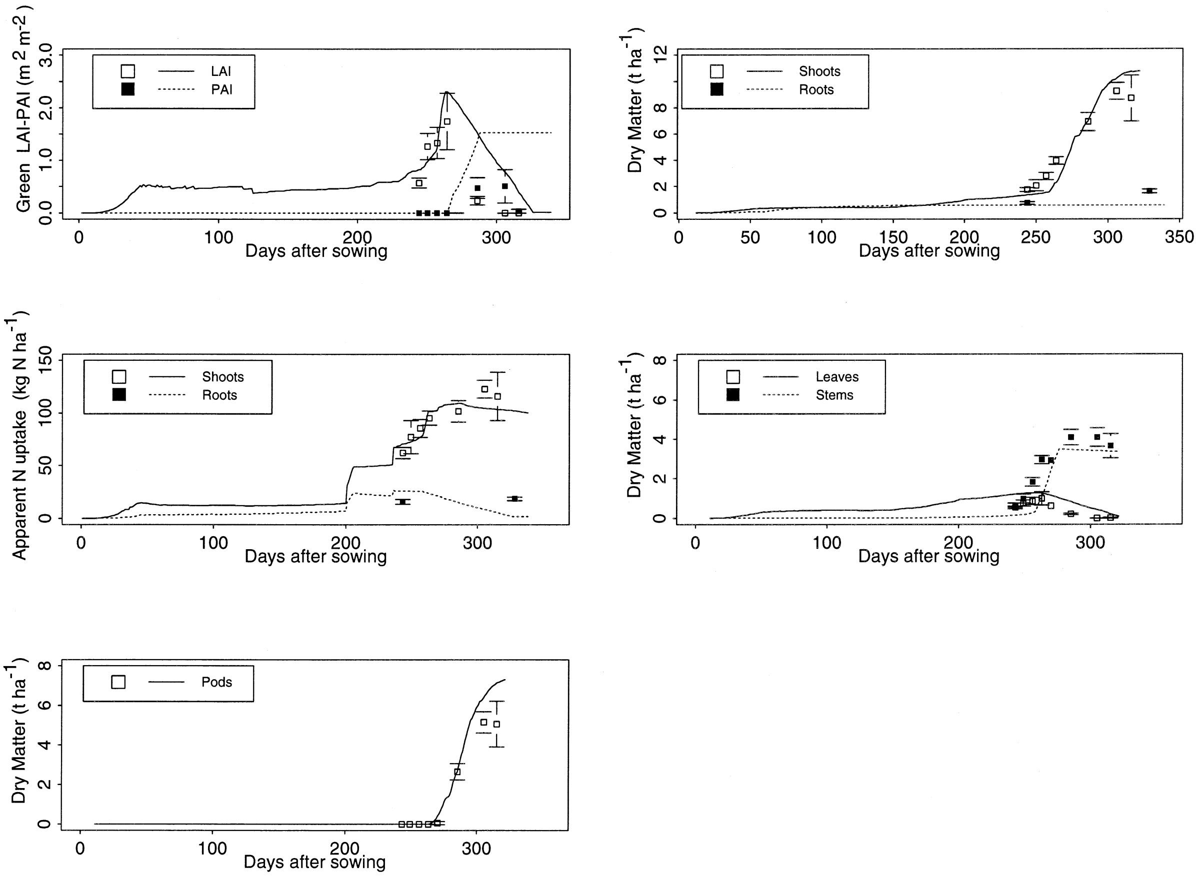

Fig. 7. Selected simulated (lines) and observed (symbols, ±s.d.) variables related to the growth of rapeseed in Jyndevad, with the CERES-Rape model for the N1 treatment.

native consisting in deriving fixed dry matter partitioning factors, as exemplified here for the stem compartment.

Lastly, in the model, DM partition to roots stopped in late winter when stems were becoming a significant sink for photosynthate, whereas in reality the roots accumulated DM for all treatments until late spring. This spring growth is surprising, since at that time rapeseed roots have been found to support the regrowth of shoots rather than to be storing additional reserves (Mendham and Salisbury, 1995). Whatever the particular physiological cause for this, stem DM was overestimated by the model as a result, implying that the partitioning factor for the stems should be reduced to allow more DM into the roots during stem elongation. To maintain agreement with the regression in Fig. 2, this factor could for instance be bounded by 0.9, limiting the strength of stems as a sink for photosynthate.

The results regarding the partitioning of N among the crop compartments are generally similar to those pertaining to DM, except for the previously mentioned underestimation of leaf N in spring in Châlons. Unfortunately, no data were available for Jyndevad.

3.2. Reproductive growth

The timing of the green LAI peak before the decline associated with the onset of pod growth was well simulated, due to the use of the measured date of flowering in the model. However, contrary to the model's hypotheses, the rate of the LAI decline did

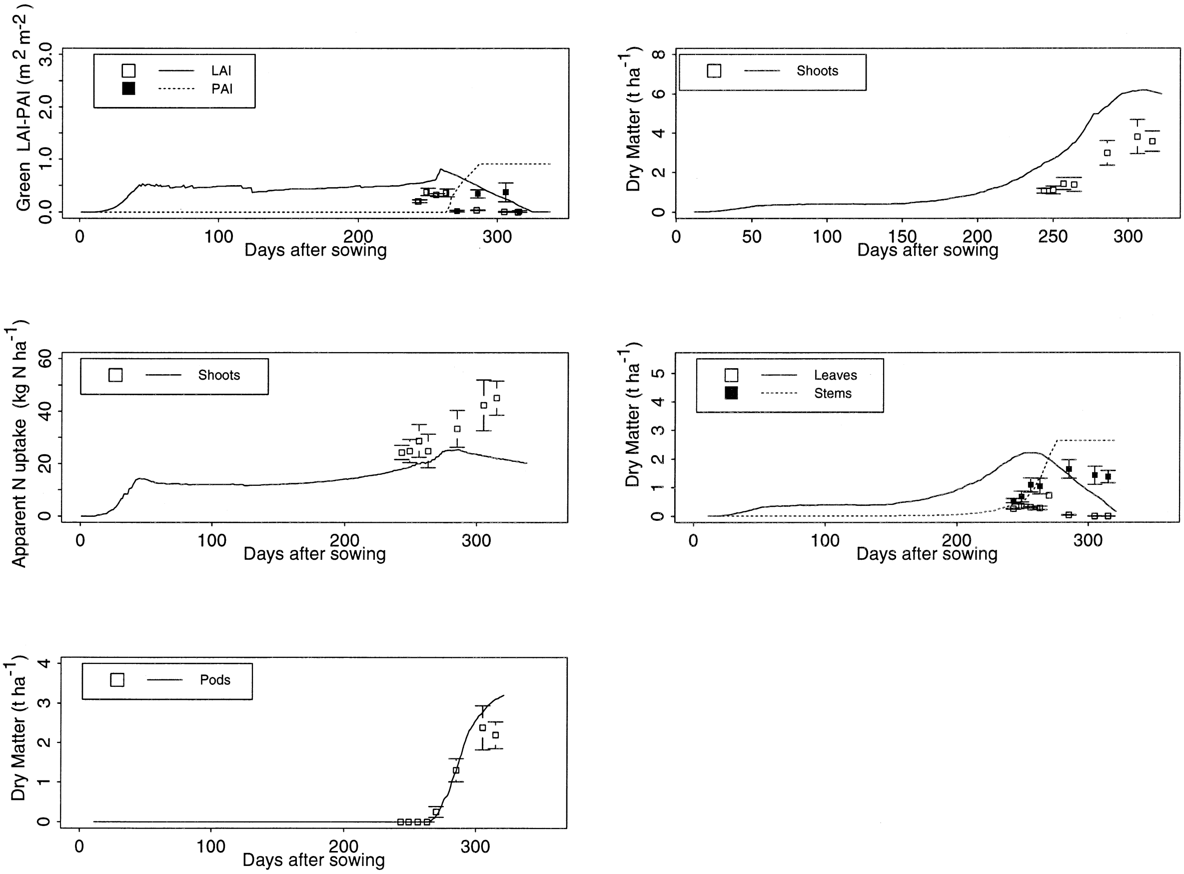

Fig. 8. Selected simulated (lines) and observed (symbols, ±s.d.) variables related to the growth of rapeseed in Jyndevad, with the CERES-Rape model for the N0 treatment.

not appear constant with respect to thermal time, and the simulation was less realistic. The base temperature of 0°C employed here may then be incorrect, although it worked fairly well for the N translocation rate itself in Châlons. The size of the pool of N mobilisable by the pods from the vegetative parts was well predicted only for the N2 crop, but for the other treatments it was strongly affected by the previously mentioned bias in total crop N. The fact that measured N concentration in stems at harvest was also variable caused additional errors in the translocation pools, since the residual contents were fixed in the model.

This resulted in significant discrepancies in the prediction of pod N content at harvest, and to a lesser extent in that of pod DM and pod area index. It appears indeed that the biases in pod N essentially affected the N content of grain, so that pod wall N was realistic enough to reflect the actual N stresses.

In Jyndevad, there were no experimental data available on pod N or grain DM, and the PAI data could not be directly compared to the simulations because these concerned total pod area, whereas the observations pertained to green PAI only. However, it seems that from the beginning of its growth, the PAI tended to be overestimated, which resulted in pod DM being also overestimated. Measured PAI was systematically lower in Jyndevad than in Châlons, implying that the maximum final PAI value, set at 2.5 in Châlons, should be reduced for cv. Ceres used in Jyndevad. Despite the closely controlled irrigation, temporary water stresses cannot also be ruled out on the well-drained sandy soil under the high evaporative demands encountered

Table 2
Measured (± s.d. in brackets) and simulated yield components for the rapeseed crops in Châlons and Jyndevad

Location and treatment	Grain DM yield (t DM ha^{-1})	Grain N yield (kg N ha^{-1})	Oil content (t oil ha^{-1})	Straw yield (t DM ha^{-1})	Straw N (kg N ha^{-1})
Châlons N2					
Measured	4.87 (0.33)	155.8 (24.6)	2.43	11.28 (0.97)	93.8 (6.8)
Simulated	4.69	162.1	1.78	12.16	57.2
Châlons N1					
Measured	4.13 (0.45)	100.6 (12.7)	2.16	9.52 (0.85)	39.0 (1.6)
Simulated	3.99	125.9	1.60	11.01	52.0
Châlons N0					
Measured	2.80 (0.43)	62.5 (11.7)	1.49	6.07 (0.72)	25.8 (2.8)
Simulated	2.46	25.0	1.37	8.46	18.1
Jyndevad N2					
Measured	2.40 (0.34)	80.6 (10.8)	1.06 (0.17)	5.36 (0.33)	30.4 (2.8)
Simulated	5.06	97.4	2.49	7.97	21.7
Jyndevad N1					
Measured	2.34 (0.17)	65.2 (4.7)	1.09 (0.08)	4.79 (0.35)	19.8 (2.5)
Simulated	4.24	83.4	2.07	7.04	18.2
Jyndevad N0					
Measured	1.25 (0.16)	33.3 (4.4)	0.60 (0.08)	2.09 (0.29)	7.8 (1.6)
Simulated	1.73	14.7	0.99	4.71	10.2

The straw refers to unharvested parts as a whole (including chaff, roots and pod walls).

during pod growth. Nevertheless, assuming a fixed maximum PAI for an indeterminate plant such as rapeseed remains a crude simplification, because, for instance, the number of pods generated is regulated by the availability of photosynthate from the rest of the plant. A more biological approach to determine the maximum PAI should be considered.

Lastly, for the Châlons data, it is difficult to judge the partitioning of N and DM between pod walls and grains because of the bias in pod N. The relative proportions of N and DM partitioned to grains and pod walls seemed to be reasonably well simulated by the model, despite variations in the observed grain to total pod DM and N ratios.

3.2.1. Yield components

Measured and simulated yield components are presented in Table 2. In Châlons, simulated grain DM yield matched observations within 15%, but grain N content was markedly too low or too high for the N0 or N1 and N2 treatments, respectively. This could be expected from the previously mentioned bias in pod N for N0 and N1, but for N2 it should be ascribed to an incorrect partitioning of N between grain and pod walls at harvest. The model also predicted too much DM in straw, and more specifically in stems, for which the simulated final decrease in biomass was too small. The latter may be ascribed to a mobilisation of photosynthate from stems, along with some respiration in the structural tissues that was not accounted for by the model.

At Jyndevad, DM yield was nearly two-fold overpredicted, whereas N yields were within 30% of observations with a positive bias. These errors are much larger than those pertaining to pods DM and crop total N content, visible as displayed in Figs. 6–8, underlining the model's shortcomings in partitioning pod assimilates between pod walls and grains. The yield discrepancies should however be smaller because (i) an estimated 20% of pods and seeds was lost at harvest and (ii) a short drought period at the beginning of the pod filling phase may have impaired grain yield (Andersen et al., 1996).

As a consequence of the errors on yields, oil contents were overestimated in Jyndevad, although Eq. (11) was partly derived from the Jyndevad data. This relationship was also barely successful in Châlons, where the simulated yields were closer to the observed ones, except for the N0 treatment. The chemical composition of grains strongly depends on their growing and nutrition conditions, thus Eq. (11) applied best to the Châlons N0 treatment because its yields were in the range of those on which the equation was calibrated.

4. Conclusion

This paper presents an attempt at simulating the major processes determining the C and N assimilation of a winter oilseed rape crop throughout its growing season, based on commonly-used principles regarding leaf area development and senescence, net photosynthesis at the canopy level, and translocation of N to reproductive organs, together with the effects of limited soil N availability. Although the equations employed have allowed successful predictions of canopy status for a number of crops (Jones and Kiniry, 1986; Sinclair and Amir, 1992), their application to rape presented additional challenges such as the simulation of a high turnover of leaves or of the mechanisms of pod and grain growth as triggered by an indeterminate flowering. Although few previous modelling exercises have covered the whole growing season or taken N nutrition effects into account, values for most parameters could be assessed from literature or additional data.

In the vegetative phase, the time courses of most of the variables of interest (LAI, dry matter and N contents within the various plant compartments) were well simulated, with the restriction that the model tended to underestimate crop N content, especially for the low N treatments. For the latter, LAI was conversely overestimated, pointing at a tendency to overpredict leaf elongation under N stress, thus overestimating net photosynthesis and ultimately the DM and N loss due to leaf senescence. However, this bias could not be dealt with in the calibration phase, implying that new equations for N stress should be derived from data covering a wider range of conditions than the present set.

In the reproductive phase, despite the use of the observed dates for the onset of flowering, the dynamics of pod and grain growth revealed some shortcomings of the current model. Notable errors occurred in the simulation of pod growth, essentially deriving from previous errors in crop N content, which made it difficult to test the module that partitions pod assimilate to grain. However, the fact that the fluxes of N between vegetative parts and pods and between pod walls and grains were driven by tissue N concentrations interfered with the N stress factors that affect photosynthesis, also determined by N concentrations, making the corresponding parameters very sensitive. An alternative approach, employed for maize and sunflower (Jones and Kiniry, 1986; Villalobos et al., 1996) would consist in calculating a N demand for grains as a driving variable. However, while this scheme is more stable, it cannot account for the variability in grain N content when N is highly available.

While some of its modules, particularly in the reproductive phase, deserve further testing, CERES-Rape provided a sound basis for the modelling of the growth of winter rape, as related to soil N status. Although it might well be outranked by a simple statistical predictor as regards grain yields, it should prove a relevant tool for analysing the time course of C–N balances within the soil–crop system, as already used by Gabrielle (1996) in a study of N losses to the atmosphere and to groundwater under rape.

Along with the identification of varietal parameters, the effects of drought could be included in a later version, as is the case with other models from the CERES family. Further work on the model would be facilitated by its scheduled integration into the DSSAT framework (IBSNAT, 1990).

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