Weed Research, 1997, Volume **37,** 325–341

Modelling crop:weed interactions in wheat with ALMANAC

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Received: 8 May 1996
Revised version accepted: 24 April 1997

Summary

ALMANAC is a dynamic model for plant growth, water balance and soil nitrogen dynamics that can simulate on a daily basis two or more competing species. The simulation of competition for light is based on Beer's law, allowing a different extinction coefficient (k) for each species. Light is partitioned between species based on k-values, leaf area index and plant heights. Total biomass is simulated with radiation use efficiency and grain yield with a harvest index approach, sensitive to water stress. The model simulates competition for water and nutrients based on each species' current rooting zone and demand by each species. The effect of crop management on the competition issue can be simulated. The model was evaluated in Dijon (France) using 4 years of experimental data on wheat:oat mixtures, differing in oat (*Avena sativa* L.) densities, the period of oat emergence, the date of weed suppression by herbicides and the wheat (*Triticum aestivum* L.) genotype. Additional data on oilseed rape (*Brassica napus* L.) and vetch (*Vicia sativa* L.) competition in spring wheat were also used. The wheat grain yield was reasonably simulated with a root mean square error (RMSE) of 0.10–0.35 t ha^{-1}. Corresponding values for oats were 0.10–0.55 t ha^{-1}. The competitiveness of oats, oilseed rape and vetch was correctly simulated. The model appears as a reasonable tool for estimating damage thresholds in integrated weed control programmes.

Introduction

Optimization of weed control programmes depends on early and reliable prediction of the impact of weeds on crop yield. Numerous empirical models describe the crop losses (or the expected yields) as a single function of one or several factors, including weed density, relative leaf area and relative time of weed emergence (Cousens, 1985; Cousens *et al.*, 1987; Kropff & Spitters, 1991). These statistical and static regression models have been intended for practical applications, such as predicting the damage threshold for bispecific weed:crop combinations in given locations (Caussanel, 1989). Nevertheless, extrapolation of such models to years and locations often gives unrealistic results because of the initial single calibration and the lack of environmental variables. Additional factors important in weed:crop competition, such as crop density, crop cultivar and soil fertility (Moss, 1985; Ampong-Nyarko & de Datta, 1993; Christensen, 1995), are assumed to be constant or not important in most of the regression models.

Process-oriented models developed recently simulate weed competition or more generally intercropping systems in a wider range of conditions (Kropff, 1988; Caldwell, 1993). On the

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basis of existing crop simulation models, dynamic models were developed to simulate competition for light, water and/or nutrients between a crop and a selected weed at a process level (Spitters & Aerts, 1983; Graf *et al.*, 1990; Wilkerson *et al.*, 1990; Kropff & Spitters, 1992; Ball & Shaffer, 1993). Economic aspects of spraying decisions can rely on plant process modelling (Dunan *et al.*, 1994). Such models help the interpretation of responses to climate in experimental data. Once validated, these models can generate new data sets because they are valid for a wide range of conditions (Assemat, 1990; Kropff *et al.*, 1993). However, the great number of parameters and the difficulty in deriving them from previously published data make validation a challenge. Therefore, these mechanistic models are generally not appropriate for current management. Furthermore, as they were developed for specific crop:weed mixtures, the models may not be easily adapted to different combinations.

The ALMANAC model (Kiniry *et al.*, 1992) is a process-orientated simulator of interplant competition and, in comparison with other dynamic competition models, remains of intermediate complexity. Using a limited number of sensitive parameters, it was intended for practical applications, such as the definition of integrated damage thresholds or the evaluation of weed control programmes on crop yield. More evaluation on data from detailed competition experiments is needed before such applications are feasible. The objective of the current research was to evaluate the ALMANAC model on various bispecific weed and wheat combinations using 4 years of detailed data.

Materials and methods

Model overview

The ALMANAC model, like EPIC (Williams *et al.*, 1989), from which it was derived, simulates daily crop and weed growth and grain yield using climatic data and soil and crop management inputs. It uses a generic approach for a wide range of crops and weeds. Water and nutrient movement and dynamics in soil have been described in detail previously (Williams *et al.*, 1989). The potential biomass, including root fraction, is a function of intercepted solar radiation and the radiation use efficiency (RUE) for the plant species (Kiniry *et al.*, 1989). Mean RUE for wheat is 2.8 g MJ^{-1} m^2 (3.5 including roots) before grain filling. Higher values were observed for C_4 grasses and lower for C_3 legumes (Gosse *et al.*, 1986). Economic yield is predicted from the above-ground biomass using a harvest index (HI) approach. HI is the dry weight of the seed divided by the dry weight of the total above-ground plant at maturity. HI_0 is defined as the HI value in a monospecific dense stand, without water and nitrogen stress. In the model, harvest index is sensitive to water stress but not to nitrogen deficiency. In ALMANAC, a module was added to simulate the competition for light, water and nutrients using two or more species (maximum 9) in an intercropping pattern (Kiniry *et al.*, 1992). A brief summary of model functions is presented below and a schematic diagram of daily and annual functioning is presented in Fig. 1.

Competition for light

The model simulates light interception by leaf canopies, using Beer's law (Monsi & Saeki, 1953) and leaf area index (LAI) of the total canopy, assuming a random spatial arrangement of leaf area. The model divides the intercepted light between the two species using the system of Spitters & Aerts (1983). The total interception is calculated with the LAI of each species, weighted by their light extinction coefficients (*k*). At a given *k*, the higher the value of *k* for a species, the more greatly that species will intercept light and the more effectively that species will compete for light. The daily incoming solar radiation intercepted by the total leaf canopy (IPAR, MJ m^{-2}) is:

$$\mathrm{IPAR} = \mathrm{PAR}_0 \times [1 - \exp(-k_\mathrm{c} \times \mathrm{LAI}_\mathrm{c} - k_\mathrm{w} \times \mathrm{LAI}_\mathrm{w})] \qquad (1)$$

where PAR_0 = photosynthetically active solar radiation above the canopy (MJ m^{-2}), k_c, k_w = light extinction coefficient for crop and weed and LAI_c, LAI_w = leaf area index for crop and weed.

The total IPAR is partitioned between the crop and the weed by a ratio (*R*) of the LAI of each species, weighted by *k* for each species and by the fraction of light transmitted to half the height of the plant species, $\exp(-k_n\ \mathrm{LAIHF}_n)$:

$$R = [\mathrm{LAI}_\mathrm{c} \times k_\mathrm{c} \times \exp(-k_1 \times \mathrm{LAIHF}_1)] / [\mathrm{LAI}_w \times k_\mathrm{w} \times \exp(-k_2 \times \mathrm{LAIHF}_2)] \qquad (2)$$

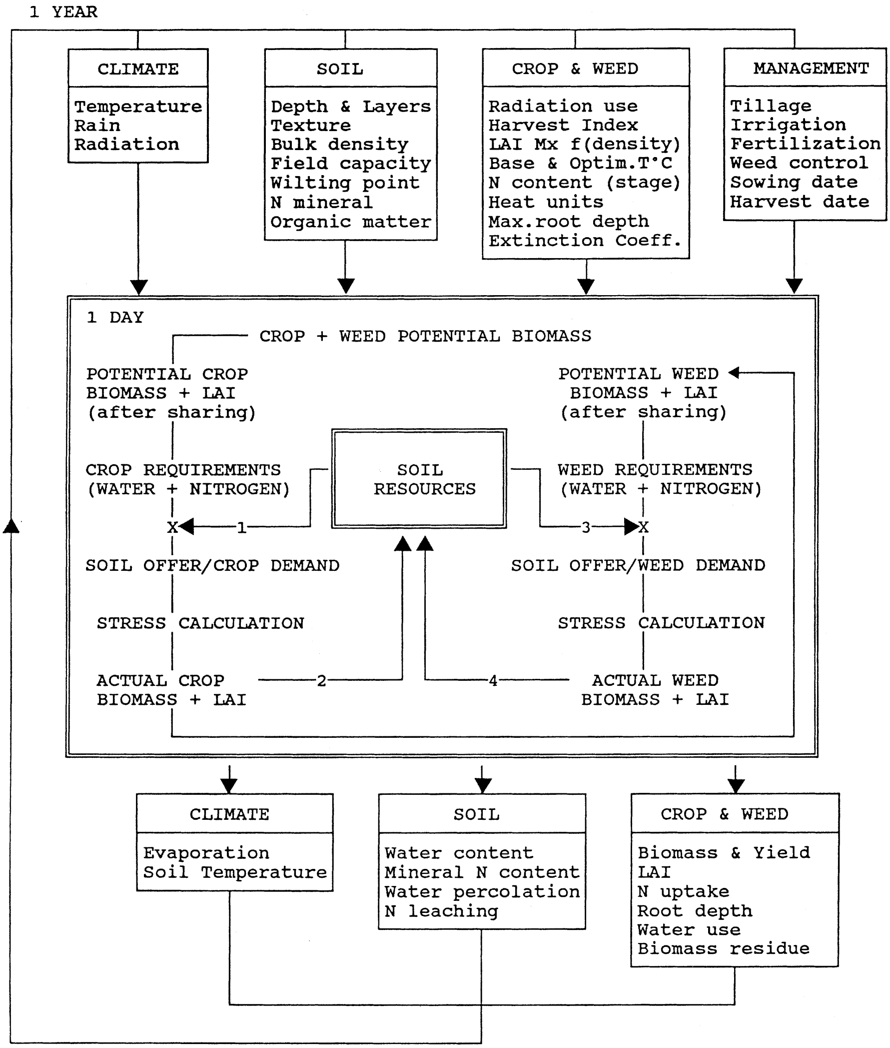


Fig. 1. Schematic diagram of the ALMANAC model.

where k_1, k_2 = estimated extinction coefficient of the combined leaf canopy above half the height of crop (1) and weed (2) and LAIHF_1, LAIHF_2 = values for combined LAI above half the height of each species.

According to Spitters & Aerts (1983), light at this height estimates the average illuminance throughout the leaf canopy of a species. Thus, taller species and species with greater values for k are given preference for light interception. Parameters k_1 and k_2 are weighted means of the k-values for both crop and weed, the weights being determined by the relative species composition of the LAI above half the height of each species. The vertical leaf area distribution was assumed to be uniform. The fraction of IPAR partitioned to the crop is $R_c = R/(R+1)$ and $R_w = 1 - R_c$ for the weed. The value of k changes greatly with the canopy architecture, the planting pattern and the solar angle (Flénet *et al.*, 1996). For plants with rather erect leaves, such as wheat or grass weeds, values of 0.6–0.7 are commonly reported (Kiniry *et al.*, 1989), whereas plants with predominantly horizontal leaves, such as sunflower (*Helianthus annuus* L.) or numerous broad-leaved weeds, have higher values (0.8–0.9). The maximum plant height (H_{mx}) of the canopy is important for simulating the competition for light. A range of values have been observed for wheat cultivars (0.6–1.2 m). Daily plant height (H_i) is estimated with the allometric relationship:

$$H_i = H_{mx} \times \sqrt{(LAI_i/LAI_{mx})} \quad (3)$$

where LAI_i = daily value of leaf area index and LAI_{mx} = potential LAI at a given population density.

Leaf area index simulation

Accurate simulation of light interception depends on realistic values of LAI for both species. This requires that the leaf area be sensitive to population density. Three variables are used in ALMANAC to simulate maximal LAI (LAI_{mx}) of each species at different population densities (PPO). First is the LAI at high densities (LAI_{mx0}) without limiting factors, in general, eight for wheat. The other two variables are data points (PPO1 and PPO2) used to fit a sigmoid-curve function for a zero-to-one factor which reduces LAI_{mx0} at different population densities. The following adjustment was suggested for wheat (Kiniry *et al.*, 1992):

$$LAI_{mx} = LAI_{mx0} \times \{PPO/[PPO + \exp(6.23 - 0.015 \times PPO)]\} \quad (4)$$

Simulation of light competition also requires accurate description of leaf area production and decline. The model estimates LAI under non-stress conditions (LAI_{pot}), up to the point of maximum LAI for the growing season (LAI_{mx}), by using a function similar to eqn (4). In this case, two data points (LAP1 and LAP2), expressing the evolution of LAI_{pot} with time, are used; the time-course of LAI_{pot} is described as a function of relative heat units (RHUs). RHUs are a fraction of PHUs (potential heat units) from emergence to maturity. The following adjustment was suggested for winter wheat (Debaeke *et al.*, 1996), but more variation is expected among cereal species and cultivars

$$LAI_{pot\,i} = LAI_{mx} \times \{RHU_i/[RHU_i + \exp(4.79 - 20.16 \times RHU_i)]\} \quad (5)$$

Natural loss of leaf area late in the season is described by the input variable RLAD (rate of leaf area decline), and the decrease in RUE in later growth stages is simulated similarly with RBMD (rate of biomass decline). This occurs after an input fraction (XDLAI) of PHU has accumulated (Williams *et al.*, 1989).

The effect of water stress or nitrogen deficiency on daily leaf expansion was computed for each species with the equations (Williams *et al.*, 1989):

$$LAI_i = LAI_{i-1} + \Delta LAI$$

$$\Delta LAI = \Delta LAI_{pot} \times \{1 - \exp[5 \times (LAI_{i-1} - LAI_{mx})]\} \times \sqrt{STR_i} \quad (6)$$

where STR_i = minimum plant stress factor (day *i*) ranging from 0 (no growth) to 1 (no limitation).

Competition for water and nutrients

The water balance consists of separate transpiration calculations for each species. Each species is assumed to use the water it needs if sufficient water is present in its current rooting zone (defined by a specific rooting shape and a potential root depth without a root-restricting soil layer, RD_{mx}). A similar approach is followed for nitrogen and phosphorus uptake. A complete description of these biophysical processes is found in Williams *et al.* (1989). A change in a soil resource will restrict the growth of a species (first LAI, then biomass) in proportion to the demand by the species and its ability to extract the resource (most limiting factor approach) (Fig. 1). A dilution curve, which is different for C_3 and C_4 plants, is used to define the N and P plant content for maximal growth as a function of PHU.

Temperature requirements

The base temperature for germination and growth (T_B,°C) is important in a multispecies competition model because the emergence date and the rate of development early in the season are critical for simulating interaction of the two species. T_B is assumed to be the same for all growth stages and all organs. Higher optimum temperature (T_O, °C) values can increase competitiveness later in the season when temperatures are greater. The potential heat units (or sum of day degrees) from emergence to maturity

(PHU) control how long a plant species can compete and how late season stresses can affect seed yield. Adjusted values for T_B are 0 °C for cool-season grasses, winter and spring cereals; values of T_0 are 13 °C for winter cereals and 15 °C for early spring crops.

Date of emergence is determined from simulated values of moisture and temperature in the uppermost soil layer with three fixed parameters: (1) duration of the period from sowing to emergence in the absence of water constraint (150 day–degrees for wheat); (2) minimum value of soil water content to initiate germination in the sowing layer (15%); and (3) critical value of soil temperature for germination and emergence (0 °C). For practical purposes, as the weed control decision is taken at weed emergence and because of the difficulty to predict correctly the emergence date, the simulation starts when the first species has emerged.

Field study to obtain data for model calibration and evaluation

Results used for model calibration and evaluation come from a 4-year experiment conducted at the INRA experimental station of Epoisses near Dijon (east central France) from 1984 to 1987 on a calcareous silty clay soil. A range of winter and spring wheat genotypes (*Triticum aestivum* L.) were grown in association with different crops used as weeds: spring and winter oats (*Avena sativa* L.), spring oilseed rape (*Brassica napus* L.) and spring vetch (*Vicia sativa* L.). Some results were published in a preliminary ALMANAC evaluation (Debaeke et al., 1993).

Experiment 1: Incidence of weed density (D_X*) and post-emergence control on crop yield (Kafiz, 1989; Caussanel* et al.*, 1993).* Six densities (0, 10, 20, 40, 80, 160 plants m^{-2}) of a spring oat cv. Selma were established with spring wheat cv. Bastion in alternate rows on 8 March 1984, 8 March 1985 and 14 April 1986. Competition design was additive and wheat sowing density was 350 plants m^{-2}. Row width was 15 cm. On half the experimental plots, oats were removed by spraying diclofop-methyl (Illoxan CE, 360 g a.i. L^{-1}) at 1080 g a.i. ha^{-1} at the three-tiller wheat stage. Application was made using a Berthoud commercial field sprayer delivering 300 L ha^{-1} at 300 kPa. Crop and weed dry aerial biomass were measured four times in the season on five replicates. At maturity (mid-August), wheat and oat grain yield were measured on each plot. The evolution of plant densities was recorded during the crop cycle. Wheat and oat densities at early tillering were kept as the population values for LAI_{mx} estimation of each species, because the plant population remained stable thereafter.

Experiment 2: Incidence of wheat genotype, weed density and weed emergence period on crop yield (Mondragon, 1988; Mondragon et al.*, 1989).* Three densities (0, 10, 20 plants m^{-2}) of winter oats cv. Fringante were established on 29 October 1985, together with four winter wheat genotypes (cv. Capitole, Castan, Fidel and Talent) sown at 250 plants m^{-2} in alternate rows. Seven densities (0, 2.5, 5, 7.5, 10, 12.5, 15 plants m^{-2}) of a spring oat cv. Selma were sown on 9 March 1987 in each of the four previous wheat genotypes sown on 24 October 1986. In agreement with GEVES (1992), the four genotypes differ in (1) their ability to produce reproductive tillers (Talent > Fidel > Capitole = Castan), (2) their straw height (Capitole = Fidel > Castan > Talent), (3) their earliness to reach stem elongation (Castan > Fidel > Capitole = Talent), (4) maturity (Castan > Talent > Capitole > Fidel) and (5) their tolerance to frost (Capitole > Fidel > Talent > Castan). At maturity (end of July), oat and wheat yields were assessed on each plot. The evolution of plant densities was recorded during the crop cycle as in Experiment 1.

Experiment 3: Incidence of weed species, weed density and timing of weed control (Caussanel et al.*, 1990).* Spring wheat (cv. Bastion) was sown on 9 March 1985 at a density of 350 plants m^{-2} with spring oat (cv. Selma), spring oilseed rape (cv. Brutor) and spring vetch (cv. Sylphie) used as ‘weeds’ in alternate rows 15 cm apart. Weed densities were 0, 20, 40 plants m^{-2}. Oats were suppressed at different periods by diclofop-methyl at 1080 g a.i. ha^{-1}) and oilseed rape and vetch by ioxynil plus mecoprop (Actril M, 150 + 375 g a.i. L^{-1}, Sedagri) at 375 + 938 g a.i. ha^{-1} or 2,4-D (U46D, 480 g a.i. L^{-1}, BASF) at 480 g a.i. ha^{-1}. The broad-leaved weed control treatments were applied using a propane-powered hand-held sprayer in 500 L water ha^{-1} at 250 kPa. Four durations of weed competition were compared for each wheat:weed type of infestation: (1) sowing –

beginning of tillering; (2) sowing – mid-tillering; (3) sowing – beginning of stem elongation; and (4) sowing – maturity.

Climatic conditions

Contrasting spring seasons were encountered: 1984 was relatively dry, 1985 was cold after sowing and 1986 was very wet, which delayed the sowing until April. The winter periods in 1985–86 and 1986–87 were extremely cold. Previous crops were oats in 1984, wheat in 1985, and peas (*Pisum sativum* L.) in 1986 and 1987.

Model input data

Major input data (Fig. 1) include:

1. daily weather data – global radiation, maximum and minimum air temperature, precipitation, air relative humidity and wind speed;
2. soil data (by layer) – texture, bulk density, organic and mineral nitrogen, percentage of rough particles, water content at field capacity and wilting point, and initial water profile;
3. crop management and weed emergence – crop and weed density, planting and harvest dates, N fertilizer (rates and dates) and spraying dates;
4. crop parameters – a standard file, calibrated in Toulouse for major crops (Cabelguenne *et al.*, 1990) was used to initiate the calibration.

To account for uncertainties in initial soil conditions, we manipulated soil depth and mineral N each year to match simulated yields with measured yields in weed-free plots (D0). Soil depths were within the range reported on maps. Initial mineral N values were based on previous crops and soil depths. Thus, we assumed 0.75 m depth and 90 kg N ha^{-1} in 1984 after barley. In 1985, we assumed 0.60 m depth and 40 kg N ha^{-1} after wheat. In 1986 and 1987, we assumed 1.40 m depth and 100 kg N ha^{-1} after pea. After obtaining reasonable simulations of weed-free plot yields, we tested the simulation of yield depression by weeds.

Model output data

Output data available at a daily step (Fig. 1) concern biomass, LAI, N uptake and root depth. The model also predicts yield for both weed and crop. Soil water and nitrogen are simulated throughout the profile. Total intercepted light, cumulative water and nitrogen stress from emergence to harvest are used as indicators for crop diagnosis. Only biomass and grain yield of both plants were evaluated in this study.

Root mean square error (RMSE) was used to evaluate the performance of the model in the different wheat:weed combinations. For the evaluation of yield, in an experiment with n observations, RMSE was defined by the following identity:

$$\mathrm{RMSE} = \sqrt{1/n \times \sum_{j=1}^{n}((\mathrm{Yield}_{\mathrm{mes}} - \mathrm{Yield}_{\mathrm{sim}})^2}$$

Determination of weed and crop parameters

Several parameters are either the same for all plant species or the same for all C_3 species and for all C_4 species. Others are specific for a crop or a weed. Crop parameters were kept identical for both spring cereals, except plant height and duration of green leaf area, both slightly greater for oats. The main parameters were derived from previous studies on EPIC and ALMANAC (Cabelguenne *et al.*, 1990; Kiniry *et al.*, 1992) and summarized in Table 1.

Spring cereals

As no major limiting factor was observed in 1986, this growing season was used to calibrate the crop and weed response (Experiment 1). The soil was deep enough and the nitrogen sufficiently high to permit a good expression of potential yield by spring wheat (85 dt ha^{-1}). The emergence conditions were satisfactory with 345 wheat plants m^{-2} and a rapid emergence. First, the calibration of wheat parameters was attempted on D0 plots and the initial set of parameters adopted for oats and then tested on the range of densities. The simulation of wheat and oat grain and shoot biomass at maturity was satisfactory on the experimented range of oats density measured at tillering (Fig. 2a and b). However, at very high density (D5), the wheat yield was overestimated, in relation with a slight underestimation of oat yield. Accumulation of wheat and oat biomass was simulated from stem

Table 1. Input parameter values for different crop species and cultivars

	Spring oats	Winter oats	Spring wheat	Winter wheat				Spring oilseed rape	Spring vetch
	Selma	Fringante	Bastion	Capitole	Castan	Fidel	Talent	Brutor	Sylphie
RUE (g MJ^{-1} m^2)	3.0	3.0	3.0	3.0	3.0	3.0	3.0	2.5	2.5
HI	0.45	0.45	0.45	0.42	0.44	0.45	0.45	0.25	0.55
LAI_{mx0}	7.5	7.5	7.5	7.5	7.5	7.5	8.0	5.0	6.0
LAP1	15.05	15.05	15.05	15.04	15.07	15.06	15.05	15.02	20.05
LAP2	50.95	50.95	50.95	50.99	50.99	50.99	50.99	50.95	60.99
XDLAI	0.80	0.80	0.60	0.60	0.60	0.60	0.60	0.65	0.60
PPO1	125.60	125.60	125.60	125.60	125.60	125.60	125.60	10.30	10.40
PPO2	250.95	250.95	250.95	250.95	250.95	250.95	250.95	20.70	20.85
H_{mx}(m)	1.2	1.2	1.0	1.0	0.9	1.1	0.8	1.3	0.8
k	0.70	0.70	0.65	0.60	0.60	0.70	0.65	0.80	0.65
RD_{mx} (m)	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.7	1.2
FRO1	5.001	5.001	5.001	15.001	5.001	10.001	10.001	5.010	5.010
FRO2	25.010	25.010	15.010	25.010	15.010	20.010	20.010	15.100	15.500

RUE, radiation use efficiency; HI, harvest index (for grain); LAI_{mx0}, maximum leaf area index in a dense unstressed crop; LAP1, 2, parameters for LAI curve (15.05 means that 5% of the maximum LAI is reached at 15% of the cycle); XDLAI, fraction of the cycle when leaf area index starts declining; PP01, 2, plant population parameters (125.60 means that 60% of the maximum LAI is reached for 125 plants m^{-2}); H_{mx}, maximum plant height; k, extinction coefficient; RD_{max}, maximum root depth; FRO1, 2, parameters for frost sensitivity (5.001 means that 0.1% of LAI and biomass are suppressed when the air temperature reaches −5 °C).

elongation to maturity with reasonable accuracy (Fig. 3a and b). Oat biomass was underestimated by the model throughout the growing season for the highest weed density.

Winter cereals

Genotype characteristics were determined using breeding catalogues and adjusted in 1986 on D0 plots (Experiment 2) as discussed earlier (Table 1). The set of genotypic parameters was comprehensive enough to describe the response of cultivars competing with winter oats at two moderate densities (five and 10 plants m^{-2}) (Fig. 4a–d). The overall value of RMSE was 0.19 t ha^{-1} after calibration of D0 plots.

Model evaluation

Crop and weed production as related to weed density

Grain yield. Moderate water stress occurred in 1984 that reduced the weed-free measured yield of wheat to 75 dt ha^{-1}. Emergence was not as rapid as in 1986 but sufficient for potential yield (339 plants m^{-2} on D0 plots). Using the 1986 calibration, simulated yields were similar to measured yields for both species throughout the range of oats densities (Fig. 5a).

The year 1985 was cold after sowing, which led to a delayed and staggered emergence of wheat (257 plants m^{-2}). In addition, soil nitrogen is generally low after a wheat crop (N immobilization by straw) and stem diseases may have appeared. As a consequence, the observed grain yield was only 45 dt ha^{-1}. In these conditions, the model simulated wheat more reasonably than oats for all densities (Fig. 5b). Oat grain yield was consistently underestimated by the model. The pattern of emergence could have been responsible for these underestimations.

Shoot biomass. Simulated aerial biomass showed reasonable trends in response to increased oat densities, but the errors were generally greater than for grain yield (Fig. 5c and d). The model frequently underestimated the growth of both oats and wheat, in particular at high densities. The simulated and measured harvest index were compared for wheat (Fig. 6). The model slightly overestimated the harvest index, mainly for high densities of oats, which compensated for the underestimation of the wheat above-ground biomass (Figs 2b, 5c and d).

Crop production as related to crop or weed competitive ability

Experiment 2: Winter wheat genotypes x spring oats interaction. The effect of spring oats on winter wheat yield was simulated in 1987 for four wheat genotypes (Fig. 7a–d). In the reported experiment, no significant effect on wheat yield was shown by sowing the spring oats at the three-leaf

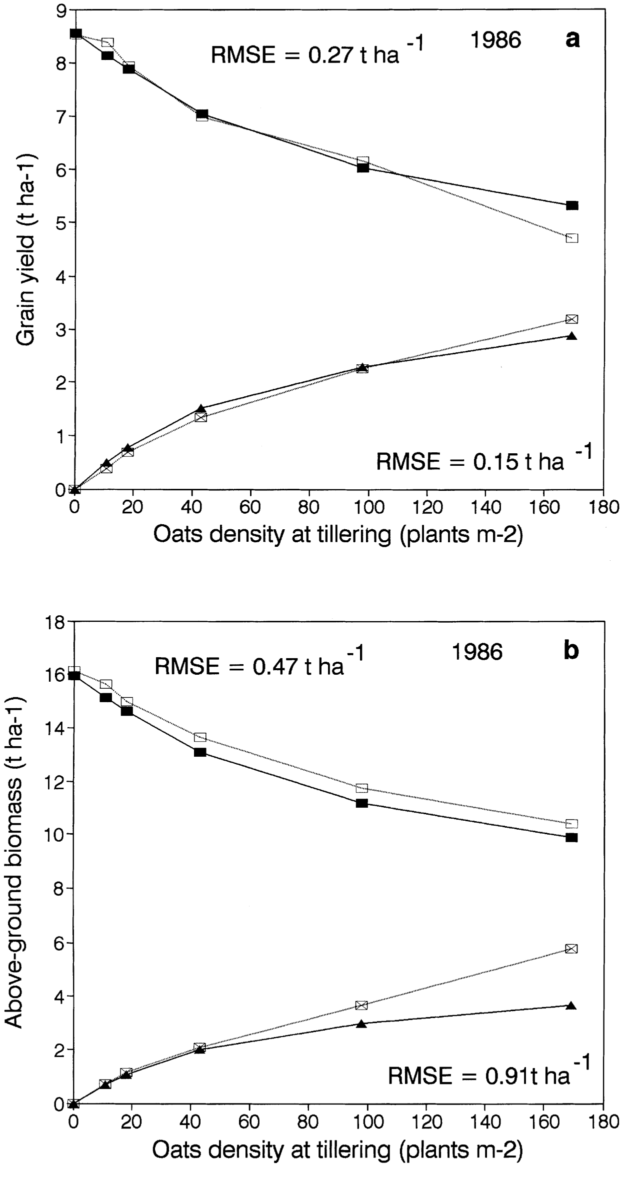


Fig. 2. Simulated and observed responses of spring wheat and spring oats production to increasing densities of oats measured at the start of wheat tillering (1986). (a) Grain yield (15% moisture) and (b) Above-ground biomass. -■- Wheat (sim); -⊟-, wheat (obs); -▲-, oats (sim); -⊠-, oats (obs).

stage of wheat at a range density of 0–16 oat plants m^{-2}. The variability among replicates within oat density treatments was responsible for the absence of measured effect. The simulation indicated a slight effect of oat density over the experimental range, which supports the statistical conclusions. Low values of RMSE (0.09–0.17 t ha^{-1}) were observed. The effect of the weed emergence date was correctly described by the model because more effect on yield was simulated for autumn-sown oats in 1986 (Fig. 4a–d).

Experiment 3: Spring wheat (spring oat:oilseed rape:vetch interaction.) The effects of three different weeds on spring wheat grain yield were simulated in 1985 for two weed densities (20 and 40 plants m^{-2}). The model reproduced reasonably the observed competitiveness ranking: oats

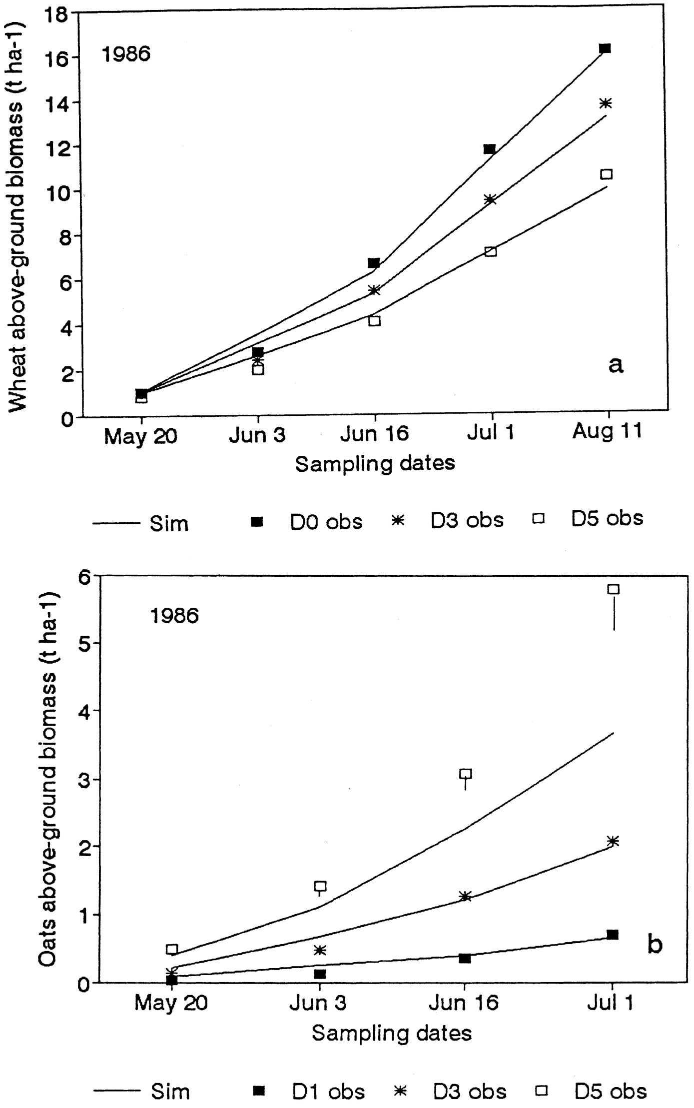


Fig. 3. Simulated and observed responses of wheat and oats above-ground biomass throughout the 1986 growing season. D0 (wheat alone); D3 (40 plants m^{-2}); D5 (160 plants m^{-2}). (a) Wheat biomass and (b) Oat biomass (at D1: 10 plants m^{-2}).

> oilseed rape > vetch (Fig. 8). The effect of the two weed densities was also correctly predicted.

Crop production as related to weed suppression date

Experiment 1: Spring wheat × spring oat interaction. In the reported experiment, oats were completely suppressed 5 days after an application of diclofop-methyl at wheat tillering. Under this assumption for simulation, the response of wheat grain yield to different densities of oats at tillering was correctly predicted with ALMANAC (Fig. 9). Errors in simulations were slightly greater at high densities. The ability of the model to reasonably describe the wheat recovery after oat control was suggested by this comparison.

Experiment 3: Spring wheat × spring oilseed rape interaction. The crop recovery, after the

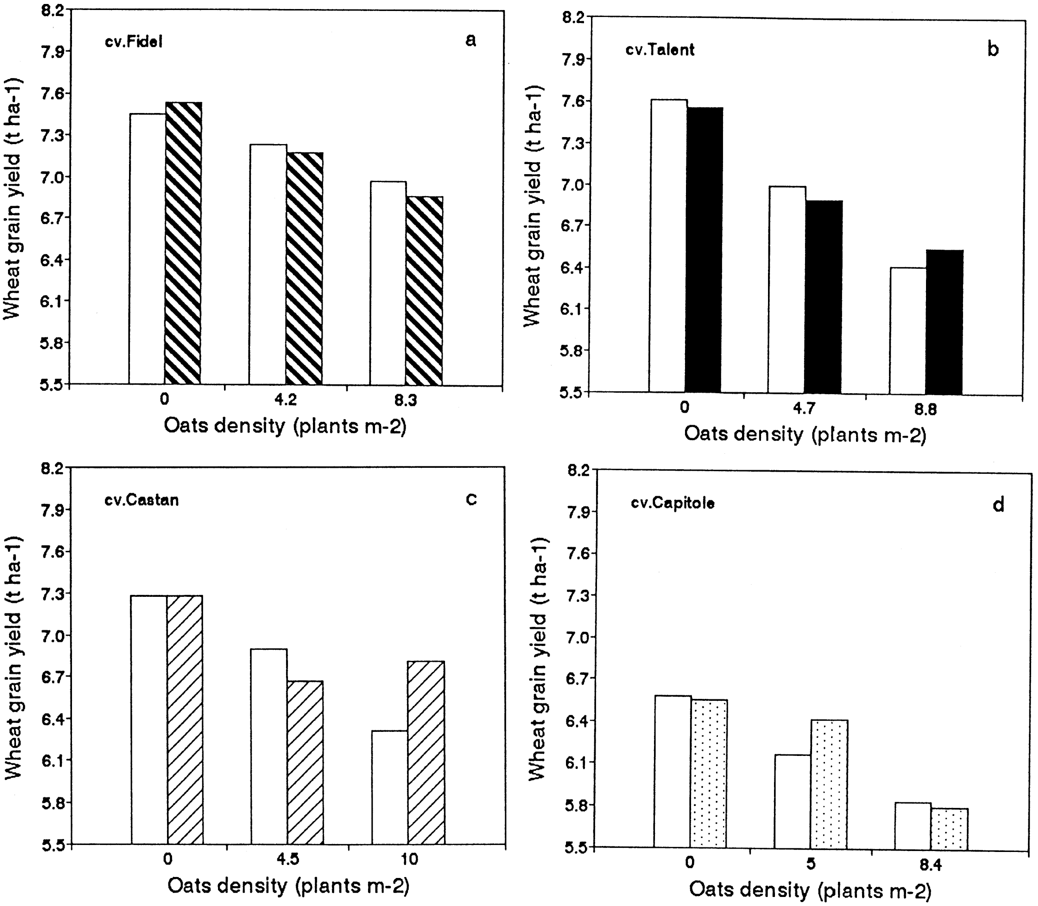


Fig. 4. Simulated and observed grain yield responses of 4 genotypes of winter wheat competing with 2 densities of winter oats (1986). (a) cv. Fidel, (b) cv.Talent, (c) cv. Castan and (d) cv.Capitole. □, Simulated; ▧, Fidel (obs); ■, Talent (obs); ▨, Castan (obs); ▩, Capitole (obs).

herbicide applications that suppressed oilseed rape at three different dates in the season, was reasonably simulated for the ioxynil + mecoprop mixture (Fig. 10); the model overestimated the wheat recovery for the later-applied 2,4-D treatment. Oilseed rape suppression was probably less rapid and may have been incomplete after this late 2,4-D application.

Sensitivity analysis

The yield response of spring wheat (300 plants m^{-2}) competing with spring oats (30 plants m^{-2}) to systematic 10% variations (±) of the nine main crop and weed parameters was analysed using 1986 climatic data (similar to Experiment 1). RUE and HI, directly related to biomass accumulation or grain yield, were known to be the most sensitive crop parameters in EPIC (Debaeke *et al.*, 1996). The variation in a wheat parameter generally had a greater effect on wheat yield than variation in the corresponding oats parameter (Fig. 11a and b). LAP2, which governs the shape of the LAI during stem elongation, was the most sensitive parameter for both wheat and oats. Variation in PHU, which indicates the duration of the weed cycle, had a strong effect on wheat yield, probably because the time-course of leaf area was parameterized as a fraction of the cycle. The increase in LAI_{mx}, LAP1 and LAP2 (rate of LAI establishment), H_{mx} (crop height), PPO2 (LAI per plant), and k (light interception) increased the wheat yield from 2% to 6%.

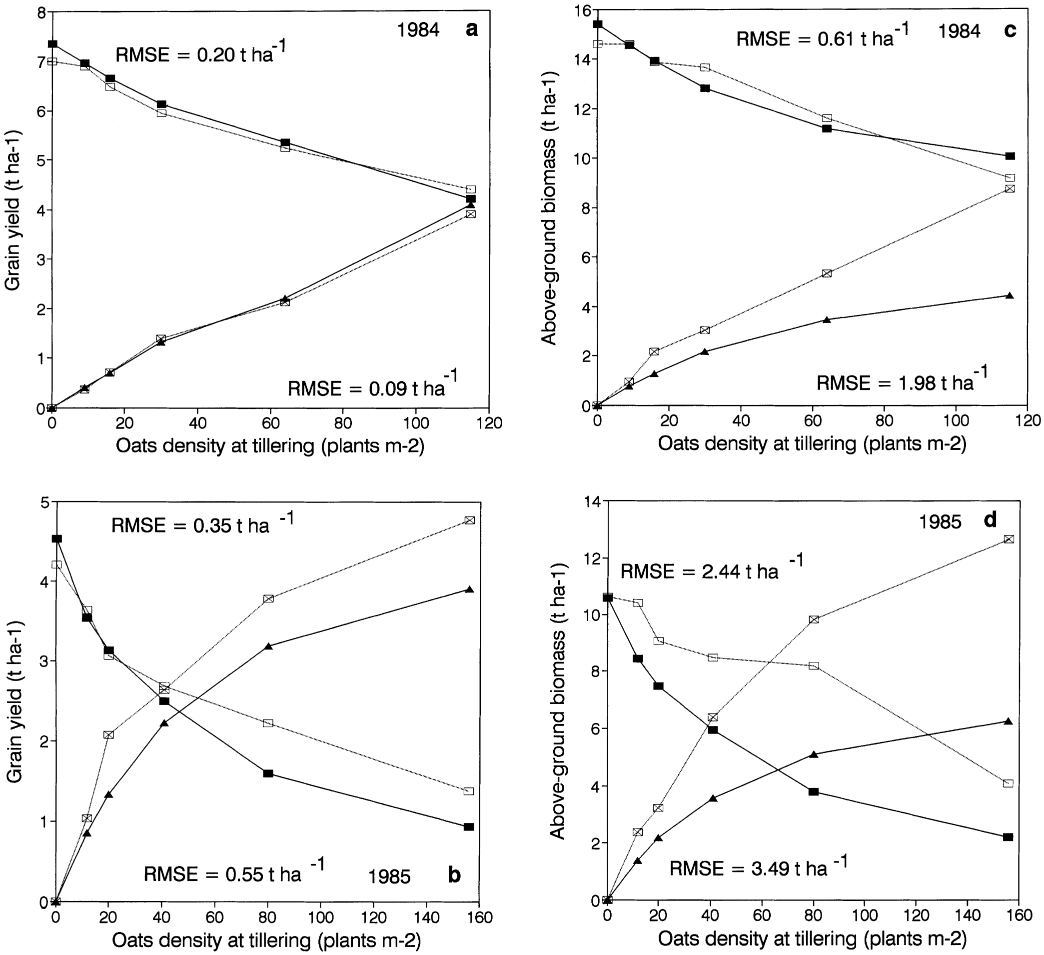
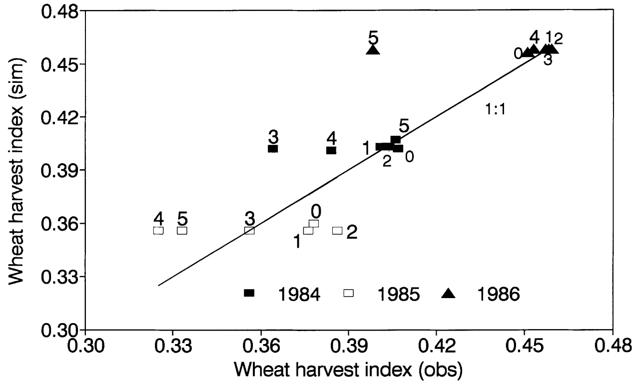


Fig. 5. Simulated and observed responses of spring wheat and spring oats production to increasing densities of oats. Grain yield: (a) 1984, (b) 1985. Above-ground biomass: (c) 1984, (d) 1985. -■-, Wheat (sim); -□-,Wheat (obs); -▲-, Oats (sim); -⊠-, Oats (obs).



n indicates the class of oats density

Fig. 6. Comparison of simulated and observed harvest index for spring wheat (1984–86).

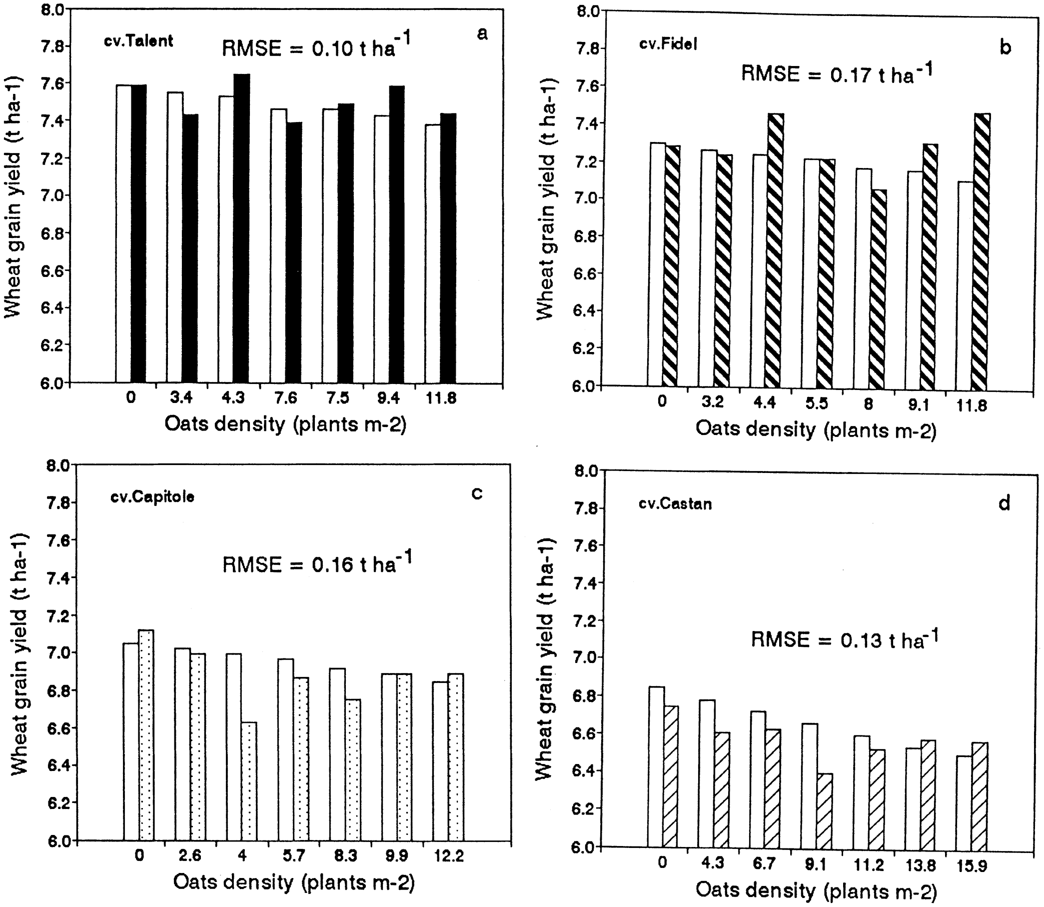


Fig. 7. Simulated and observed grain yield responses of 4 genotypes of winter wheat competing with 6 densities of spring oats (1987). (a) cv. Talent, (b) cv. Fidel, (c) cv. Capitole and (d) cv. Castan. □, Simulated; ■, Talent (obs); ▧, Fidel (obs); ▒, Capitole (obs); ▨, Castan (obs).

Discussion

The ALMANAC model was developed to express in terms of crop yield the interplant competition between a crop and one or more weeds (Kiniry *et al.,* 1992). It uses a limited number of sensitive parameters, and particularly the crop parameter table contained in the EPIC plant growth model, which was widely evaluated for crop yield prediction (Williams *et al.*, 1989; Cabelguenne *et al.*, 1990). The aim of the related work was to test a wide range of wheat:weed interactions in simulating the yield and above-ground biomass of each plant in association. As weed parameters are not yet determined in the literature, crop plants, such as oats, oilseed rape and vetch, were used as 'standard weeds' to mimic weed competition. The simulation of crop yield by the ALMANAC model gave a reasonable representation of the competition issue in most of the experiments reported, with a sufficient sensitivity to weed density, in relation to various management strategies, including sowing date, wheat genotype choice and herbicide application. Some results are discussed in relation to their importance in prediction when making application decisions.

The simulations of oat:wheat combinations showed that the yields of the wheat crop were reasonably predicted, with a root mean square error from 1.0 to 3.5 dt ha^{-1}, depending on years and experiments. Errors on wheat yield were greater in the lowest yielding year (1985) and for the greatest oat densities (D5). Similar conclu-

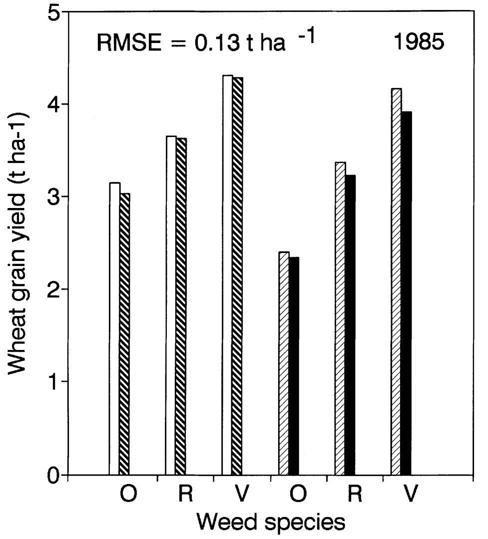


Fig. 8. Simulated and observed responses of spring wheat grain yield at 2 densities (20 and 40 plants m^{-2}) of spring oats, spring oilseed rape and spring vetch (1985). Weed density; □, 20 plants m^{-2} (sim); ▧, 20 plants m^{-2} (obs); ▨, 40 plants m^{-2} (sim); ■, 40 plants m^{-2} (obs). O, oats; R, rape; V, vetch.

sions were drawn for oats. One reason could be the choice of oat density observed at wheat tillering to estimate the value of LAI_{mx} in the

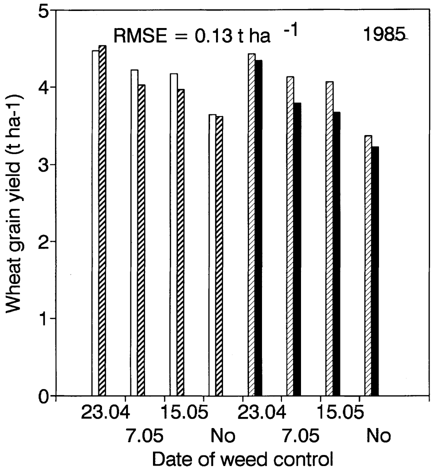


Fig. 10. Simulated and observed responses of spring wheat grain yield to different densities of seed rape (20 and 40 plants m^{-2}) after control with ioxynil + mecoprop and 2,4-D (1985). Rape density: □, 20 plants m^{-2} (sim); ▧, 20 plants m^{-2} (obs); ▨, 40 plants m^{-2} (sim); ■, 40 plants m^{-2} (obs).

model. Depending on years and initial densities, the mortality of weed populations from emergence to wheat tillering varied from 6% to 31%, with the highest rates corresponding to the highest oat densities (Kafiz, 1989). The under-

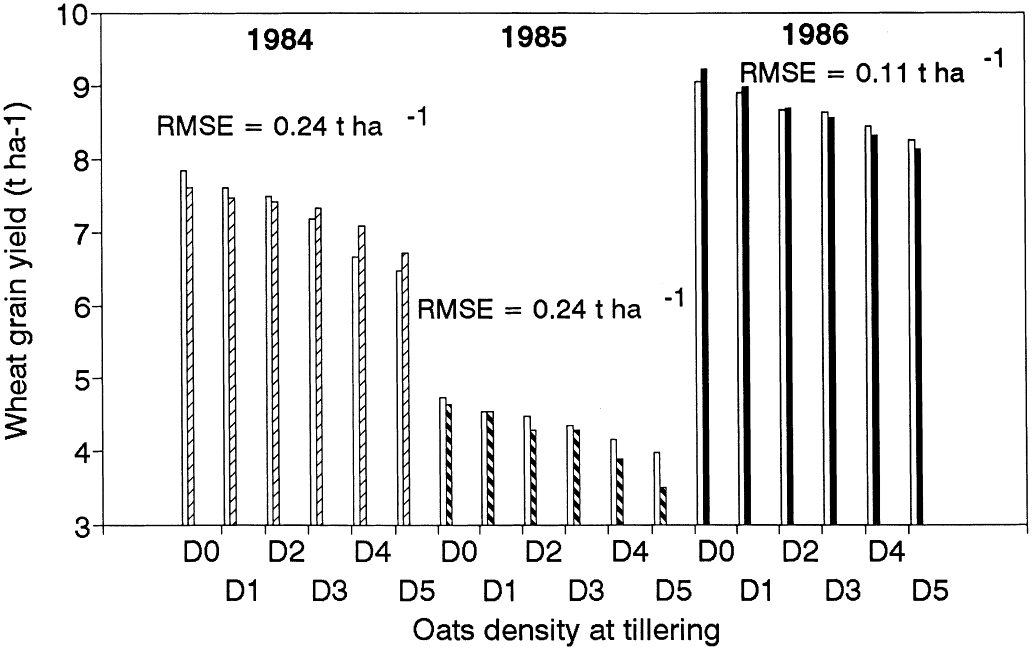


Fig. 9. Simulated and observed responses of spring wheat grain yield to different densities of oats after control with diclofop-methyl applied at tillering time (1984–86). □, Simulated; ▨, observed 1984; ▧, observed 1985; ■, observed 1986.

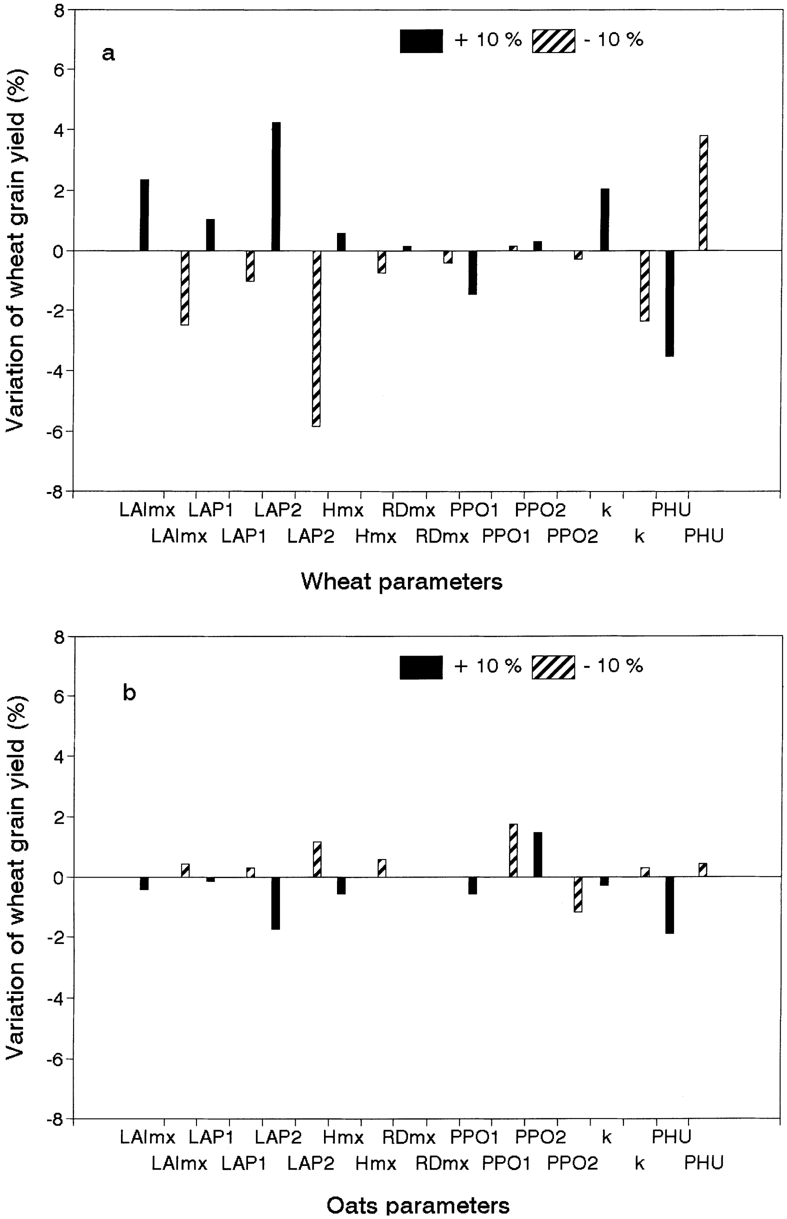


Fig. 11. Response of wheat grain yield to 10% variations of the main crop parameters of ALMANAC. (a) Wheat parameters and (b) oat parameters.

estimation of effective oat populations at high weed densities could explain the difference between observed and measured yield values for both wheat and oats (Figs 2a and 5b). Furthermore, in 1985, oat density increased continuously between wheat emergence and tillering stage because of low temperatures, which delayed and staggered the emergence process. In these conditions, the definition of a single emergence date was not acceptable because it led to greater errors using ALMANAC. Although the simulation of the impact of high weed densities on crop yield loss is unsatisfactory, this is probably not so important in practice because weed control is generally justified in such situations. The model's ability to simulate realistically the impact of low or moderate weed densities is more useful for post-emergence spraying decisions.

The differences in sensitivity of four crops to the presence of a standard weed (oats) were shown to be dependent on the year (Lutman *et al.*, 1994). The experiments reported here confirm these results for the wheat:oat competition. The competitive ability of oilseed rape and vetch in a spring wheat crop was also correctly predicted, as was the density effect.

With a small number of genetic parameters (rate of ground cover, final crop height, light interception as related to leaf angle, growth duration) ALMANAC described the effects of different wheat genotypes on weed suppression. Verschwele & Niemann (1993) observed good correlations between crop cover, leaf area, and leaf angle and the ability of the wheat crop to suppress weeds. Christensen (1995) showed that a model comprising parameters of maximum canopy height, maximum light interception and temporal displacement of light interception provided a good description of the weed suppression ability of spring barley varieties. As these variables are simulated by the model, ALMANAC could guide plant breeders in selecting new genotypes for low-input management.

With the hypothesis of a complete suppression of the weed some days after an application of herbicide, the recovery of wheat after early weed suppression was reasonably simulated using ALMANAC. When the herbicide application was delayed in time, the model overestimated the wheat recovery partly because the herbicide efficacy was not complete on fully developed weeds. ALMANAC could contribute to a better definition of the critical period of weed control (the period of weed-free maintenance and the period before weed removal) (Nieto *et al.*, 1968), provided that the herbicide efficacy is correctly represented.

Several hypotheses used in ALMANAC could restrict its scope of application. Assuming a regular distribution of weeds within the crop inter-row, the model ignores the patchiness often present in natural infestations or the presence of weeds on the row after mechanical weeding. Results of computer simulations have shown that spatial distribution can have a substantial effect on calculated thresholds for weed control (Thornton *et al.*, 1990). Likewise, in previous simulations, we simulated a single planting date of the weeds, causing a single flush of simulated weed emergence. This was acceptable because the weed seeds in our experiments were sown at the same depth and were not dormant. But in natural weed populations, a wide distribution of emergence dates is generally observed, because of the variability of seed depth and seed dormancy. Multispecific competition (or the effect of successive flushes of weed emergence) could be simulated by the model using the same routine as for bispecific mixtures, but this procedure has not been yet evaluated.

In ALMANAC, when plant-available soil moisture is less than the potential evapo-transpiration, the first-planted species is able to use the available water in its current rooting zone. Then the second-planted species (in the input file) is able to use the water left in its current rooting zone. A similar situation occurs for nitrogen and phosphorus. Because it is a daily time step model, the planting order problem should only affect the initiation of stress by, at most, one day. To reduce the problem of order in resource uptake, the mean of two different simulations was taken while alternating the planting order. However, to improve the model the hourly step might be chosen for more realistic calculations.

The model was developed to simulate weeds over a wide range of environmental conditions and to account for differences in type of leaf canopy, plant height, rooting depth and population density. Its dynamic aspect permits a survey of factors influencing competition, such as soil resources, climatic sequence, fertilizer amount or date of spraying, in relation with crop and weed stands (genotype, date of emergence, density). However, more work is required to thoroughly evaluate the model in different conditions of water and nitrogen availability.

A major application of such a model, once validated, could be the definition of biological damage thresholds for weed control in selected weed:crop associations to motivate the spraying decision in relation to the overall crop management (Debaeke, 1995). As these thresholds are defined by statistical differences of yield with weed-free plots, a further determination of the error associated with the model prediction is necessary. By its simulation of weed seed production at a crop rotation level, ALMANAC could be connected to a seedbank population model to simulate long-term yields trends.

Acknowledgements

The authors gratefully thank M. Bourlier for his technical assistance and the staff of the Epoisses Experimental Station for their help in experimentation. This simulation work was supported by INRA grants through a concerted action (AIP) on 'Input Management in Agronomic Crops'.

References

Ampong-Nyarko K & De Satta SK (1993) Effects of nitrogen application on growth nitrogen use efficiency and rice–weed interaction. *Weed Research* **33,** 269–6.

Assemat L (1990) Simulation de la nuisibilité des mauvaises herbes: interactions date de levée – densité – climat. *Annales 14ème Conférence COLUMA, ANPP*, Versailles, 227–34.

Ball DA & Shaffer MJ (1993) Simulating resource competition in multispecies agricultural plant communities. *Weed Research* **33,** 299–310.

Cabelguenne M, Jones CA, Marty JR, Dyke PT & Williams JR (1990) Calibration and validation of EPIC for crop rotations in southern France. *Agricultural Systems* **33,** 153–71.

Caldwell RM (1993) Simulation models for intercropping systems. In: *Ecophysiology of Tropical Intercropping* (eds H Sinoquet & P Cruz), pp. 353–68. Science update, INRA, Paris.

Caussanel JP (1989) Nuisibilité et seuils de nuisibilité des mauvaises herbes dans une culture annuelle: situation de concurrence bispécifique. *Agronomie* **9,** 219–40.

Caussanel JP, Kafiz B & Carteron A (1993) Yield response of spring wheat to increasing densities of spring oats and various forms of postemergence weed control. *Agronomie* **13,** 815–27.

Caussanel JP, Kafiz B, Carteron A & Schiex J (1990) Influence de la densité d'une avoine, d'un colza ou d'une vesce sur la perte de rendement d'un blé de printemps en relation avec la date de désherbage chimique ou la structure spatiale du peuplement. *Proceedings 7th EWRS Symposium on Integrated Weed Management in Cereals,* Helsinki, 255–62.

Christensen S (1995) Weed suppression ability of spring barley varieties. *Weed Research* **35,** 241–7.

Cousens R (1985) A simple model relating yield loss to weed density. *Annals of Applied Biology* **107,** 239–52.

Cousens R, Brain P, O'Donovan JT & O'Sullivan A (1987) The use of biologically realistic equations to describe the effects of weed density and relative time of emergence on crop yield. *Weed Science* **35,** 720–5.

Debaeke P (1995) Apport d'un modèle de simulation de la concurrence au raisonnement du désherbage des cultures. *Annales 16ème Conférence du Columa, ANPP*, Reims (France), 355–62.

Debaeke P, Kiniry JR, Caussanel JP & Kafiz B (1993) An integrated model of crop-weed interaction: application to wheat-oats mixtures. *Proceedings 8th EWRS Symposium on Quantitative Approaches in Weed and Herbicide Research and their Practical Application,* Braunschweig, 5–15.

Debaeke P, Cabelguenne M, Casals ML & Puech J (1996) Elaboration du rendement du blé d'hiver en conditions de déficit hydrique. II. Mise au point et test d'un modèle de simulation de la culture de blé d'hiver en conditions d'alimentation hydrique et azotée variées: EPICPHASE-Blé. *Agronomie* **16,** 25–46.

Dunan CM, Moore III FD & Westra P (1994) A plant process–economic model for wild oats management decisions in irrigated barley. *Agricultural Systems* **45,** 355–68.

Flenet F, Kiniry JR, Board JE, Westgate ME & Reicosky DC (1996) Row spacing effects on light extinction coefficients of corn, sorghum, soybean and sunflower. *Agronomy Journal* **88,** 185–90.

Geves (1992) *Bulletin des Variétés. Céréales.* GEVES, Guyancourt (France).

Gosse G, Varlet-Grancher C, Bonhomme R, Chartier R, Allirand M & Lemaire G (1986) Production maximale de matière sèche et rayonnement solaire intercepté par un couvert végétal. *Agronomie* **6,** 47–56.

Graf B, Gutierrez AP, Rakotobe O, Zahner P & Delucchi V (1990) A simulation model for the dynamics of rice growth and development. II. The competition with weeds for nitrogen and light. *Agricultural Systems* **32,** 367–92.

Kafiz B (1989) *Contribution à l'étude des seuils biologiques de nuisibilité de l'avoine (*Avena sativa *L.) dans une céréale de printemps (*Triticum vulgare *L.) en relation avec le désherbage chimique et à l'étude de l'interaction entre le diclofopméthyl et le 2, 4-D.* Thèse, Université de Nancy I, 317 pp.

Kiniry JR, Jones CA, O'Toole JC, Blanchet R, Cabelguenne M & Spanel DA (1989) Radiation use efficiency in biomass accumulation prior to grain filling for five grain crop species. *Field Crops Research* **20,** 51–64.

Kiniry JR, Williams JR, Gassman PW & Debaeke P (1992) A general, process-orientated model for two competing plant species. *Transactions of the ASAE* **35,** 801–10.

Kropff MJ (1988) Modelling the effects of weeds on crop production. *Weed Research* **28,** 465–71.

Kropff MJ & Spitters CJT (1991) A simple model of crop loss by weed competition from early observations on relative leaf area of the weeds. *Weed Research* **31,** 97–105.

Kropff MJ & Spitters CJT (1992) An eco-physiological model for interspecific competition, applied to the influence of *Chenopodium album* L. on sugar beet. I. Model description and parametrization. *Weed Research* **32,** 437–50.

Kropff MJ, Lotz LAP & Weaver SE (1993) Practical applications. In: *Modelling Crop–Weed Interactions* (eds MK Kropff & HH van Laar). pp. 149–67. CAB International, Wallingford.

Lutman PJJW Dixon FL & Risiott R (1994) The response of four spring-sown combinable arable crops to weed competition. *Weed Research* **34,** 137–46.

Mondragon G (1988) *Contribution à l'étude des seuils de nuisibilité biologique de quelques espèces d'avoine dans une culture de blé.* Thèse Docteur-Ingénieur, ENSA Rennes, 137 pp. + annexes.

Mondragon G, Caussanel JP, Aujas C, Carteron A & Schiex J (1989) Sensibilité variétale d'un blé d'hiver à la concurrence d'une avoine adventice: influence sur le seuil biologique de nuisibilité. *Agronomie* **9,** 809–18.

Monsi M & Saeki T (1953) Uber den lichtfaktor in den pflanzengesellschaften und seine bedeutung für die stoffproduktion. *Japan Journal of Botany* **14,** 22–52.

Moss SR (1985) The influence of crop variety and seed rate on *Alopecurus myosuroides* competition in winter cereals. *Proceedings British Crop Protection Conference – Weeds, Brighton*, 701–8.

Nieto JH, Brando MA & Gonzalez JT (1968) Critical periods of the crop growth cycle for competition from weeds. *PANS (C)* **14,** 159–66.

Spitters CJT & Aerts R (1983) Simulation of competition for light and water in crop-weed associations. *Aspects of Applied Biology* **4,** 467–83.

Thornton PK, Fawcett RH, Dent JB & Perkins TJ (1990) Spatial weed distribution and economic thresholds for weed control. *Crop Protection* **9,** 337–42.

Verschwele A & Niemann P (1993) Indirect weed control by selection of wheat cultivars. *Proceedings 4th International Conference I.F.O.A.M on Non Chemical Weed Control,* Dijon (France), 269–73.

Wilkerson GG, Jones JW, Coble HD & Gunsolus JL (1990) SOYWEED: a simulation model of soybean and common cocklebur growth and competition. *Agronomy Journal* **82,** 1003–10.

Williams JR, Jones CA, Kiniry JR & Spanel DA (1989) The EPIC crop growth model. *Transactions of the ASAE* **32,** 497–511.