ENDURE

European Network for Durable Exploitation of crop protection strategies

Project number: 031499

Network of Excellence
Sixth Framework Programme

Thematic Priority 5
FOOD and Quality and Safety

Deliverable DR2.3

Mechanistic Winter Wheat Simulation model (WHEATPEST) linking European production situations and injury profiles to crop losses

Due date of deliverable: M18

Actual submission date: M18

Start date of the project: January 1st, 2007 **Duration**: 48 months

Organisation name of lead contractor: INRA

Revision: V2

The published reference of this deliverable is:

Willocquet L, Aubertot JN, Lebard S, Robert C, Lannou C, Savary S. 2008 Simulating multiple pest damage in varying winter wheat production situations. Field Crops Research, 107 (1), p.12-28.

Project co-funded by the European Commission within the Sixth Framework Programme (2002-2006)	
Dissemination Level	
PP Restricted to other programme participants (including the Commission Services)	**X**

Table of contents

Summary

The production situation–injury profile paradigm can be used as a framework to assess the harmfulness of multiple-pest complexes in a changing agriculture. A mechanistic simulation model for wheat, WHEATPEST, was developed to incorporate drivers of (i) variable production situations and (ii) their related injury profiles. The model simulates the harmful effects of pathogens, pests, and weeds in a simple, open, generic manner. Simulation drivers were derived from published reports, in particular through a meta-analysis of highly detailed farmers' field surveys in the United Kingdom and the Netherlands. Preliminary analysis of the model's performances indicates that WHEATPEST conforms to available published reports in a range of production situations and injury profiles. While improvement on some components of the model are discussed, this work points at the need for the collection of cross-disciplinary, reasonably accurate, and standardised data at a system's level, and at the usefulness of modelling tools for basic research and policy.

1. Introduction

The agricultural area under wheat production in the EU is approximately 24 10^6 ha for a yield output of 121 x 10^6 t and national average yields (in 2005) ranging from 0.66 to 8.57 t ha^{-1} (FAO, 2007). Recently, needs and policies within the EU have emerged (e.g., Directorate-General for Agriculture, 2003), which strengthen the challenge of a sustainable wheat production that respects the environment, and lead to the need for novel plant and crop management research.

A production situation (PS) can be defined as the bio-physical and socio-economic environment under which a crop is grown (De Wit and Penning de Vries, 1982; Breman and De Wit, 1983; Rabbinge, 1993). PS can in turn be operationally determined on the basis of the combination of crop management practices occurring in a given field. This is because strategies and tactics for crop management are reflections of the physical (soil and climate), biological (genotypes, cultivars, and biotic environment), social and economical (e.g., markets) environment where a crop is grown (Savary et al., 2000a). An injury profile can be defined as the combination of injury levels caused by the multiple pests (pathogens, insects, weeds) that affect a crop during a growing cycle (Savary et al., 2000a, 2006a). The concepts of production situation and injury profile can be used for developing research for pest management that is suitable to specified agricultural contexts and production objectives. This is because production situations and injury profiles are strongly linked (Zadoks, 1984), as has been shown in a number of production systems, including rice-, coffee-,groundnut-, or wheat-based (Savary, 1987; Daamen et al., 1989; Savary et al., 2000a; Avelino et al., 2006). The case of the wheat-based system in Western Europe however remains to be quantitatively documented. This relationship between production situations and injury profiles has manifold implications: (i) it indicates that crop management practices are key to explaining the varying combination of pests that may affect a crop, (ii) it suggests that changes in crop management, and therefore in production situations, are likely to strongly influence the nature (composition, intensities) of injury profiles, and (iii) it opens ways for research where pest management, being integrated to crop management, might choose not to use unsustainable components, including heavy reliance on pesticides.

The production situation–injury profile paradigm also provides a framework for mechanistic simulation modelling, where relatively simple models may successfully be developed to address complex, multivariate issues, and explore management options (e.g., Johnson, 1992; Willocquet et al., 2004). Modelling yield losses due to multiple pests in wheat in Europe using such a framework should: (i) allow assessing the individual and combined effects of harmful organisms on performances of wheat in Europe, (ii) help detecting where priorities for management lie, (iii) provide a basis to develop new management strategies that are congruent to both varying production situations and evolving plant protection practices, and (iv) guide research for integrated crop and pest management strategies in a context of global (economic, policy, environmental) change (Herdt, 2006).

WHEATPEST, a simulation model for multiple-injury yield losses in wheat was developed in order to (1) use a generic structure that can potentially be adapted to a range of crops and pests, (2) be simple and transparent, (3) consider a wide range of wheat pests, and (4) incorporate in a simple way the effect of production situations on crop growth and yield. We report here (1) the overall structure of WHEATPEST and the hypotheses underlying the model structure, and (2) the performances of this model under a set of crop and injury drivers.

2. Materials and methods

2.1. Model structure

2.1.1. Model overall structure

WHEAPEST is a simple agrophysiological model which incorporates damage mechanisms (Rabbinge and Vereijken, 1980; Boote et al., 1983; Kropff et al., 1995), that is, which simulates the physiological effects of injury on crop growth and yield. The general structure of WHEATPEST is derived from RICEPEST, a model developed for rice yield loss analysis (Willocquet et al., 2000, 2002, 2004), and from a model developed by Johnson (1992) for potato multiple pests. The acronyms used in the model are listed in Table 1, and the model structure is shown in Fig. 1. The model incorporates harmful effects of weeds, aphids, viruses, brown rust, yellow rust, powdery mildew, Septoria tritici blotch, Septoria nodorum blotch, take-all, eyespot, sharp eyespot, Fusarium stem rot, and Fusarium head blight, on wheat crop physiology. Model inputs consist of weather data (daily temperature and radiation) and drivers for production situation and for injury profile. The driver for production situation (Willocquet et al., 2004) includes an array of driving functions that can vary over time (e.g., RUE), and parameters. Similarly, the driver for injury profile consists of an array of driving functions or parameters that represent the dynamics (or maximum levels) of individual injuries during a cropping season. These combined injury time-courses represent the injury profile a given crop stand has been exposed to during its cycle. Model outputs are series of dynamic variables over time: development stage (DVS; Table 1), dry biomass of organs, Leaf Area Index (LAI); and final yield.

2.1.2. Modelling attainable growth and yield

2.1.2.1. System characteristics and initial values of state

The system considered is 1 m^2 of winter wheat crop, with a simulation time step of 1 day. Simulation starts at 200 °8C day (base temperature of 0°C) from January 1, which corresponds to the start of spring growth (Spitters et al., 1989) and ends at crop maturity. Initial values of leaves, stems, roots, and ears biomass were set to 10, 6, 5, and 0 g m^{-2}, respectively.

2.1.2.2. Weather data

Weather data used as input are daily mean temperature (°C) and daily global radiation (MJ m^{-2}). For the purpose of this study, the weather data used as input are mean values over the 1951–1980 period at the Wageningen meteorological station (Spitters et al., 1989).Weather data were mainly used to generate reasonable inputs for the different scenarios addressed, which correspond to wheat crops grown in the Netherlands and in the United Kingdom over several years. Only one weather data set was used, so as to perform as simple as possible scenario analyses, and also because production situations are not site-, nor year-specific (e.g., Savary et al., 2006a).

2.1.2.3. Development stage

Development is expressed as development stage (DVS), a dimensionless variable having the value 0 at seedling emergence (DVS0), 1 at flowering (DVS1) and 2 at maturity (DVS2, Spitters et al., 1989). Development stage increases linearly with temperature, with two phases: prior and after anthesis. Thermal time between DVS0 and DVS1, and between DVS1 and DVS2, were set to 1600 °C day (Gate, 1995) and 910 °C day (Spitters et al., 1989), respectively, with a base temperature of 0 °C.

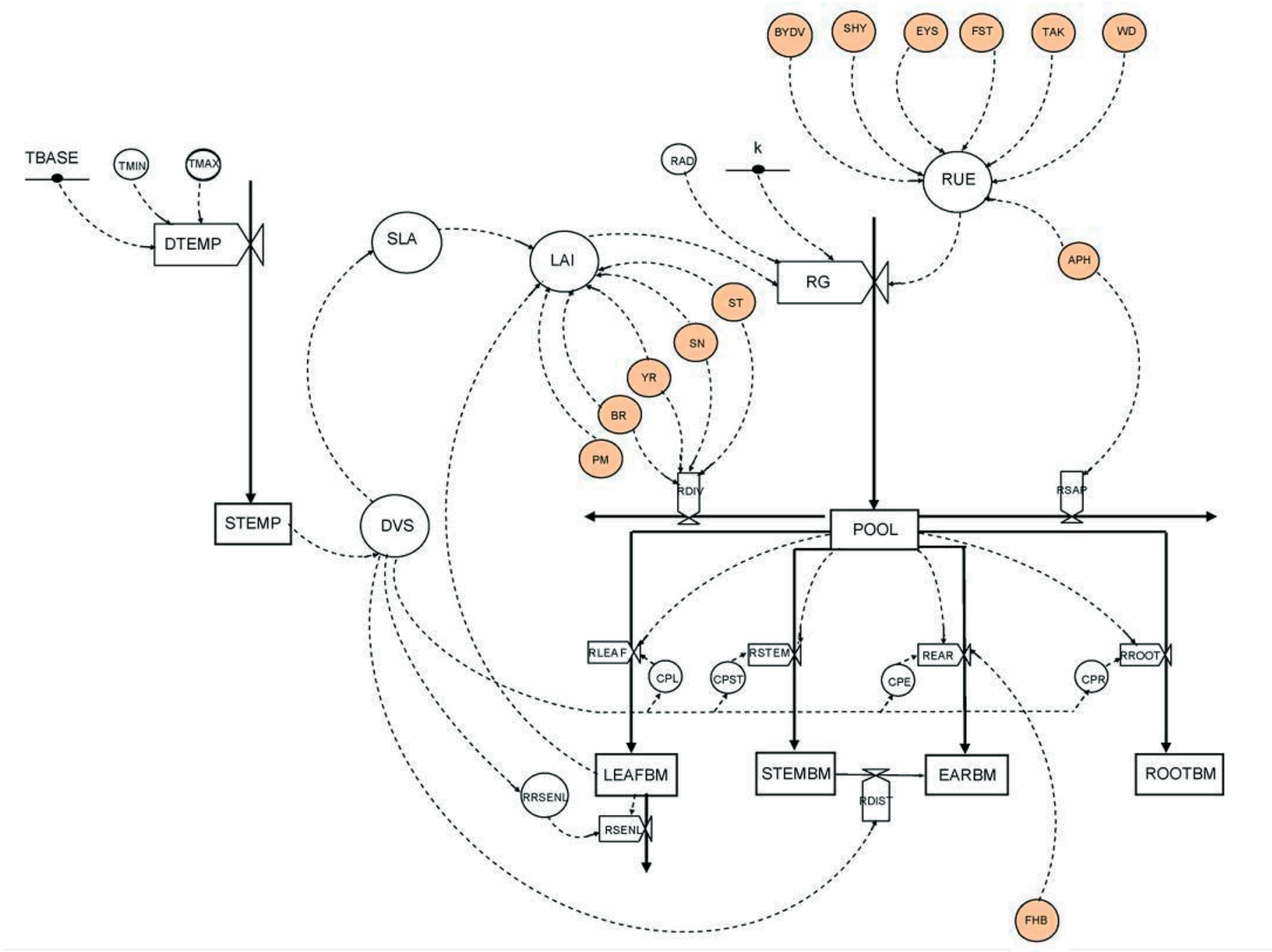

Fig. 1. Simplified representation of the structure of WHEATPEST. Squares represent state variables; arrows with plain lines represent flows of quantities; arrows with dotted lines represent flows of information; grey circles represent pest injuries; other circles represent intermediate variables; valves represent rate variables; plainines represent parameters (symbolism from Forrester, 1961); see Table 1 for definition of acronyms.

Table 1. Acronyms, units, and meanings of WHEATPEST main variables

Acronym	Unit	Meaning
		Crop model variables
CPE	–	Coefficient of assimilate partitioning towards leaves (=f(DVS))
CPR	–	Coefficient of assimilate partitioning towards roots (=f(DVS))
CPST	–	Coefficient of assimilate partitioning towards stems (=f(DVS))
DTEMP	°C	Daily increase in thermal time (base of 0 °C)
DVS	–	Development stage
EARBM	$g\ m^{-2}$	Dry biomass of ears
k	–	Coefficient of light extinction
LAI	$m^2 m^{-2}$	Leaf area index
LEAFBM	$g\ m^{-2}$	Dry biomass of green leaves
POOL	$g\ m^{-2}$	Pool of assimilates
RAD	$MJ\ m^{-2}\ day^{-1}$	Daily radiation
RDIST	$g\ m^{-2}\ day^{-1}$	Daily rate of starch translocated from stem to ears
RDIV	$g\ m^{-2}\ day^{-1}$	Daily rate of assimilate diversion to foliar pathogen lesions (=f(DVS))
REAR	$g\ m^{-2}\ day^{-1}$	Daily rate of increase in ear dry biomass
RFi	–	Reduction Factor for RUE caused by injury i
RG	$g\ m^{-2}\ day^{-1}$	Daily rate of increase in crop biomass
RLEAF	$g\ m^{-2}\ day^{-1}$	Daily rate of increase in leaf dry biomass
ROOTBM	$g\ m^{-2}$	Dry biomass of roots
RROOT	$g\ m^{-2}\ day^{-1}$	Daily rate of increase in root dry biomass
RRSENL	$m^{-2}\ day^{-1}$	Daily relative rate of leaf senescence (=f(DVS))
RSTEM	$g\ m^{-2}\ day^{-1}$	Daily rate of increase in stem dry biomass
RUE	$g\ MJ^{-1}$	Radiation Use Efficiency (=f(DVS))
SLA	$g^{-1}m^{-2}$	Specific Leaf Area (=f(DVS))
STEMBM	$g\ m^{-2}$	Dry biomass of stems (sheath+culm)
STEMP	°C day	Thermal time (base of 0 °C)
		Pests and injuries variables
APH	m^{-2}	Aphids density
BR	%Leaf surface	Brown rust severity
BYDV	%Plant nb	BYDV incidence
EYS	%Tiller nb	Eyespot incidence
FHB	%Kernel nb	Fusarium head blight incidence
FST	%Tiller nb	Fusarium stem rot incidence
PM	%Leaf surface	Powdery mildew severity
SHY	%Tiller nb	Sharp eyespot incidence
SN	%Leaf surface	Septoria nodorum blotch severity
ST	%Leaf surface	Septoria tritici blotch severity
TAK	%Root surface	Take-all severity
WD	$g\ m^{-2}$	Weed biomass
YR	%Leaf surface	Yellow rust severity

2.1.2.4. Biomass production

Biomass production through photosynthesis is proportional to the radiation intercepted by the canopy (Monteith, 1977), which can be derived from the LAI using Beer's law (Monsi and Saeki, 1953)

$$RG = RAD \times RUE \times (1 - e^{-k \times LAI}) \qquad (1)$$

where RG is the daily rate of growth, k is a dimensionless light extinction coefficient, and RAD is the daily global radiation. A conservative value for k of 0.65 was chosen (Monteith, 1969; Kiniry et al., 1989). For most crops grown under good conditions, RUE is approximately 1.4 g MJ^{-1} (Monteith, 1977). RUE may vary over the course of a crop cycle, and is generally lower during the reproductive than the vegetative phases (Sinclair andMuchow, 1999;Willocquet et al., 2002). RUE depends on cropping practices, and decreases when growth conditions are less favourable.

2.1.2.5. Leaf area

Leaf area is computed as

$$LAI = LEAFBM \times SLA \qquad (2)$$

where LEAFBM is the leaf dry biomass and SLA is the specific leaf area (Table 1). SLA is a function of DVS. Values used for rice are used here, following Meinke et al. (1998).

2.1.2.6. Partitioning of assimilates

Assimilates produced by photosynthesis are partitioned towards the different organs of the plant (roots, stems, leaves, ears). The fractions allocated to each organ depend on the development stage, and values from Spitters et al. (1989) were used (Fig. 2). The general form of the equation describing the increase in organ dry biomass, RO, at each time step is

$$RO = RG \times CPi \qquad (3)$$

where CPi is the coefficient of assimilate partitioning towards organs: i = R, L, ST, and E for roots, leaves, stems, and ears, respectively. For instance, the increase in leaf dry biomass is computed as

$$RLEAF = RG \times CPL \qquad (4)$$

Grain yield is set to 85% of ear biomass at harvest (Penning de Vries et al., 1989).

2.1.2.7. Carbohydrates remobilization

Carbohydrates are temporarily stored in stems during the vegetative phase, and are partly redistributed to ears during the reproduction phase (DVS > 1) (Penning de Vries et al., 1989). About 20%of wheat stem biomass at flowering consists of remobilizable carbohydrates (Groot, 1987).

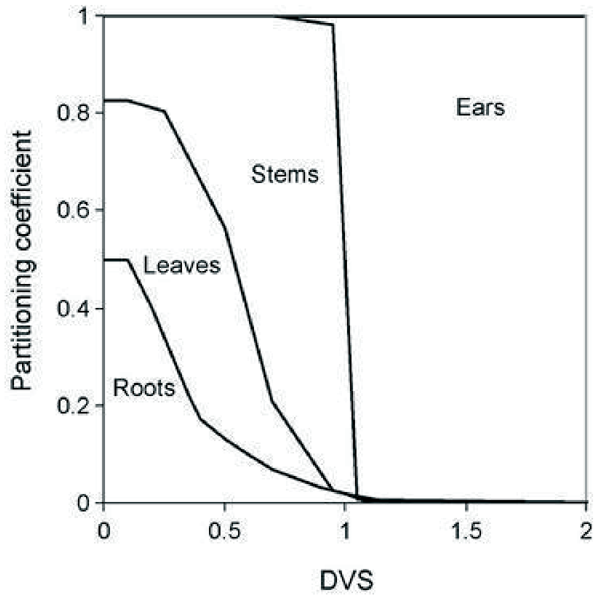

Fig. 2. Partitioning of assimilates to wheat organs as a function of development stage (DVS). Derived from Spitters et al. (1989).

2.1.2.8. Leaf senescence

Senescence refers to the loss of capacity to carry out essential physiological processes and to the loss of biomass. Leaf senescence occurs mainly after flowering (Penning de Vries et al., 1989). The relative rate of leaf senescence (RRSENL) was determined from Groot (1987) as an interpolation function with values of: 0, 0.01, 0.04, 0.1, and 0.1 day^{-1} for DVS = 1, 1.2, 1.6, 1.8, and 2, respectively.

2.1.3. Modelling damage mechanisms

2.1.3.1. Aphids

Sitobion avenae, an aphid often found in cereals in Europe, affects growth of winter wheat by two mechanisms: (1) uptake of phloem sap, and (2) decrease in net photosynthesis due to honeydew deposition (Rossing, 1991). The daily rate of assimilate sapping by aphids (RSAP) was written as

RSAP = RRSAP x APHBM x APH (5)

where RRSAP is the relative feeding rate, which is dependant on development stage based on Rossing (1991). APHBM is the fresh biomass of an individual aphid, which also depends on DVS (Mantel et al., 1982); and APH is the (dynamic) number of aphids per m^2 of wheat crop.

Honeydew deposition corresponds to 35% of the phloem sapped (Rossing, 1991). Honeydew decreases the rate of carbon dioxide assimilation at light saturation, and increases the rate of dark respiration (Rossing, 1991). The maximum reduction of carbon dioxide assimilation is 2% per g of honeydew, which is achieved 15 days after honeydew deposition. This process was translated by multiplying RUE by a reduction factor (RFAPH) that is proportional to honeydew dry mass accumulated, and remaining in the canopy at a rate of 1.5% per g of honeydew on a 1 m^2 wheat crop. This rate averages the increase in rate from 0 to 15 days after honeydew deposition, followed by a constant, i.e., the maximum rate of 2% (Rossing, 1991). Although the impact of honeydew on photosynthesis can be decreased due to wash-off caused by rainfall or dew, this was not included for the sake of simplicity. Furthermore, the decrease in RUE cannot exceed 20% (Rossing, 1991). Honeydew production, and reduction of RUE caused by honeydew deposition, were thus included in the model as

$$RHONEY = 0{:}35 \times RSAP \quad (6)$$

$$RFAPH = MAX(1 – (HONEY \times 0.015); 0{:}8) \quad (7)$$

where RHONEY is the daily rate of honeydew accumulation, and HONEY is the mass of accumulated honeydew.

2.1.3.2. Weeds

Weeds affect wheat growth through competition for light, nutrients, and water (Spitters, 1989). The overall effect of weeds on wheat physiology can be reflected as a reduction factor of RUE (RFWEED), which depends on weed biomass (Willocquet et al., 2000). We used in WHEATPEST the same parameter as in RICEPEST

$$RFWD = e^{-0.003 \times WD} \quad (8)$$

where WD is the dry biomass of weeds per m^2 of wheat crop.

2.1.3.3. BYDV

Barley Yellow Dwarf Viruses (BYDV) are transmitted by aphids and occur in phloem cells (Wiese, 1991). Disruption of phloem functioning may imply reduction in water and nutrient uptake, and a reduction in photosynthesis efficiency. This mechanism is reflected by multiplying RUE by a reduction factor (RF_{BYDV}). Based onMcKirdy et al. (2002) and Perry et al. (2000), the reduction factor for BYDV was set to

$$RF_{BYDV} = 1 – (0.0035 \times BYDV) \quad (9)$$

where BYDV is the percentage of diseased plants.

2.1.3.4. Take-all

Take-all disease, caused by *Gaeumannomyces graminis* var. *tritici*, is characterized by lesions on roots that affect the phloem vessels (Clarkson et al., 1975), leading to a reduction of nitrogen uptake (Schoeny et al., 2003). Reduction in water uptake may also be hypothesized. Compensation for nitrogen uptake is possible, and depends on nitrogen availability in the neighbourhood of healthy roots (Schoeny et al., 2003). For the sake of simplicity, however, no compensation was considered here. Damage mechanisms (reductions of N and water uptake) for take-all were synthesized by multiplying RUE by a reduction factor, RF_{TAK}, which equals

$$RF_{TAK} = 1 - 0.01 \times TAK \quad (10)$$

where TAK is the root disease severity defined as the percentage of diseased root length.

2.1.3.5. Eyespot.

Eyespot, caused by *Oculimacula yallundae and O. acuformis* (formerly *Tapesia yallundae* and *T. acuformis*; anamorph: *Pseudocercosporella herpotrichoides*), infects outer leaf sheaths, and then penetrates successive leaf sheaths. After stem extension has begun, the fungus may colonise the stem itself (Fitt et al., 1988). Lesions on sheaths cause negligible damage as compared to lesions on stems (Fitt et al., 1988), and thus are not considered here. Infection has direct effects on host physiology: disturbance of water and nutrients movement through the base of stem; and an indirect lodging effect (Scott and Hollins, 1974; Fitt et al., 1988). Three types of damaged tillers with symptoms on stems can be distinguished (Scott and Hollins, 1974): (1) tillers with 'slight' symptoms on stems: one or more lesions occupying in total less than half the circumference of the stem; (2) tillers with 'moderate' symptoms on stems: one or more lesions occupying at least half the circumference of the stem; and (3) tillers with 'severe' symptoms on stems: stem completely girdled by lesions; tissue softened. The direct effect of eyespot was summarized by reducing the RUE from stem elongation to harvest, proportionally to the fraction of tillers with slight, moderate and severe symptoms

$$RF_{EYS} = 1 – 0.01 \times (a \times EYS1 + b \times EYS2 + c \times EYS3) \qquad (11)$$

where RF_{EYS} is the reduction factor of RUE due to eyespot; EYS1, EYS2 and EYS3 are percentages of tillers with slight, moderate and severe eyespot symptoms, respectively.

Yield loss on tillers with slight, moderate, and severe symptoms at harvest are 1.2, 12.5, and 35%, respectively (Clarkson, 1981). The fraction of diseased tillers for each type of disease symptoms generally increases linearly from booting to maturity (Scott and Hollins, 1978). Parameters a, b and c were set to 0.03, 0.28, and 0.78, respectively, based on data from Clarkson (1981).

The indirect effect of eyespot on crop, i.e., lodging, causes 15% of yield loss on tillers with severe symptoms (Scott and Hollins, 1974, 1978). This was accounted for by decreasing ear dry biomass from DVS = 1.8–2 (maturity), so as to achieve a 15% yield loss at maturity. The ear dry biomass reduced by lodging was proportional to EARBM, which allows accounting for the interaction with other injuries that affect ear dry biomass (which reduce EARBM and thus the effect of lodging).

2.1.3.6. Sharp eyespot

Sharp eyespot, caused by *Rhizoctonia cerealis*, causes lesions on the stem base of wheat plants (Clarkson and Cook, 1983). It was assumed that sharp eyespot damage mechanisms were the same as those for eyespot, except for the lodging effect, which seldom occurs for this disease. The effect of sharp eyespot was thus reflected by reducing the RUE from stem elongation to harvest, proportionally to the fraction of tillers with slight, moderate, and severe symptoms

$$RF_{SHY} = 1 – 0.01 \times (a \times SHY1 + b \times SHY2 + c \times SH3) \qquad (12)$$

where RFSHY is the reduction factor of RUE due to sharp eyespot; SHY1, SHY2 and SHY3 are percentages of tillers with slight, moderate, and severe sharp eyespot symptoms, respectively.

Yield loss on tillers with slight, moderate, and severe symptoms at harvest are 2.8, 5.4, and 26.4%, respectively (Clarkson and Cook, 1983). Based on these data, parameters a, b, and c were set to 0.07, 0.14, and 0.65, respectively.

2.1.3.7. Fusarium stem rot

Fusarium stem rot is associated to *Fusarium* species (mainly *Fusarium graminearum*, *F. culmorum*), and *Microdochium nivale* (Daamen et al., 1991), and causes roots, crown and lower nodes and internodes to turn brown (Wiese, 1991). As for eyespot and sharp eyespot, the damage mechanisms for this injury were reflected by reducing RUE. The magnitude of RUE reduction depends on the type of symptom: tillers with slight symptoms correspond to tillers with browning up to the second node; and tillers with severe symptoms correspond to browning up to the third node or above. These categories of tillers correspond to categories D1 and D2, and D3 and D4 described by Smiley et al. (2005), which are associated with 11% and 29% yield losses, respectively (Smiley et al., 2005). Reduction of RUE by Fusarium stem rot was incorporated in the model as

$$RF_{FST} = 1 – 0.01 \times (a \times FST1 + b \times FST2) \quad (13)$$

where RF_{FST} is the reduction factor of RUE due to Fusarium stem rot; FST1 and FST2 are percentages of tillers with slight and severe Fusarium stem rot symptoms, respectively; a and b were set to 0.26 and 0.67, respectively, based on data from Smiley et al. (2005).

2.1.3.8. Fusarium head blight

Fusarium head blight (FHB) is associated in Europe with at least four *Fusarium* species (*F. graminearum, F. culmorum, F. avenaceum,* and *F. poae*), and with *M. nivale* (Parry et al., 1995). The fungi colonise grains and reduce yield. They also produce mycotoxins that are harmful to animals and humans, but this effect will not be considered here. It is hypothesized that the increase in grain dry biomass is reduced proportionally to the fraction of kernels infected by the fungi involved in FHB, by multiplying it by a reduction factor RF_{FHB}. The reduction parameter value (1.1) was derived from Mesterhazy et al. (2003, 2005), and RF_{FHB} is computed as

$$RF_{FHB} = 1 – 0.01 \times (1.1 \times FHB) \quad (14)$$

where FHB is the percentage of diseased kernels.

2.1.3.9. Foliar diseases

Lesions on leaves can affect crop physiology through four main mechanisms (Rabbinge and Vereijken, 1980; Boote et al., 1983; Savary et al., 1990):

(i) Foliar diseases cause lesions which decrease the photosynthetic area: photosynthesis does not occur on leaf parts covered by lesions.

(ii) (ii) Photosynthesis can also be decreased in areas surrounding lesions. This can be reflected by using the concept of virtual lesion (Bastiaans, 1991). A virtual lesion is the area including the visual lesion, and the symptomless zone around the visual lesion, where photosynthesis is impaired. For a low fraction of virtual lesion (<20%), the fraction of photosynthetically active area can be written as $(1 - x)^{\beta}$, where x is disease severity and β represents the ratio of the virtual lesion area over the actual lesion area. The effect is introduced in the model as a fraction of reduction of the (green) LAI.

$$LAIdis = LAI \times (1-x)^{\beta} \quad (15)$$

(iii) Assimilates can be diverted to the lesions for production of reproduction propagules.
(iii) Foliar lesions can cause an acceleration of leaf senescence.

Septoria nodorum blotch
Septoria nodorum blotch, caused by *Septoria nodorum*, causes lesions which decrease the photosynthetic area. The effects of lesions (and senesced tissue expanding from the lesions) on gross photosynthesis correspond to a beta value of 1 (Scharen and Taylor, 1968; Rooney, 1989).

A fraction of 22% of the assimilates produced by the crop is diverted to the lesions for the formation of pycnidia for diseased leaves with a severity of 35% (Scharen and Taylor, 1968). Assuming a linear relationship between disease severity and assimilate uptake for pycnidia formation, this was included in the model by reducing the quantity of assimilates produced daily as

$$RDIVSN = 0.01 \times RG \times 0.63 \times SN \tag{16}$$

where RDIVSN is the daily rate of assimilate diversion, RG is the rate of crop growth, and SN is severity of Septoria nodorum blotch.

Septoria tritici blotch
Septoria tritici blotch, caused by *Mycosphaerella graminicola*, causes lesions which decrease
the photosynthetic area. The effects of lesions (and senesced tissue in their neighbourhood) on gross photosynthesis correspond to a beta value of 1.25 (Robert et al., 2006). Diversion of assimilates for pycnidia production was included in the model in the same way as for Septoria nodorum blotch.

Brown rust
Brown (leaf) rust is caused by *Puccinia triticina*. Lesions do not affect photosynthesis on symptomless leaf tissues, that is, a beta value of 1 is used (Spitters et al., 1990; Robert et al., 2005). For this type of rust, the carbohydrate uptake for spore production is proportional to the number of pustules (Mehta and Zadoks, 1970; Savary et al., 1990).

$$RDIVBR = 4.62 \times 10^{-6} \times NPUSBR \tag{17}$$

with

$$NPUSBR = 0.01 \times BR \times LAI / SURFBR \tag{18}$$

where NPUSBR is the number of pustules of brown rust per m^2 of wheat crop, BR is brown rust severity, SURFBR is the area of a pustule of leaf rust, and was set to 10^6 m^2.

Yellow rust:
Yellow (stripe) rust, caused by *Puccinia striiformis*, causes lesions which decrease the photosynthetic area. The effects of lesions of this type of rust with a systemic growth on maximum photosynthesis correspond to a beta value of 1.5 (Yang and Zeng, 1988). Daily carbohydrate diverted for spore production was included in the same way as for brown rust.

Powdery mildew
Powdery mildew, caused by *Blumeria graminis*, causes lesions that decrease the photosynthetic area. The photosynthesis of the area surrounding the lesion is also impaired. The corresponding beta value depends on the incident radiation, and increases as radiation increases (Rabbinge et al., 1985). As powdery mildew generally develops in the lower part of

the canopy, a beta value corresponding to that fraction of the canopy was derived from Rabbinge et al. (1985), which is 2.5.

2.1.3.10. Interaction between injuries

The combined effects of injuries on crop physiology are represented in WHEATPEST by the product of the corresponding reduction factors affecting a same variable. For example, the reduction factors for LAI due to the different leaf pathogens were multiplied and Eq. (2) becomes

$$LAI = LEAFBM \times SLA \times 0.01 \times (1 - SN) \times (0.01 \times (1 - ST))^{1.25} \times 0.01 \times (1 - BR) \times (0.01 \times (1 - YR))^{1.5} \times (0.01 \times (1 - PM))^{2.5} \quad (19)$$

The model therefore assumes that one pathogen does not affect a leaf area that has already been injured by another one (Johnson, 1990), as in the case e.g., of bean rust and anthracnose (Lopes and Berger, 2001), and of wheat leaf rust and Septoria tritici blotch (Robert et al., 2004). The multiplication of reduction factors also assumes that injuries are spatially distributed randomly. Less-than-additive damage interactions between pests having identical damage mechanisms are thus modelled.

2.2. Drivers for injury profiles

Wheat injury profiles and production situations that would be representative of a range of contexts of attainable growth and yield, and of yield reductions in Europe are necessary to judge the performances of the model. In this study, our aim was not to compare observed and simulated attainable yields and losses with any accuracy, but rather to provide an assessment of the model's behaviour. In order to do so, a limited data set was considered sufficient.

There is a large body of literature reporting results from pest surveys in winter wheat in Europe (e.g., King, 1977; Zadoks and Rijsdijk, 1984; Daamen and Stol, 1990; Polley and Thomas, 1991; Hyvonen et al., 2003). Reports from the literature were sought, which would meet the following requirements: (i) be recent, (ii) cover the entire range of organisms that are harmful to wheat, (iii) provide accurate, if not precise, information on production situations, and (iv) share the same, or similar, sampling and assessment methods in order to enable compatibility across data sets.

No reported study actually met all these four criteria, especially the third one. The latter aspect, where the effects of production situations on injury profiles are considered, is available however in the literature (Daamen et al., 1989; Debaeke, 1990; Savary et al., 2006b). The second criterion was partly met by some studies; however, there was a clear distinction between farmers' field studies that deal with diseases and/or insects, and studies dealing with weeds. The decision was then made to proceed in four steps
- first, combine studies that would meet criteria i and iv, where overall injury profiles would be determined, and generate a preliminary framework of injury profiles using clustering methods (these included injuries caused by fungal pathogens),
- second, overlay this framework with injuries that were not taken into account in the first step (these included weeds and vector-borne diseases),
- third, introduce the effects of production situations on injury profiles using results reported in experimental studies,
- and four, incorporate the shape of injury dynamics using reported data, since the bulk of the available material consisted of single-point injuries, and not injury dynamics data.

2.2.1. Step1: meta-analysis of country-year pest data

The first step was based on two series of studies, in England and Wales (Polley and Thomas, 1991), and in the Netherlands (Daamen, 1990; Daamen and Stol, 1990, 1992, 1994; Daamen et al., 1991, 1992). These studies provide a comprehensive and detailed account of many organisms harmful to wheat over several hundreds of farmers' fields. The former study (which covers the period 1976–1988) provides national measurements of leaf disease severities (proportion of leaf area injured), stem and root disease incidences (proportion of plants, tiller, or root systems injured), but does not however provide information on insect injuries. The latter (which covers the period 1974–1986) does provide measurement of insect injuries together with those caused by diseases, but involves a shift in assessment methods for some diseases. Moreover, the study in England and Wales makes use of (leaf disease) severities, where the two Septoria diseases are distinguished, whereas the study in the Netherlands mostly makes use of (leaf disease) incidences at the plant level, often pooling the two Septoria injuries together. Both studies, however, make use of disease prevalence (proportion of field affected), thus enabling data combination. One relationship that proved useful in combining data sets is a severity–prevalence relationship which was tested on the data generated in England and Wales. This relationship is of the form: severity = (exp(a x prevalence) - b)/(exp(b) + 1). For Septoria tritici blotch, Septoria nodorum blotch, powdery mildew, yellow rust, and brown rust, corrected R^2 values (d.f. = 9) of 0.882, 0.701, 0.869, 0.729, and 0.601, respectively, were found using the entire data set provided over the 13 covered years. Much of the Dutch data did not distinguish the two Septoria injuries, and could unfortunately not be used, except for 1983–1986. Only the data for these years were therefore used. While the study in Wales and England considered only one development stage (stage 73–75, Zadoks et al., 1974), the study in the Netherlands mostly provided data at two broad stages, first to second node, and milky-ripe stage. The milky-ripe stage was used as a common basis for combining data sets.

A hierarchical cluster analysis using the Ward criterion and a Euclidean distance was used to generate the framework for injury profiles. This analysis involved mean year-country (i.e., 15 year-countries) data pertaining to Septoria nodorum blotch, Septoria tritici blotch, powdery mildew, yellow rust, brown rust (severities), eyespot, sharp eyespot, and Fusarium stem rot (incidences) over 11 years in England and Wales and 4 years in the Netherlands. One important hypothesis in using these clusters was that the large majority of the fields surveyed both in the Netherlands and the United Kingdom were under a conventional crop management system.

2.2.2. Step 2: overlay of the meta-analysis with additional injuries

The second step, where additional injuries were included in the injury profiles, focused on weeds, barley yellow dwarf viruses, Fusarium head blight, aphids, and take-all. Weed injuries were assumed omnipresent and independent from the clustering based on fungal diseases. A baseline level of injury was derived from several sources in the literature, but this maximum level was altered with varying production situations in step 3 (below). Barley Yellow Dwarf Virus infection was assessed in a separate, comprehensive, survey in the entire United Kingdom between 1996 and 1998 (Foster et al., 2004). No equivalent data could be found which would cover the chosen range of country-years considered in the cluster analysis. A grand mean incidence (% tiller infected) for the three viruses (MAV, PAV, and RPV) was derived from this 3-year study. Fusarium head blight injuries were assessed in detail by Daamen et al. (1991) for the Netherlands across different years which were involved in the cluster analysis. Fusarium head blight injury was assumed to be homogeneous within a cluster, and mean-year values derived from these Dutch data were applied to all elements belonging to that cluster. Similarly to Fusarium head blight, the survey conducted by Daamen and Stol (1994) provides background information for aphids that covered the country-year clusters with data from the Netherlands. Aphid injury was thus assumed similar across country-years belonging to the same cluster. The same reasoning was applied in the other direction in the case of take-all injury, as the survey in England and Wales (Polley and Thomas, 1991) complemented that of the Netherlands. British data thus served as a basis to estimate mean injuries within a given country-year cluster.

2.2.3. Step 3: introduction of the effects of production situations on injury profiles

Production situations of course vary widely across Europe (e.g., Zadoks and Rijsdijk, 1984), but quantitative information linking production situations and injury profiles is scarce. The study by Daamen et al. (1989) provided a quantitative basis for introducing the considerable changes crop management generates into injury profiles. This study was conducted in on-farm experiments on a series of representative wheat varieties for 2 years, where most of the harmful organisms addressed in the present work were considered, in three crop management systems: ‘conventional’ (C), ‘integrated’ (I), and ‘biodynamic’ or ‘organic’ (O). These three crop management systems were considered to represent a range of production contexts wide enough to provide a basis for assessing the model. The conventional system included high yielding cultivars; use of nitrogen inputs, growth regulator, and pesticides. The integrated system was characterised by the use of partially resistant and weed competitive cultivars, nitrogen application, and pesticide treatment based on pest level. The organic system was associated with no pesticide use, partially resistant and weed competitive cultivars, and use of organic manure in preceding crops (Daamen et al., 1989). A two-way matrix, production systems (O, C, or I) by injury profiles (clusters), therefore was considered. Injury progress curves from the experiments on conventional, integrated, or organic production systems (Daamen et al., 1989) showed large differences in injury patterns for powdery mildew, yellow rust, brown rust, Septoria blotches, eyespot, sharp eyespot, Fusarium stem rot, and take-all. These differences in turn provided modifiers for the average injury levels mostly represented by conventional crop management systems in the cluster analysis of injuries over countries and years. Further information was also gathered for weed infestation from additional references (Debaeke, 1990; Olsen et al., 2005; Rasmussen et al., 2006).

Step 4: incorporation of the shape of injury dynamics

A dynamic simulation model requires driving functions over time, not maximal values. The on-farm experimental study by Daamen et al. (1989) also provided further information on the time-course of injuries during a cropping season. These were used to define idealised patterns of increase over time of severities (leaf diseases). Dynamics of stem diseases (tiller incidences) were derived from Scott and Hollins (1978). Idealised dynamics over time of take-all root severity, aphid numbers, and weed biomass were derived from Schoeny et al. (2001), Rossing (1991), and Wilson et al. (1995), respectively. BYDV and FHB injuries were set as parameters (i.e., maximum values) in the injury profiles.

3. Results

3.1. Modelling attainable growth and yield for different production situations

Simulated attainable grain yields were set to 1000, 850, and 700 g m^{-2} for the C, I and O systems, respectively, following Daamen et al. (1989). This corresponded in turn to simulated ear yield of 1180, 1000, and 824 g m^{-2} for the conventional, integrated, and organic systems, respectively. Attainable growth and yield was hypothesized to be mainly determined by RUE. In each system, RUE values were thus determined to achieve the targeted simulated attainable yield: RUE values were 1.4 and 1.3 g $MJ^{-1}m^{-2}$ during the vegetative and reproductive stages, respectively, in the C system; in the same way, RUE values were 1.24 and 1.14 for the I system, and 1.085 and 0.985 for the O system during the vegetative and reproductive stages, respectively.

Simulated attainable growth and yield for the three systems are shown in Fig. 3. In the conventional system, the dry biomass of leaves increases in a sigmoid shape until development stages around flowering (DVS = 1), then remains stable (340 g m^{-2}), and decreases afterwards, due to physiological leaf senescence (Fig. 3A). Stem dry biomass increases regularly until flowering, reaches nearly 1200 g m^{-2}, and then declines linearly, due to carbohydrate re-mobilization to the ears (Fig. 3A). The dry biomass of roots increases regularly until DVS 0.8, then tapers off, and remains stable at 140 g m^{-2}. Ear dry biomass starts to increase at flowering, and increases nearly linearly until maturity (DVS = 2), with a final dry biomass of 1200 g m^{-2} (Fig. 3A). The accumulated dry biomass increases regularly according to a concave curve, and final total dry biomass is 2280 g m^{-2} (Fig. 3B). LAI increases regularly until DVS = 0.7 (LAI = 7), and then declines until maturity. Similar dynamics are simulated in the integrated (Fig. 3C and D) and organic (Fig. 3E and F) systems, but with decreased values. Maximum LAI are 6 (Fig. 3D) and 5 (Fig. 3F) in the integrated and organic systems, respectively.

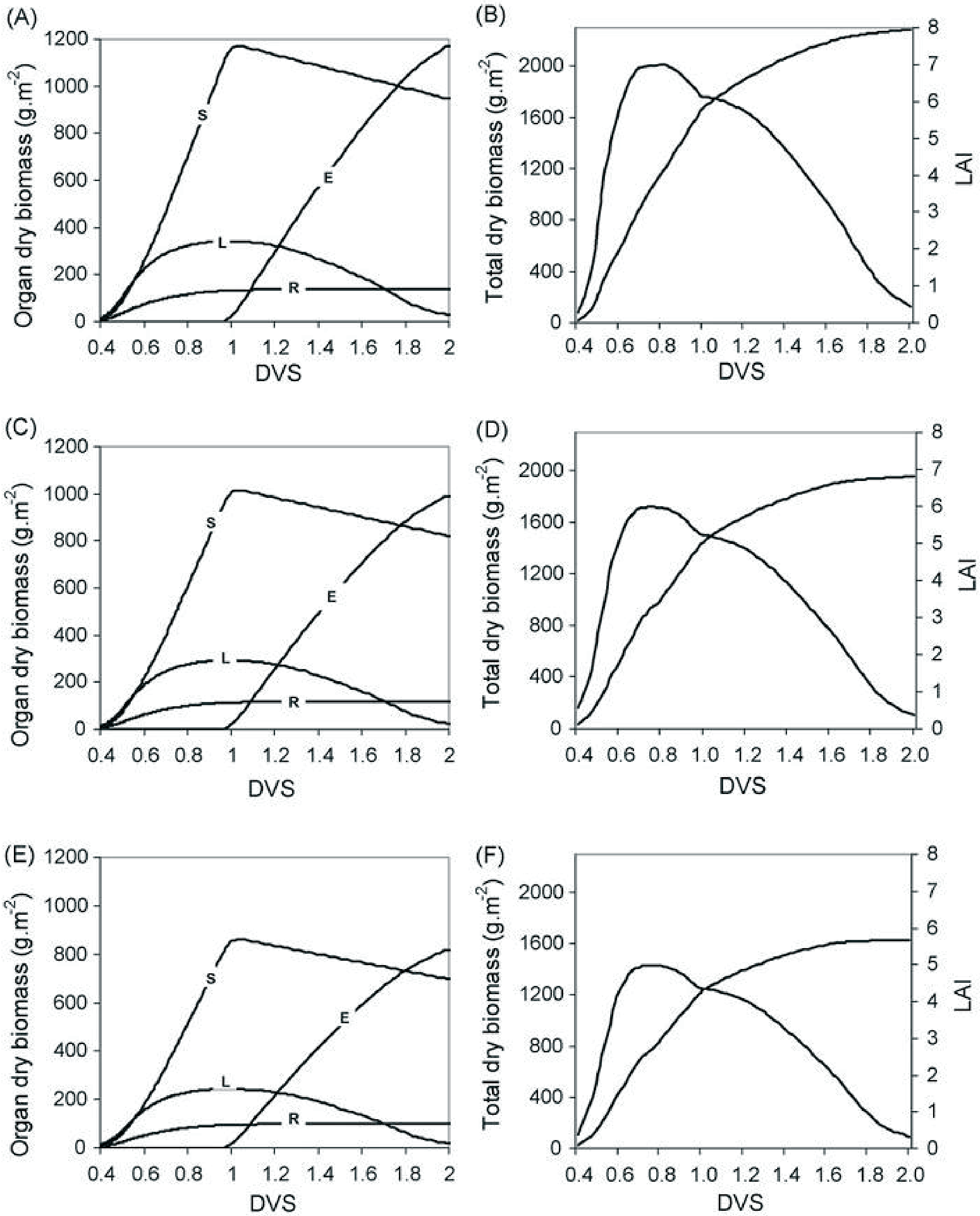

Fig. 3. Simulated dynamics of dry biomass and LAI fromWHEATPEST for the three cropping systems, Conventional (A and B), integrated (C and D), and organic (E and F). L: dry biomass of leaves; S: dry biomass of stems; R: dry biomass of roots; E: dry biomass of ears. DVS: development stage.

3.2. Drivers for injury profiles

3.2.1. Meta-analysis of country-year pest data: cluster analysis

Cluster analysis (Fig. 4) yielded three groups which differed in their levels of injuries (Table 2). Cluster A corresponds to comparatively low levels of Septoria nodorum blotch, high Septoria tritici blotch, medium powdery mildew, medium yellow rust, high brown rust, high eyespot, medium sharp eyespot, and high Fusarium stem rot; cluster B corresponds to medium level of Septoria net blotch, low Septoria tritici, high powdery mildew, low yellow rust, medium brown rust, low eyespot, low sharp eyespot, and low Fusarium stem rot; and cluster C corresponds to high Septoria nodorum, medium Septoria tritici, medium powdery mildew, medium yellow rust, medium brown rust, medium eyespot, medium sharp eyespot, and high Fusarium stem rot. In spite of the clear overall pattern shown in Fig. 4, these differences however are associated with large variances. Table 2 may be seen as a template of injury profiles for wheat in Western Europe, to be completed with additional injuries, and adjusted to account for variation in crop management.

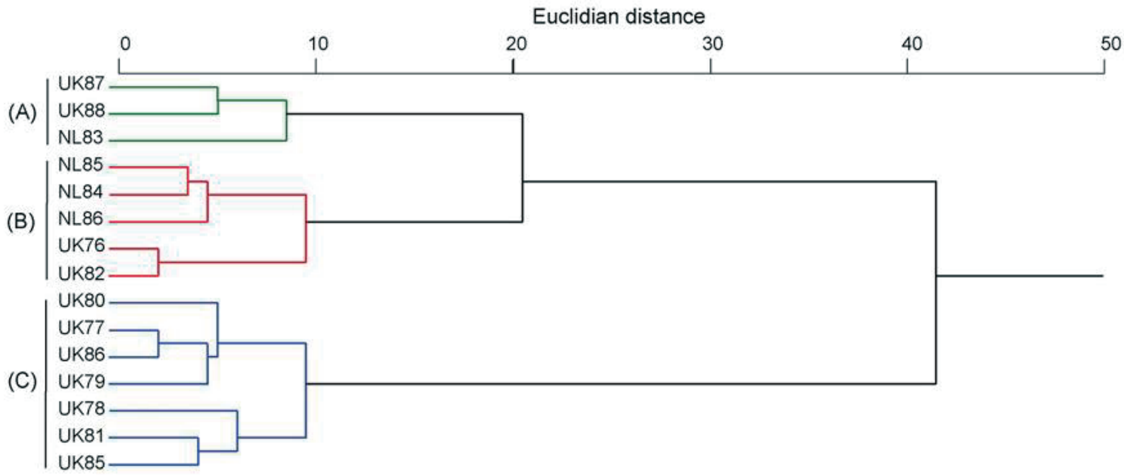

Fig. 4. Results from a hierarchical cluster analysis[a] of wheat pests from farmers' field surveys in England and Wales[b] and in the Netherlands[c].
[a] The clustering was performed on injury levels caused by a series of wheat pests (see text for details), using a Ward criterion and a Euclidian distance. Three injury profiles (A, B, and C) were identified (see text for details)
[b] From Polley and Thomas (1991): UKi
[c] From Daamen (1990), Daamen et al. (1991, 1992), and Daamen and Stol (1990, 1992, 1994): NLj

3.2.2. Overlaying results from cluster analysis with additional injuries

The maximum weed infestation level was assumed similar across clusters and was set to 3.0 g m^{-2} in the conventional system (Debaeke, 1990; Hyvonen et al., 2003; Olsen et al., 2005). BYDV injury data from Foster et al. (2004) concern a total of 623 (unprotected) fields, from which samples of 100 leaves each were taken. A total of 711 leaves were tested positive for either one of the three viruses (MAV, PAV, or RPV), thus leading to a grand mean incidence of 711/62,300 = 1.14%. This disease incidence was assumed identical for all injury profiles (A, B, and C). Percentage of grain diseased by FHB was estimated as 1.99, 0.86, and 1.16% for injury profiles A, B, and C, respectively (Daamen et al., 1991). Percent of tillers infested by aphids were estimated at 18.7, 22.3, and 20.5% for injury profiles A, B, and

C, respectively, from data reported by Daamen and Stol (1994). These incidences correspond to aphid densities per tiller of 0.58, 0.71, and 0.65, respectively, based on the incidence-density relationship reported by Rossing et al. (1994). Take-all root severity at DVS 1.6 was estimated at 3.5, 4.75, and 6%, for clusters A, B, and C, respectively, from Polley and Thomas (1991).

Table 2. Levels of injuries and statistics for levels of injuries in three clusters of injury profiles from farmers' field surveys in England and Wales[a] and in the Netherlands[b].

Group[c]		Injuries[d]							
Code	Statistics	SN	ST	PM	YR	BR	EYS	SHY	FST
A	Mean	0.64	4.81	0.66	0.12	0.76	30.8	9.4	13.0
	Min	0.15	1.25	0.15	0.00	0.10	24.3	1.5	4.0
	Max	1.60	10.2	1.39	0.25	1.69	35.0	17.3	21.5
	Standard deviation	0.83	4.73	0.65	0.12	0.83	5.69	7.9	8.76
B	Mean	1.83	1.64	3.66	0.01	0.25	7.28	6.32	9.64
	Min	0.01	0.06	1.25	0.00	0.10	1.61	2.40	4.00
	Max	6.45	6.58	6.81	0.03	0.39	16.0	12.4	17.4
	Standard deviation	2.76	2.78	2.48	0.02	0.11	5.76	3.89	6.42
C	Mean	2.63	2.39	0.87	0.13	0.29	16.2	10.8	37.7
	Min	0.41	0.11	0.20	0.00	0.00	7.60	5.70	29.3
	Max	6.80	10.1	2.35	0.50	0.55	27.0	16.4	49.7
	Standard deviation	2.15	3.50	0.77	0.22	0.23	6.55	4.69	6.45

[a] From Polley and Thomas (1991).
[b] From Daamen (1990), Daamen and Stol (1990, 1992, 1994), and Daamen et al. (1991, 1992).
[c] Three groups of injury profiles were determined based on surveys in the Netherlands and the United Kingdom (see Fig. 4, Dendrogram): A: n =3,B: n = 5, and C: n = 7 average country-years. Each country-year represents several hundred farmers' fields. See text for details.
[d] SN, ST, PM, YR, BR: severities (% leaf area injured) for Septoria nodorum blotch, Septoria tritici blotch, powdery mildew, yellow rust, and brown rust, respectively; EYS, SHY, FST: incidence (%tillers injured) for eyespot, sharp eyespot, and Fusarium stem rot, respectively. See Table 1 (list of variables and symbols) for complete list of variables.

3.2.3. Injury profiles in different crop management systems

Crop management has profound effects on the time courses and maximum levels of injuries (Daamen et al., 1989). Powdery mildew is strongly increased in the integrated I (fewer fungicide applications) compared to the conventional (C) management, and is reduced in the organic (O) management (resistant varieties). Yellow rust injury is similar in C and I, but is strongly reduced in O (resistant varieties). Brown rust injury is similar in C and I, but is increased in O. Both the septoria injuries are reduced in I compared to C (varieties and nitrogen application) and are further reduced in O. Eyespot is similar in C and I but is reduced in O (crop succession effect). The three management practices result in similar stem injury by Fusarium, as well as by sharp eyespot. Aphid infestation was higher in I than C, and was the highest in O. The levels of pests not addressed in Daamen et al. (1989) were estimated in crop managements I and O as follows. Maximum weed dry biomass was set to 11 g m^{-2} in the integrated (Debaeke, 1990), and to 16 g m^{-2} in the organic (Rasmussen et al., 2006) production systems, respectively. Take-all severity was assumed similar in C and I, but strongly reduced in O (van Bruggen and Termorshuizen, 2003). BYDV and FHB disease incidence were assumed not to be influenced by crop management (O, I, and C).

These patterns are summarized at two development stages in Table 3, where the three groups resulting from the cluster analysis are indicated, as well as the effect of crop management modifiers. Table 3 therefore summarizes the drivers for injuries which were used to run WHEATPEST.

Table 3. Summary of drivers for injuries in three clusters of injury profiles combined with three production systems

IP[a]	CM[b]	DVS[c]	Injury levels[d]												
			WD	TAK	EYS	SHY	FST	ST	SN	BR	YR	PM	APH	BYDV	FHB
A	C	0.8	1.16	0.70	3.07	0.94	1.30	0.48	0.06	0.01	0.02	0.22	0.00	1.14	1.99
A	C	1.6	3.00	3.50	30.70	9.40	13.00	4.81	0.64	0.76	0.12	0.67	0.58	1.14	1.99
A	I	0.8	4.23	0.70	3.07	0.94	1.30	0.24	0.03	0.01	0.02	0.45	0.00	1.14	1.99
A	I	1.6	11.00	3.50	30.70	9.40	13.00	2.41	0.32	0.76	0.12	1.34	1.37	1.14	1.99
A	O	0.8	6.15	0.14	0.77	0.94	1.30	0.12	0.02	0.08	0.00	0.06	0.00	1.14	1.99
A	O	1.6	16.00	0.70	7.68	9.40	13.00	1.20	0.16	7.60	0.02	0.17	4.25	1.14	1.99
B	C	0.8	1.16	0.95	0.73	0.63	0.96	0.16	0.18	0.00	0.01	1.22	0.00	1.14	0.86
B	C	1.6	3.00	4.75	7.28	6.32	9.64	1.64	1.83	0.25	0.06	3.66	0.71	1.14	0.86
B	I	0.8	4.23	0.95	0.72	0.63	0.96	0.08	0.09	0.00	0.01	2.44	0.00	1.14	0.86
B	I	1.6	11.00	4.75	7.28	6.32	9.64	0.82	0.92	0.25	0.06	7.32	1.75	1.14	0.86
B	O	0.8	6.15	0.11	0.18	0.63	0.94	0.04	0.05	0.03	0.00	0.31	0.00	1.14	0.86
B	O	1.6	16.00	0.95	1.82	6.32	9.64	0.41	0.46	2.50	0.01	0.92	7.03	1.14	0.86
C	C	0.8	1.16	1.20	1.62	1.08	3.77	0.24	0.26	0.00	0.02	0.29	0.00	1.14	1.16
C	C	1.6	3.00	6.00	16.20	10.80	37.70	2.39	2.63	0.29	0.13	0.87	0.65	1.14	1.16
C	I	0.8	4.23	1.2	1.62	1.08	3.77	0.12	0.13	0.00	0.02	0.58	0.00	1.14	1.16
C	I	1.6	11.00	6.00	16.20	10.80	37.70	1.20	1.32	0.29	0.13	1.74	1.55	1.14	1.16
C	O	0.8	6.15	0.24	0.40	1.08	3.77	0.06	0.07	0.03	0.00	0.07	0.00	1.14	1.16
C	O	1.6	16.00	1.20	4.05	10.80	37.7	0.60	0.66	2.90	0.02	0.22	5.35	1.14	1.16

[a] Injury profile
[b] Crop Management. C: conventional, I: integrated, and O: organic crop management (Daamen et al., 1989)
[c] DVS: wheat development stage (Table 1)
[d] Symbols for injuries (Table 1): WD: weed dry biomass (g m^{-2}), TAK: take-all severity (%), EYS: eyespot incidence (%tillers), SHY: sharp eyespot incidence (%tillers), FST: Fusarium Stem Rot (%tillers), ST: septoria tritici blotch severity (%), SN: septoria nodorum blotch severity (%), BR: brown rust severity(%),YR: yellow rust severity (%), PM: powdery mildew severity (%), APH: aphid density (nb m^{-2}), BYDV: Barley Yellow Dwarf Virus incidence (% plants), and FHB: Fusarium head blight (%kernels)

3.3. Modelling yield loss for different combinations of production situation by injury profile

Simulated yield losses caused by wheat injury profiles and their corresponding individual injuries for the different combinations of production situations (C, I, and O) by injury profiles (A, B, and C) are shown in Fig. 5. Relative yield losses are expressed as fractions (%) of attainable yield (YA) for each individual pest, and yield losses caused by the entire injury profile are also indicated in terms of grain dry biomass (YL IP) and fraction of grain dry biomass lost (RYL IP). Across the nine possible combinations, relative yield losses range from 11.4% (Fig. 5B; conventional, IP B) to 16.9% (Fig. 5F; integrated, IP C). In all cases, relative yield losses caused by an injury profile are lower than the accumulated yield losses caused by combined individual injuries. Yield losses in terms of grain dry biomass range from 86 (Fig. 5H; organic, IP B) to 165 g m^{-2} (Fig. 5C; conventional, IP C). These figures are to be linked to attainable yields, which increase from700 (organic) to 1000 g m^{-2} (conventional). WHEATPEST simulates varying patterns of relative yield losses, caused by the individual injuries within a given PS x IP combination, as is reflected by the differences of loss patterns shown in Fig. 5A–I. Relative yield losses caused by individual injuries are always below 6%, and are below 1% in more than 50% of the cases.

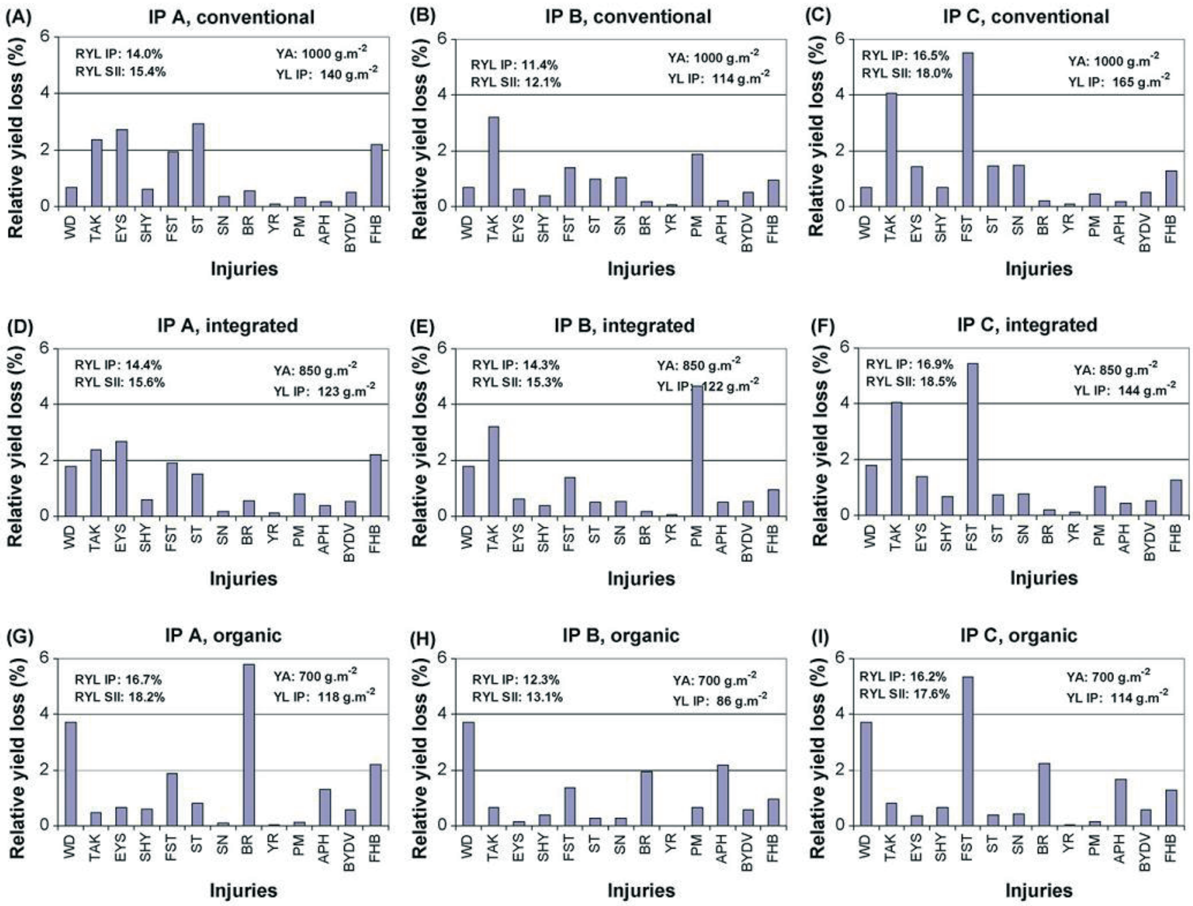

Fig. 5. Simulated wheat yield losses caused by individual injuries, and by their combination into injury profiles, for combinations of production situation by injury profile. (A–C) Conventional system; (D–F) integrated system; (G–I) organic system; (A, D and G) injury profile A; (B, E and H) injury profile B; (C, F and I) injury profile C. RYL IP: relative yield losses caused by the injury profile; RYL SII: relative yield losses cumulated over the individual injuries; YA: attainable grain yield; YL IP: grain yield loss caused by the injury profile. Symbols for injuries (Table 1): WD: weed dry biomass (g m^{-2}), TAK: take-all severity (%), EYS: eyespot incidence (%tillers), SHY: sharp eyespot incidence (%tillers), FST: FusariumStemRot (%tillers), ST: septoria tritici blotch severity (%), SN: septoria nodorumblotch severity (%), BR: brown rust severity(%),YR: yellow rust severity (%), PM: powdery mildew severity (%), APH: aphid density (nb m^{-2}), BYDV: Barley Yellow Dwarf Virus incidence (% plants), and FHB: Fusarium head blight (%kernels).

Simulated yield losses caused by injury profile A in the conventional system (Fig. 5A) are mainly caused by take-all, eyespot, Fusarium stem rot, Septoria tritici blotch, and Fusarium head blight, which individually cause relative yield losses between 2 and 3%. Other individual relative yield losses are below 0.7%. This combination is thus dominated by fungal diseases that injure roots, stems, and ears; and where Septoria tritici blotch dominates among leaf diseases. This injury profile entails relative yield losses of 14%, that is, 140 of the 1000 g m^{-2} that should have been achieved in the absence of pests. Yield losses pattern for injury profile B under a conventional system (Fig. 5B) differs from IP A (Fig. 5A). In this case, take-all represents the major biotic constraint to wheat grain production, with an individual relative yield loss of 3.2%, followed by powdery mildew, with 1.9%. Fusarium stem rot, Septoria blotches and FHB are associated with individual relative yield losses ranging between 0.9

and 1.5%. Other injuries cause relative yield losses lower than 0.7%. Simulated relative yield loss caused by injury profile B is 11.4%. Relative yield loss caused by injury profile C in the conventional system (Fig. 5C) is 16.5%, that is, the most damaging among the three injury profiles considered in the conventional system. This injury profile is associated with high relative yield losses caused by take-all and Fusarium stem rot, of 4.1 and 5.5%, respectively. Eyespot, Septoria blotches, and FHB are the next most damaging injuries in this profile. In the conventional production system, aphids, BYDV, weeds, brown rust and yellow rust individually cause less than 1% of relative yield losses, irrespective of the injury profile considered (Fig. 5A–C). Relative yield losses simulated in the integrated production system (I, Fig. 5D–F) are similar to those simulated in the conventional system for injury profiles A and C, but higher for injury profile B. Injury levels, and thus individual yield losses caused by aphids, powdery mildew, and weeds, are higher in the integrated system than in the conventional one, whereas the opposite effect occurs for Septoria blotches. These opposite trends compensate one another in injury profiles A and C, but lead to higher losses in the integrated system for injury profile B. In this case, powdery mildew is the main pest involved in the difference in yield losses found between the I and C systems.

Organic systems under injury profiles A, B, and C, are consistently associated with high yield losses caused by weeds (Fig. 5G–H). Relative yield losses caused by brown rust and aphids are strongly increased in comparison to those simulated for the conventional system, while relative yield losses caused by powdery mildew, Septoria blotches, take-all and eyespot are reduced. This leads to similar fractions of yield lost to injury profiles B and C in the organic and conventional systems. By contrast, the relative yield loss caused by injury profile A is higher in the organic system (16.7%) than in the conventional one (14%). In this last combination, yield losses caused by brown rust (5.8%) and weeds (3.7%) represent the most important reducing factors for production.

3.4. Evaluation of model behaviour

To our knowledge, there is no published report where wheat yield loss data in farmers' fields, together with the range of pests considered in WHEATPEST would be addressed. This makes a formal assessment of the model's performances very difficult. There are, however, excellent sources where one or several pests would be considered in the actual losses they cause. We therefore make use of various reports to assess the range of variations of the model, and focus on reports addressing similar production environments as those addressed in the simulations performed here with WHEATPEST. For instance, Cook et al. (1991) reported estimates of yield losses caused by several fungal diseases of wheat for England and Wales over 1985–1989, based on surveys and empirical yield loss models. Estimates of yield losses caused by eyespot were 1.5%, which falls within the range (0.4–2.7%) obtained from WHEATPEST simulations in the nine combinations of production situation by injury profile considered in our study. In the same way, ranges of simulated yield losses from this study, and estimates from Cook et al. (1991), are as follows for other fungal diseases: 0.4–0.7 versus 0.6% for sharp eyespot, 0.1–4.7% versus 2.0% for powdery mildew, 0.3–2.9% versus 2.0% for Septoria tritici blotch, 0.01–0.1 versus below 0.1% for yellow rust, and 0.2–5.8 versus below 0.1% for brown rust. In the case of take-all, the average of reported estimates for England in 1977–1979 were 2.1% (Polley and Clarkson, 1980), and simulated yield losses from WEATPEST over the nine PS x IP combinations was 0.5–4.1%. Yield losses caused by aphids for the Netherlands in 1979–1980 was estimated at 1% (Daamen, 1981), and the range simulated by WHEATPEST was 0.2–1.8%.

4. Discussion

4.1. Model hypotheses

4.1.1. Model structure

One objective of this work was to achieve synthesis and accuracy (not necessarily precision) in combining the dynamics of harmful effects of simultaneous pests on wheat crop growth and yield, using a mechanistic approach. This was made possible using (1) a simple model structure, (2) a unified representation of damage mechanisms across the diversity of pests considered, which implies (3) a generic way of representing each damage mechanism in a model.

Many agrophysiological models have been developed over the last 30 years. Some of them were developed as generic structures (e.g., SUCROS, Van Keulen et al., 1982; BACROS, Penning de Vries and Van Laar, 1982; CERES, Hoogenboom et al., 1994; STICS, Brisson et al., 2003), to be adapted for different crops. The prime objective of these models was to represent physiological processes and their outputs at the field scale. Most of these models integrated in a second step the effects of yield limiting factors (*sensu* Rabbinge, 1993) on crop growth and yield. Recently, a model for wheat growth including the effects of planting, nitrogen, residues, irrigation, and pests for tropical wheat has been developed, through a very detailed modelling of C, N, and water cycles, and the incorporation of several pests (Aggarwal et al., 2006a,b). In contrast, WHEATPEST has a much simpler structure; it includes fewer, simplified, crop physiological processes, so as to incorporate only those that are affected by injuries; it includes in a transparent way damage mechanisms for the 13 wheat injuries addressed, and by doing so provides a quantitative and operational synthesis of the knowledge accumulated over the past 40 years on damage mechanisms of wheat pests. The effect of production situation on crop physiology has been incorporated in WHEATPEST in the simplest possible way. In this respect, the structure of WHEATPEST is similar to that of RICEPEST (Willocquet et al., 2004) and of the model developed by Johnson (1992). Such similarities of structures, applied to a range of crops and pests, outline the genericity of the approach taken.

Although WHEATPEST has been parameterised for winter wheat, the general structure and the modelling of damage mechanisms are also relevant for spring wheat. Modelling of spring wheat would only require an adaptation of the simulation of the development stage. Water stress was not accounted for in the present study, because no available field data (i.e., combining water stress and pest injuries) could be mobilized to address this issue, and because the datasets used to assess the model's performance were assumed to be associated with environment with limited water stress (UK and The Netherlands in the 1980s). The structure of WHEATPEST however enables the integration of water stress effect on physiological processes, because water stress mainly reduces RUE and accelerates leaf senescence, which are represented in the structure of WHEATPEST.

Many models have been developed over the last 30 years as tools to support tactical decisions in pest management. Although most of these tools are pest-specific, several systems tools have been developed to consider simultaneously several pests injuring a crop (e.g., Zadoks, 1989; Hagelskjaer and Jorgensen, 2003; Audsley et al., 2005). These systems tools are very useful for tactical, within-season, pest management (in particular, pesticide applications), but address objectives that are very different from the objective of this study.

Fig. 1 indicates that the bulk of the damage mechanisms concern mostly LAI, RUE, and RDIV. In each case, less-than additive effects are hypothesized, following earlier reports in host-multiple pests systems such as potato (Johnson et al., 1987), groundnut (Savary and Zadoks, 1992), and rice (Savary et al., 2000b). It remains to be seen in the case of wheat pests whether such hypotheses are also valid.

4.1.2. Modelling of damage mechanisms caused by foliar diseases

Damage mechanisms caused by leaf diseases is represented here using the virtual lesion concept (Bastiaans, 1991), and the parameter beta, which represents the total host area affected by the pathogen divided by the area of the visually measurable lesion. Beta thus synthesizes the injury effect on photosynthesis, and should not be confused with assimilate diversion by the pathogen for its growth and/or propagule production. Reflecting the effect on photosynthesis, beta is sensitive to production situation, the plant nutritional status, the type of plant tissues, and to the level of compatibility between host and pathogen (i.e., a reaction type; Zadoks and Schein, 1979).

The parameter beta is usually measured at saturation radiation (e.g., Bastiaans, 1991; Lopes and Berger, 2001; Robert et al., 2005, 2006), i.e., it only reflects the effect measured on the maximum rate of assimilation (Amax, Goudriaan, 1982), and not, e.g., the effect on the initial light use efficiency (epsilon, Goudriaan, 1982). In this case, beta only partly accounts for the injury effect on photosynthesis. Beta is commonly measured in single-leaf experiments, and so does not consider an entire crop stand, possibly leading to biased estimates of injury effects (Lopes and Berger, 2001). As WHEATPEST considers 1 m^2 of crop, the use of beta needs to be pondered. Although the approach using beta has limitations, it was chosen in the present analysis for its simplicity in reflecting injury mechanisms caused by foliar lesions and affecting photosynthesis.

Our choice when modelling damage mechanisms caused by foliar pathogens therefore was (1) to consider photosynthesis reduction and carbohydrate diversion as two separate processes that co-exist; (2) make use of literature data on photosynthesis reduction and spore production to estimate beta and carbohydrate reduction, respectively, and (3) to assume the existence of lesions that extend beyond their visual limits in reducing the rate of photosynthesis (virtual lesion) as measured by severity measurements, simultaneously with the production of propagules. In the case of some biotrophic pathogens, where severity is very difficult to assess (e.g., powdery mildew), literature indicates extremely high beta values (e.g., Rabbinge et al., 1985) which probably results from severity under-estimation and/or undetectable pathogen growth.

Reduction of photosynthetic area (LAI) therefore is incorporated in the model as a reduction of GLAI (photosynthetically active area) and not as a reduction of RI (radiation interception). The assumption is therefore that the presence of lesions at any location in the canopy does not affect the photosynthetic competency (Lopes and Berger, 2001) of any green (healthy) tissue anywhere in the canopy (either through self-shading effects, or differences in physiological age).

4.2. Assessment of model behaviour

Yield losses simulated for individual and combined wheat pests injuries under combinations of three production systems by three injury profiles (Fig. 5) indicate that the model allows to account for a variety of pests and production situations. In this respect, the model fulfils one prime objective for which it was built. Estimates of national yield losses that were derived from the literature were within the ranges of simulated values using WHEATPEST in the nine production situation by injury profiles considered, for the individual pests addressed, except for brown rust. WHEATPEST thus simulates yield loss values which are in general in agreement with orders of magnitude reported under similar production environments.

Although no formal evaluation of WHEATPEST is possible at this stage, this partial evaluation suggests that both individual and combined injury effects on crop growth and yield are satisfactorily well modelled, at least within the objectives set for this modelling work. The structure of the model, and the different damage mechanisms it includes, incorporate processes that have been proven to represent satisfactorily physiological pathways involved in crop growth (e.g., Monteith, 1977; Ayres, 1981; Goudriaan, 1982; Penning de Vries et al., 1989), and in the effects of injury on crop physiology (e.g., Rabbinge and Vereijken, 1980; Boote et al., 1983). Further refinements could be added in the future, which should (1) respect a balance in the details of representation of both crop physiology and damage mechanisms process, and (2) keep the model as simple as possible.

4.3. Perspective for model use

WHEATPEST allows simulating yield losses caused by individual and combined wheat pest injuries. When run with, e.g., arrays of production situation and injury drivers that capture a diversity of European wheat fields, WHEATPEST could simulate yield losses for these sets of contexts, and thus provide a basis to rank wheat pests according to their reducing effect on crop production. In a further stage, if the efficiency of pest management tools (Savary et al., 1998) is accounted for in simulation scenarios (see, e.g., Willocquet et al., 2004), analyses from simulated outputs under specified scenarios of pest management could be used as a component to guide research priorities for wheat pest management in Europe.

Another use of WHEATPEST could be to provide a baseline to structure and guide large-scale data collection and impact assessment. Surveys conducted at the European scale to characterise production situations and injury profiles for wheat could use WHEATPEST as a framework to design standardised protocols for data collection. Recent statistical advances (including meta-analyses methodology; Rosenberg et al., 2004), bioinformatics, database management, and information networking could be mobilised to link information obtained from surveys and from simulations.

Simulation modelling allows addressing scenarios that have not been experienced in real systems. In our case, WHEATPEST could be used to address future scenarios, through the use of drivers representing important global changes that may occur in the medium or long term. This includes for example water availability and its impact on crop growth and injury profiles.

Although a large number of wheat pests have been addressed in this work, several are not yet included. This is the case, e.g., of tissue consumers (*sensu* Boote et al., 1983) such as slugs, or additional leaf diseases such as stem rust. Although the importance of this latter disease has declined worldwide in the last decades due to resistance breeding, the recent detection of new races may render this disease a future reality (Stokstad, 2007). The structure of WHEATPEST allows integration ofsuch pests, if needed.

4.4. Future needs

Many strong hypotheses have been made here to determine injury profiles in different production situations. The determination of these injury profiles in different production situations was guided here by the need to assess the ability of WHEATPEST to account for these diversities. This study points at the acute, basic, need for reasonably accurate data on injury levels in winter wheat across its diversity of production situations in Europe. This need reflects several characteristics of the information available today: (1) the lack of standardised methods (sampling and assessment) for measuring injuries in farmers' field; (2) the over-specialisation of the information gathered, which would often consider one or a few pests, but very rarely all of them; and (3) poor, when not absent, information related to production situations, including cropping practices (among which the use of pesticides and the choice of varieties are integral parts).

Information including both production systems characteristics and multiple pests would enable to better characterise links between ranges of production situations and of injury profiles in wheat in Europe, and thus exploit tools such as WHEATPEST to explore management options, present or future.

5. References

Aggarwal, P.K., Banerjee, B., Daryaei, M.G., Bhatia, A., Bala, A., Rani, S., Chander, S., Pathak, H., Kalra, N., 2006a. InfoCrop: a dynamic simulation model for the assessment of crop yields, losses due to pests, and environmental impact of agro-ecosystems in tropical environments. II. Performance of the model. Agric. Syst. 89, 47–67.

Aggarwal, P.K., Kalra, N., Chander, S., Pathak, H., 2006b. InfoCrop: a dynamic simulation model for the assessment of crop yields, losses due to pests, and environmental impact of agro-ecosystems in tropical environments. I. Model description. Agric. Syst. 89, 1–25.

Audsley, E., Milne, A., Paveley, N., 2005. A foliar disease model for use in wheat disease management decision support systems. Ann. Appl. Biol. 147,161–172.

Avelino, J., Zelaya, H., Merlo, A., Pineda, A., Ordonez, M., Savary, S., 2006. The intensity of a coffee rust epidemic is dependent on production situations. Ecol. Model. 197, 431–447.

Ayres, P.G., 1981. Effects of Disease on the Physiology of the Growing Plant. Cambridge University Press, Cambridge.

Bastiaans, L., 1991. Ratio between virtual and visual lesion size as a measure to describe reduction in leaf photosynthesis of rice due to blast. Phytopathology 81, 611–615.

Boote, K.J., Jones, J.W., Mishoe, J.W., Berger, R.D., 1983. Coupling pests to crop growth simulators to predict yield reductions. Phytopathology 73, 1581–1587.

Breman, H., DeWit, C.T., 1983. Rangeland productivity and exploitation in the Sahel. Science 221, 1341–1347.

Brisson, N., Gary, C., Justes, E., Roche, R., Mary, B., Ripoche, D., Zimmer, D., Sierra, J., Bertuzzi, P., Burger, P., Bussiere, F., Cabidoche, Y.M., Cellier, P., Debaeke, P., Gaudillere, J.P., Henault, C., Maraux, F., Seguin, B., Sinoquet, H., 2003. An overview of the crop model STICS. In: van Ittersum, M.K., Donatelli, M. (Eds.), Eur. J. Agron. 3/4, pp. 309–332.

Clarkson, J.D.S., 1981. Relationship between eyespot severity and yield loss in winter wheat. Plant Pathol. 30, 125–131.

Clarkson, J.D.S., Cook, R.J., 1983. Effect of sharp eyespot (*Rhizoctonia cerealis*) on yield loss in winter wheat. Plant Pathol. 32, 421–428.

Clarkson, D.T., Drew, M.C., Ferguson, I.B., Sanderson, J., 1975. The effect of the take-all fungus, *Gaeumannomyces graminis* var. tritici, on the transport of ions by wheat plants. Physiol. Plant Pathol. 6, 75–84.

Cook, R.J., Polley, R.W., Thomas,M.R., 1991. Disease-induced losses in winter wheat in England and Wales 1985–1989. Crop. Prot. 10, 504–508.

Daamen, R.A., 1981. Surveys of diseases and pests of winter wheat in the Netherlands, 1979–1980. Mededelingen van de Faculteit Landbouwwetenschappen. Rijksuniversiteit Gent 46, 933–937.

Daamen, R.A., 1990. Surveys of cereal diseases and pests in the Netherlands. 1. Weather and winter wheat cropping during 1974–1986. Neth. J. Plant Pathol. 96, 227–236.

Daamen, R.A., Stol, W., 1990. Surveys of cereal diseases and pests in the Netherlands. 2. Stem-base diseases of winter wheat. Neth. J. Plant Pathol. 96, 251–260.

Daamen, R.A., Stol, W., 1992. Surveys of cereal diseases and pests in the Netherlands. 5. Occurrence of Septoria spp. in winter wheat. Neth. J. Plant Pathol. 98, 369–376.

Daamen, R.A., Stol, W., 1994. Surveys of cereal diseases and pests in the Netherlands. 6. Occurrence of insect pests in winter wheat. Neth. J. Plant Pathol. 99 (Suppl. 3), 51–56.

Daamen, R.A.,Wijnands, F.G., Vliet, G., van, der., 1989. Epidemics of diseases and pests of winter wheat at different levels of agrochemical input. A study on the possibilities for designing an integrated cropping system. J. Phytopathol. 125, 305–319.

Daamen, R.A., Langerak, C.J., Stol, W., 1991. Surveys of cereal diseases and pests in the Netherlands. 3. Monographella nivalis and Fusarium spp. In winter wheat fields and seed lots. Neth. J. Plant Pathol. 97, 105–114.

Daamen, R.A., Stubbs, R.W., Stol, W., 1992. Surveys of cereal diseases and pests in the Netherlands. 4. Occurrence of powdery mildew and rusts in winter wheat. Neth. J. Plant Pathol. 98, 301–312.

De Wit, C.T., Penning de Vries, W.W.T., 1982. L'analyse des systèmes de production primaire. In: Penning de VriesW.W.T., Djiteye, M.A. (Eds.), La productivité des pâturages sahéliens. Agricultural Research Report 918. Pudoc, Wageningen, The Netherlands, pp. 275–283.

Debaeke, P., 1990. Effets de systèmes diversement intensifiés sur la composition et la dynamique de la flore adventice des céréales d'hiver. In: Proceedings EWRS Symposium on Integrated Weed Management in Cereals, Helsinki, pp. 143–152. Directorate-General for Agriculture, European Commission, 2003. Agriculture and the environment, http://ec.europa.eu/agriculture/publi/fact/envir/2003_en.pdf.

FAO, 2007. FAOSTAT http://faostat.fao.org.

Fitt, B.D.L., Goulds, A., Polley, R.W., 1988. Eyespot (*Pseudocercosporella herpotrichoides*) epidemiology in relation to prediction of disease severity and yield loss in winter wheat—a review. Plant Pathol. 37, 311–328.

Forrester, J.W., 1961. Industrial Dynamics. MIT Press, MIT, and JohnWiley & Sons, New York.

Foster, G.N., Blake, S., Tones, S.J., Barker, I., Harrington, R., 2004. Occurrence of barley yellow dwarf virus in autumn sown cereal crops in the United Kingdom in relation to field characterisation. Pest Manage. Sci. 60, 113–125.

Gate, P., 1995. Ecophysiologie du blé. Lavoisier. Paris and ITCF, Paris. Goudriaan, J., 1982. Potential production processes. In: Penning de Vries, F.W.T., van Laar, H.H. (Eds.), Simulation of Plant Growth and Crop Production. Pudoc, Wageningen, pp. 98–113.

Groot, J.J.R., 1987. Simulation of nitrogen balance in a system of winter wheat and soil. Simulation Report CABO-TT nr. 13, Wageningen.

Hagelskjaer, L., Jorgensen, L.N., 2003. A web-based decision support system for integrated management of cereal pests. Bull. OEPP 33, 467–471.

Herdt, R.W., 2006. Priorities for plant disease epidemiology and developing world food security. In: Plant Disease Epidemiology: Facing Challenges of the 21st Century. Cooke, M., Savary, S. (Eds), Eur. J. Plant Pathol. Special Issue 115, 75–93.

Hoogenboom, G., Jones, J.W., Wilkens, P.W., Batchelor, W.D., Bowen, W.T., Hunt, L.A., Pickering, N.B., Singh, U., Godwin, D.C., Bear, B., Boote, K.J., Ritchie, J.T., White, J.W., 1994. Crop Models, DSSAT Version 3.0. In: International Benchmark Sites Network for Agrotechnology Transfer. University of Hawaii, Honolulu.

Hyvonen, T., Ketoja, E., Salonen, J., 2003. Changes in the abundance of weeds in spring cereal fields in Finland. Weed Res. (Oxford) 43, 348–356.

Johnson, K.B., 1990. Assessing multiple pest populations and their effects on crop yield. In: Crop Loss Assessment in Rice, IRRI, Los Banõs, Philippines, pp. 203–213.

Johnson, K.B., 1992. Evaluation of a mechanistic model that describes potato crop losses caused by multiple pests. Phytopathology 82, 363–369.

Johnson, K.B., Teng, P.S., Radcliffe, E.B., 1987. Analysis of potato foliage losses caused by interacting infestations of early blight, Verticilium wilt, and potato leafhopper; and the relationship to yield. Z. PflKrankh. PflSchutz. 94, 22–33.

King, J.E., 1977. Surveys of diseases of winter wheat in England and Wales, 1970–1975. Plant Pathol. 26, 8–20.

Kiniry, J.R., Jones, C.A., O'Toole, J.C., Blanchet, R., Cabelguenne,M., Spanel, D.A., 1989. Radiation-use efficiency in biomass accumulation prior to grain-filling for five grain crop species. Field Crops Res. 20, 51–64.

Kropff, M.J., Teng, P.S., Rabbinge, R., 1995. The challenge of linking pest and crop models. Agric. Syst. 49, 413–434.

Lopes, D.B., Berger, R.D., 2001. The effects of rust and anthracnose on the photosynthetic competence of diseased bean leaves. Phytopathology 91, 212–220.

Mantel, W.P., Rabbinge, R., Sinke, J., 1982. Effecten van bladluizen op de opbrengst van wintertarwe. Gewasbescherming 13, 115–124.

McKirdy, S.J., Jones, R.A.C., Nutter Jr., F.W., 2002. Quantification of yield losses caused by Barley yellow dwarf virus in wheat and oats. Plant Dis. 86, 769–773.

Mehta, Y.R., Zadoks, J.C., 1970. Uredospore production and sporulation period of *Puccinia recondita* f. sp. *triticina* on primary leaves of wheat. Neth. J. Plant Pathol. 76, 267–276.

Meinke, H., Hammer, G.L., van Keulen, H., Rabbinge, R., 1998. Improving wheat simulation capabilities in Australia from a cropping systems perspective. III. The integrated wheat model (I_WHEAT). Eur. J. Agron. 8, 101–116.

Mesterhazy, A., Bartok, T., Lamper, C., 2003. Influence of wheat cultivar, species of Fusarium, and isolate aggressiveness on the efficacy of fungicides for control of Fusarium head blight. Plant Dis. 87, 1107–1115.

Mesterhazy, A., Bartok, T., Kaszonyi, G., Varga, M., Toth, B., Varga, J., 2005. Common resistance to different Fusarium spp. causing Fusarium head blight in wheat. Eur. J. Plant Pathol. 112, 267–281.

Monsi, M., Saeki, T., 1953. Uber den Lichtfaktor in den Pflanzengesellschaften und sein Bedeutung fur die Stoffproduktion. Jpn. J. Bot. 14, 22–52.

Monteith, J.L., 1969. Light interception and radiative change exchange in crop stands. In: Eastin, J.D. (Ed.), Physiological Aspects of Crop Yield. American Society of Agronomy, Madison, WI, pp. 89–111.

Monteith, J.L., 1977. Climate and the efficiency of crop production in Britain. Phil. Trans. Roy. Soc. Lond. 281, 277–294.

Olsen, J., Kristensen, L.,Weiner, J., 2005. Effects of density and spatial pattern of winter wheat on suppression of different weed species. Weed Sci. 53, 690–694.

Parry, D.W., Jenkinson, P., Mc Leod, L., 1995. Fusarium ear blight in small grain cereals—a review. Plant Pathol. 44, 207–238.

Penning de Vries, F.W.T., Van Laar, H.H., 1982. Simulation of growth processes and the model BACROS. In: Penning de Vries, F.W.T., van Laar, H.H. (Eds.), Simulation of Plant Growth, Crop Production. Pudoc, Wageningen, pp. 114–135.

Penning de Vries, F.W.T., Jansen, D.M., ten Berge, H.F.M., Bakema, A. (Eds.), 1989. Simulation of ecophysiological processes of growth in several annual crops. IRRI, Los Banõs, and Pudoc, Wageningen.

Perry, K.L., Kolb, F.L., Sammons, B., Lawson, C., Cisar, G., Ohm, H., 2000. Yield effects of barley yellow dwarf virus in soft red winter wheat. Phytopathology 90, 1043–1048.

Polley, R.W., Clarkson, J.D.S., 1980. Take-all severity and yield in winter wheat: relationship established using a single plant assessment method. Plant Pathol. 29, 110–116.

Polley, R.W., Thomas, M.R., 1991. Surveys of diseases of winter wheat in England and Wales, 1976–1988. Ann. Appl. Biol. 119, 1–20.

Rabbinge, R., 1993. The ecological background of food production. In: Chadwick, D.J., Marsh, J. (Eds.), Crop Protection and Sustainable Agriculture. John Wiley and Sons., Chichester, UK, pp. 2–29.

Rabbinge, R., Vereijken, P.H., 1980. The effect of diseases or pests upon the host. Z. Pflkrankh. Pflschutz 87, 409–422.

Rabbinge, R., Jorritsma, I.T.M., Schans, J., 1985. Damage components of powdery mildew in winter wheat. Neth. J. Plant Pathol. 91, 235–247.

Rasmussen, I.A., Askegaard, M., Olesen, J.E., Kristensen, K., 2006. Effects on weeds of management in newly converted organic crop rotations in Denmark. Agric. Ecosyst. Environ. 113, 184–195.

Robert, C., Bancal, M.O., Nicolas, P., Lannou, C., Ney, B., 2004. Analysis and modelling of effects of leaf rust and Septoria tritici blotch on wheat growth. J. Exp. Bot. 55, 1079–1094.

Robert, C., Bancal,M.O., Ney, B., Lannou, C., 2005.Wheat leaf photosynthesis loss due to leaf rust, with respect to lesion development and leaf nitrogen status. New Phytol. 165, 227–241.

Robert, C., Bancal, M.O., Lannou, C., Ney, B., 2006. Quantification of the effects of Septoria tritici blotch on wheat leaf gas exchange with respect to lesion age, leaf number, and leaf nitrogen status. J. Exp. Bot. 57, 225–234.

Rooney, J.M., 1989. Biomass production and gas exchange of winter wheat as affected by flag leaf inoculations with Septoria nodorum. New Phytol. 112, 229–234.

Rosenberg, M.S., Garrett, K.A., Su, Z., Bowden, R.L., 2004. Meta-analysis in plant pathology: synthesizing research results. Phytopathology 94, 1013–1017.

Rossing, W., 1991. Simulation of damage in winter wheat caused by the grain aphid Sitobion avenae. 2. Construction and evaluation of a simulation model. Neth. J. Plant Pathol. 97, 25–54.

Rossing, W.A.H., Daamen, R.A., Jansen, M.J.W., 1994. Uncertainty analysis applied to supervised control of aphids and brown rust in winter wheat. Part 1. Quantification of uncertainty in cost-benefit calculations. Agric. Syst. 44, 419–448.

Savary, S., 1987. Enquête sur les maladies fongiques de l'arachide (*Arachis hypogaea*) en Côte-d'Ivoire. I. Méthodes d'enquête et étude descriptive : les conditions culturales et les principales maladies. Neth. J. Plant Pathol. 93, 167–188.

Savary, S., Zadoks, J.C., 1992. Analysis of crop loss in themultiple pathosystem groundnut-rust-late leaf spot. I. Six experiments. Crop. Prot. 11, 99–109.

Savary, S., De Jong, P.D., Rabbinge, R., Zadoks, J.C., 1990. Dynamic simulation of groundnut rust: a preliminary model. Agric. Syst. 32, 113–141.

Savary, S., Elazegui, F.A., Teng, P.S., 1998. Assessing the representativeness of data on yield losses due to rice diseases in tropical Asia. Plant Dis. 82, 705–709.

Savary, S., Willocquet, L., Elazegui, F.A., Teng, P.S., Du, P.V., Zhu, D., Tang, Q., Lin, X., Singh, H.M., Srivastava, R.K., 2000a. Rice pest constraints in tropical Asia:

characterization of injury profiles in relation to production situations. Plant Dis. 84, 341–356.

Savary, S.,Willocquet, L., Elazegui, F.A., Castilla, N.P., Teng, P.S., 2000b. Rice pest constraints in tropical Asia: quantification of yield losses due to rice pests in a range of production situations. Plant Dis. 84, 357–369.

Savary, S., Teng, P.S.,Willocquet, L., Nutter Jr., F.W., 2006a. Quantification and modeling of crop losses: a review of purposes. Ann. Rev. Phytopathol. 44, 89–112.

Savary, S.,Mille, B., Rolland, B., Lucas, P., 2006b. Patterns and management of crop multiple pathosystems. Special Issue: Plant disease epidemiology: facing challenges of the 21st Century. In: Savary, S., Cooke, B.M. (Eds.), Eur. J. Plant Pathol. 115, 123–138.

Scharen, A.L., Taylor, J.M., 1968. CO2 assimilation and yield of Little Club wheat infected by Septoria nodorum. Phytopathology 58, 447–451.

Schoeny, A., Jeuffroy, M.H., Lucas, P., 2001. Influence of take-all epidemics on winter wheat yield formation and yield loss. Phytopathology 91, 694–701.

Schoeny, A., Devienne-Barret, F., Jeuffroy, M.H., Lucas, P., 2003. Effect of take-all root infections on nitrate uptake in winter wheat. Plant Pathol. 52, 52–59.

Scott, P.R., Hollins, T.W., 1974. Effects of eyespot on the yield of winter wheat. Ann. Appl. Biol. 78, 269–279.

Scott, P.R., Hollins, T.W., 1978. Prediction of yield loss due to eyespot in winter wheat. Plant Pathol. 27, 125–131.

Sinclair, T.R., Muchow, R.C., 1999. Radiation-use efficiency. Adv. Agron. 65, 215–265.

Smiley, R.W., Gourlie, J.A., Easley, S.A., Patterson, L.M., Whittaker, R.G., 2005. Crop damage estimates for crown rot of wheat and barley in the Pacific Northwest. Plant Dis. 89, 595–604.

Spitters, C.J.T., 1989. Weeds: population dynamics, germination and competition. In: Rabbinge, R., Ward, S.A., van Laar, H.H. (Eds.), Simulation and Systems Management in Crop Protection. Pudoc, Wageningen, the Netherlands, pp. 182–217.

Spitters, C.J.T., van Keulen, H., van Kraalingen, D.W.G., 1989. A simple and universal crop growth simulator: SUCROS87. In: Rabbinge, R., Ward, S.A., van Laar, H.H. (Eds.), Simulation and Systems Management in Crop Protection. Pudoc, Wageningen, The Netherlands, pp. 147–181.

Spitters, C.J.T., van Roermund, H.J.W., van Nassau, H.G.M.G., Schepers, J., Mesdag, J., 1990. Genetic variation in partial resistance to leaf rust in winter wheat: disease progress, foliage senescence and yield reduction. Neth. J. Plant Pathol. 96, 3–15.

Stokstad, E., 2007. Deadly wheat fungus threatens world's breadbaskets. Science 315, 1786–1787.

van Bruggen, A.H.C., Termorshuizen, A.J., 2003. Integrated approaches to root disease management in organic farming systems. Aust. Plant Pathol. 32, 141–156.

Van Keulen, H., Penning de Vries, F.W.T., Drees, E.M., 1982. A summary model for crop growth. In: Penning de Vries, F.W.T., van Laar, H.H. (Eds.), Simulation of Plant Growth and Crop Production. Pudoc, Wageningen, pp. 87–97.

Wiese, M.V., 1991. Compendium ofWheat Diseases, 2nd ed. APS Press, Saint Paul, p. 112.

Willocquet, L., Savary, S., Fernandez, L., Elazegui, F., Teng, P.S., 2000. Development and evaluation of a multiple-pest, production situation specific model to simulate yield losses of rice in tropical Asia. Ecol. Model. 131, 133–159.

Willocquet, L., Savary, S., Fernandez, L., Elazegui, F.A., Castilla, N., Zhu, D., Tang, Q., Huang, S., Lin, X., Singh, H.M., Srivastava, R.K., 2002. Structure and validation of RICEPEST, a production situation-driven, crop growth model simulating rice yield response to multiple pest injuries for tropical Asia. Ecol. Model. 153, 247–268.

Willocquet, L., Elazegui, F.A., Castilla, N., Fernandez, L., Fischer, K.S., Peng, S., Teng, P.S., Srivastava, R.K., Singh, H.M., Zhu, D., Savary, S., 2004. Research priorities for rice disease and pest management in tropical Asia: a simulation analysis of yield losses and management efficiencies. Phytopathology 94, 672–682.

Wilson, B.J., Wright, K.J., Brain, P., Clements, M., Stephens, E., 1995. Predicting the competitive effects of weed and crop density on weed biomass, weed seed production and crop yield in wheat.Weed Res. (Oxford) 35, 265–278.

Yang, X., Zeng, S., 1988. Studies on crop loss caused by stripe rust on winter wheat II. Effect of disease on the leaf photosynthesis. Sci. Sin. (Ser. B) 31, 726–733.

Zadoks, J.C., 1984. A quarter century of disease warning, 1958–1983. Plant Dis. 68, 352–355.

Zadoks, J.C., 1989. EPIPRE, a computer-based decision support systemfor pest and disease control in wheat: its development and implementation in Europe. In: Leonard, K.J., Fry, W.E. (Eds.), Plant Disease Epidemiology, vol. II. McGraw-Hill Publishing Company, New York, pp. 3–29.

Zadoks, J.C., Rijsdijk, F.H., 1984. Agroecological Atlas of Cereal Growing in Europe. Atlas of Cereal Diseases and Pests in Europe, vol. III. Pudoc, Wageningen.

Zadoks, J.C., Schein, R.D., 1979. Epidemiology and Plant Disease Management. Oxford University Press, New York.

Zadoks, J.C., Chang, T.T., Konzak, C.F., 1974. A decimal code for the growth stages of cereals. Weed Res. 14, 415–421.