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Simulating crop–parasitic weed interactions using APSIM: Model evaluation and application

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Abstract

The parasitic weed *Orobanche crenata* inflicts major damage on faba bean, lentil, pea and other crops in Mediterranean environments. The development of methods to control *O. crenata* is to a large extent hampered by the complexity of host–parasite systems. Using a model of host–parasite interactions can help to explain and understand this intricacy. This paper reports on the evaluation and application of a model simulating host–parasite competition as affected by environment and management that was implemented in the framework of the Agricultural Production Systems Simulator (APSIM). Model-predicted faba bean and *O. crenata* growth and development were evaluated against independent data. The APSIM-Fababean and -Parasite modules displayed a good capability to reproduce effects of pedoclimatic conditions, faba bean sowing date and *O. crenata* infestation on host–parasite competition. The r^2 values throughout exceeded 0.84 (RMSD: 5.36 days) for phenological, 0.85 (RMSD: 223.00 g m^{-2}) for host growth and 0.78 (RMSD: 99.82 g m^{-2}) for parasite growth parameters. Inaccuracies of simulated faba bean root growth that caused some bias of predicted parasite number and host yield loss may be dealt with by more flexibly simulating vertical root distribution. The model was applied in simulation experiments to determine optimum sowing windows for infected and non-infected faba bean in Mediterranean environments. Simulation results proved realistic and testified to the capability of APSIM to contribute to the development of tactical approaches in parasitic weed control.
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1. Introduction

An array of parasitic organisms inflict damage on global agricultural production. Parasitic weeds compete with host plant organs mainly for water and assimilates, leading to decreased resource availability for host growth and yield formation. One of the most noxious parasitic weeds in Mediterranean environments is *Orobanche crenata* (crenate broomrape), which frequently causes substantial yield losses in faba bean (*Vicia faba*), lentil (*Lens culinaris*), pea (*Pisum sativum*), carrot (*Daucus carota*) and other crops (Sauerborn, 1991; Riches and Parker, 1995). The extent of water and assimilate diversion from the host plant to *O. crenata* results from complex interactions of host genotype, parasite infestation level, environmental conditions and agronomic practices (Manschadi et al., 2001; Rubiales et al., 2003a). In faba bean crops, *O. crenata* acts like an additional plant organ mainly competing with pods for assimilate and thereby causing large yield losses (Manschadi et al., 2001). Sole applications of cultural, chemical, physical or biological control measures (Jacobsohn et al., 1980; Foy et al., 1989; Linke et al., 1990, to cite just a few) have proven either insufficient or impracticable, mainly due to the intimate connectivity of host and parasite. Delayed sowing of host crops can reduce the severity of *O. crenata* infection, presumably through effects of soil temperature on germination and early development of the parasite (Mesa-García and García-Torres, 1986; Sauerborn, 1989; Rubiales et al., 2003b; Grenz et al., 2005). However, this practice can also cause the seed filling period to extend into the Mediterranean dry season, thereby reducing yield potential. Site-specific optimum sowing strategies yet remain to be developed. Control of *O. crenata* is likely to be achieved through strategies integrating several approaches (Linke and Saxena, 1991; Pieterse et al., 1994). Experimental evaluations of such strategies are

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hindered by constraints of time, resources and complexity. An eco-physiological model allowing the quantification of environment – crop – parasitic weed interactions (Spitters, 1989; Kropff and Lotz, 1992) could improve our understanding of the system and facilitate assessments of the potential efficacy of possible control strategies.

A model simulating the faba bean—*O. crenata* system as affected by environment and management was developed by Manschadi et al. (2001) and integrated into the Agricultural Production Systems Simulator (APSIM) as the APSIM-Parasite module (Manschadi et al., 2003, 2004). The APSIM framework combines biophysical and management modules with a central engine to simulate crops and rotations and has been applied to various situations (Wang et al., 2003; Keating et al., 2003). APSIM-Parasite can be applied in a generic manner to all crop modules and is the first module allowing the simulation of effects of biotic stress in APSIM.

The objectives of this study were to (i) evaluate the performance of APSIM for predicting damage effects of *O. crenata* on faba bean and (ii) test the capability of the model to contribute to control strategy development. Model-predicted growth and development of faba bean and *O. crenata* were evaluated against independent field data. The applicability of APSIM-Parasite in control strategy development will be tested by using the model to determine optimum faba bean sowing windows as affected by environment and *O. crenata* infestation.

2. Materials and methods

2.1. Model description

A configuration of APSIM version 3.2, including the SoilWat2-, SoilN2-, Residue2- and Fababean-modules (Probert et al., 1998; Turpin et al., 2003), was used to simulate non-parasitised faba bean. This configuration predicts dynamics and interactions of carbon, nitrogen and water within the crop–soil system as driven by daily weather information. APSIM-Fababean is based upon the generic APSIM-Legume template that simulates crop phenology, leaf area expansion, biomass accumulation, partitioning and senescence, as well as nitrogen and water uptake (Robertson et al., 2002). Since *O. crenata* mainly affects host yield via reductions of pod number (Manschadi et al., 2001; Grenz et al., 2005), a version of APSIM-Fababean employing a cohorting approach to yield simulation was used (Manschadi et al., 2004). During flowering, new pod cohorts are initiated daily. The number of pods in each cohort is a function of assimilate supply and the genotype-specific minimum supply required to set a pod (Stützel, 1995). Assimilates are allocated to cohorts in descending order of physiological age. Pod growth depends on physiological age of the cohort, maximum pod weight of the genotype, potential duration of the reproductive phase and potential pod growth rate, modified by temperature and assimilate supply. Pod detachment is based on the ratio of assimilate supply to demand (Batchelor et al., 1994).

To simulate parasitised crops, APSIM-Soiltemp, which calculates soil temperature, and a version of APSIM-Parasite configured for *O. crenata* were added. APSIM-Parasite calculates *O. crenata* phasic development based on the assumption that development rate is mainly a function of soil temperature (Mesa-García and García-Torres, 1986; Arjona-Berral et al., 1987). Parasite cohorts are initiated daily. Parasite number in each cohort is a function of host root length density and initial parasite seedbank level. Potential carbon demand of each parasite depends on a stage-dependent growth rate, modified by ambient temperature. Assimilate partitioning to parasites is the minimum of total parasite demand and assimilate supply by the host, with parasites having higher sink priority than vegetative faba bean organs and newly formed pods, but lower priority than pods in the seed filling phase (Fig. 1) (Manschadi et al., 2001). In infected
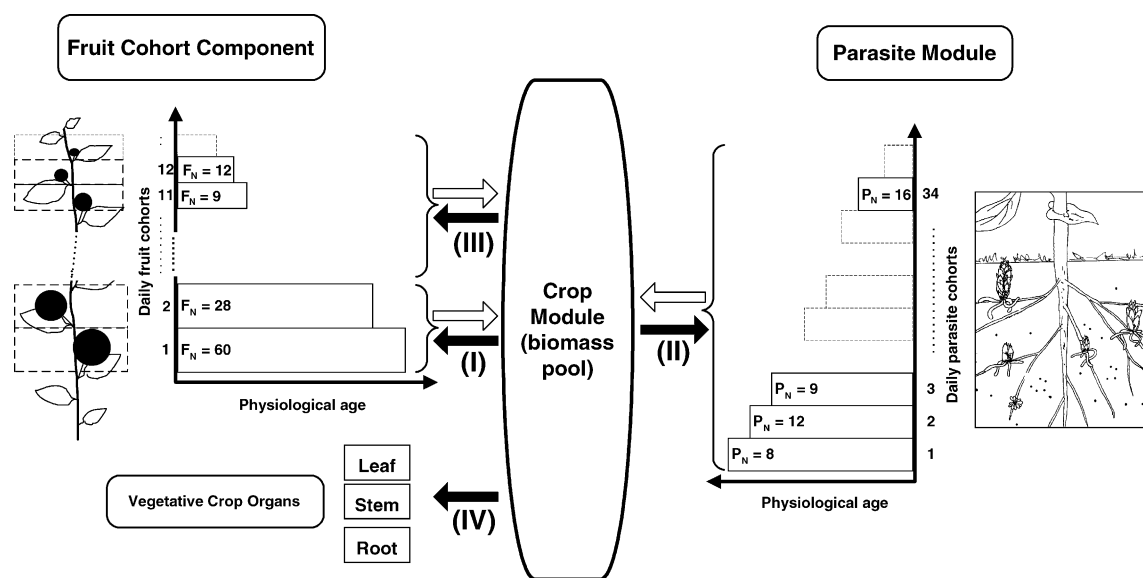

Fig. 1. Schematic representation of the simulation of cohorts of crop fruits and parasites. F_N and P_N indicate the number of fruits and parasites in each cohort, respectively; arrows represent carbon demand (open) and supply (closed); roman numerals show the priority order for assimilate partitioning. From Manschadi et al. (2004).

Table 1
Location characteristics and experimental factors of trials used in calibration and evaluation of APSIM-Fababean and -Parasite

Experiments				Treatments			
No.[a], symbol	Year	Location	Soil texture[b] (%)	Irrigation (mm)	Infestation[c]	Sowing date[d] (DOY)	Cultivar[e]
C1, ♦	1993–1994	Tel Hadya (36.0°N 37.0°E)	60/30/10	30, 180	0	11/10, 12/20	I
C2, ●	1994–1995	Tel Hadya (36.0°N 37.0°E)	60/30/10	30, 256	0, 50, 200, 600	11/7, 12/12	I
E1, ●	2000–2001	Balcali (37.0°N 35.4°E)	47/25/28	20	0, 25, 200	12/3, 1/4	I, S
E2, ■	2000–2001	Yumurtalik (36.8°N 35.8°E)	25/35/40	15	0, 25, 200	12/4, 1/6	I, S
E3, ▲	2001–2002	Balcali (37.0°N 35.4°E)	47/25/28	20	0, 25, 200	11/5, 12/13	A, S
E4, ▼	2001–2002	Hacihasan (36.6°N 35.4°E)	30/55/15	0	0	11/8, 1/26	A, S

[a] C: calibration, E: evaluation.
[b] Clay/silt/sand.
[c] Viable *O. crenata* seeds kg^{-1} soil in 0–15 cm depth.
[d] Month/day.
[e] I = ILB 1814, S = Sakiz, A = Aquadulce.

crops, assimilate availability to younger pods is reduced, leading to increased pod abortion (Manschadi et al., 2004).

The following modifications to APSIM-Fababean were implemented:

- APSIM-Legume does not account for effects of drought stress on post-flowering phenological development (Robertson et al., 2002). However, water stress can accelerate maturation and shorten the seed filling period of legumes (Desclaux and Roumet, 1996, on soybean (*Glycine max*); De Costa et al., 1997, on faba bean). This can result in smaller seeds and lower grain yield (Loss and Siddique, 1997; Loss et al., 1997). Moreover, development rates of faba bean and *O. crenata* have a major influence on host–parasite competition (Grenz et al., 2005). Therefore, table look-up functions were added to make post-flowering crop development responsive to soil water availability.
- Root growth as calculated by APSIM-Legume is vertically homogeneous, with the option to include root branching. Faba bean roots in fact are concentrated in the topsoil (Manschadi et al., 1998; Sau and Mínguez, 2000). Since the probability of parasite germination depends on host root length density in the infested layer (ter Borg and van Ast, 1991; Manschadi et al., 2001), accurate predictions of faba bean root growth are required to correctly simulate parasite infection. Therefore, the approach of Jones et al. (1991) was adopted by introducing

a factor allowing vertical root distribution to exponentially decrease with root depth.

2.2. Model evaluation

2.2.1. Experimental data

Data for model evaluation were collected in on-station experiments conducted at the University of Cukurova in Adana (Turkey) during the 2000–2001 and 2001–2002 growing seasons (Table 1; Grenz et al., 2005). Balcali (37°N 35.4°E) is located in the centre of the Cukurova plain in southern Turkey, while Yumurtalik and Hacihasan are situated at 110 and 40 km distance, respectively, from Balcali. Experiments were designed as split–split-plots with four replications, with *O. crenata* infestation as main plot, sowing date as subplots and faba bean cultivar as sub-subplots. Plots were artificially infested to 15 cm depth with 25 or 200 viable *O. crenata* seeds kg^{-1} soil, or left as an untreated control. Faba bean was sown at 5 cm depth at a rate of 20 seeds m^{-2} with 50 cm row spacing, fertilised with diammonium-phosphate at 20 kg N and 22 kg P ha^{-1} and irrigated with 12–30 mm water at sowing, depending on soil moisture status. Air temperature, soil temperature at 10 cm depth, rainfall and solar radiation were continuously recorded by weather stations (μ-Metos, Pessl Instruments, Austria) installed in the fields. Soil moisture from 0 to 90 cm depth was measured fortnightly by a time domain reflectometry tube probe
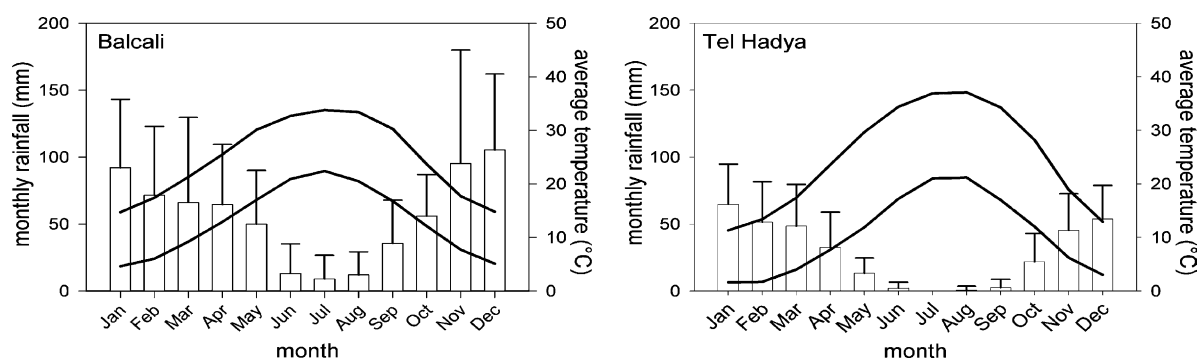
Fig. 2. Climatic conditions at Balcali and Tel Hadya from 1979 to 2000. Symbol meanings: curves, monthly averages of maximum and minimum air temperature, columns, average monthly rainfall (±1S.D.).
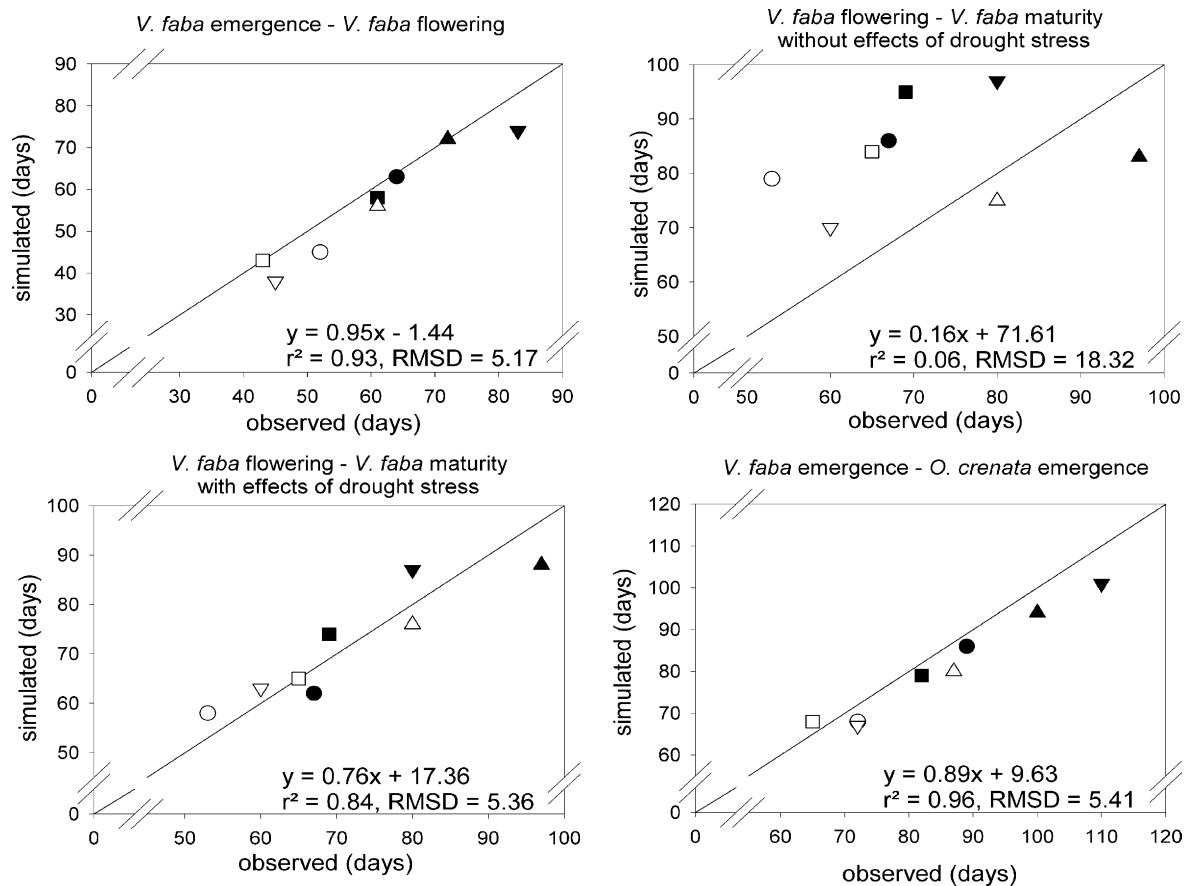
Fig. 3. Linear regressions of simulated vs. observed durations of faba bean and *O. crenata* development phases. Symbol meanings: see Table 1. Full and hollow symbols represent early and late-sown crops, respectively.

system (TRIME-T3, IMKO, Germany) in the first and gravimetrically in the second season. Host and parasite phenology were recorded weekly. Sequential biomass harvests as described by Manschadi et al. (2001) were carried out 4 weekly, starting 3 weeks after emergence. Soil cores were taken to 45 cm depth from beneath and beside one plant per non-infested plot to determine root length density and weight. Only data collected from faba bean cultivars ILB 1814 and Aquadulce were used in the evaluation.

2.2.2. Model parameterisation

Information on soil hydrological characteristics, N status and clay content required to parameterise APSIM-SoilWat2, -SoilN2 and -Soiltemp was derived from the field data. Crop husbandry was programmed according to the agronomic practice applied in the field. Species-specific constants and cultivar-specific parameters for faba bean cultivar ILB 1814 were set to values employed during calibration of APSIM-Fababean (Turpin et al., 2003) and -Parasite (Manschadi et al., 2004). In the second season

Table 2
Ranges of rainfall received and growth parameter results obtained from calibration and evaluation trials

Trials		Results				
No.	Data sets[a] (*n*)	Rainfall[b] (mm)	Host biomass[c] (g m^{-2})	Grain yield[c] (g m^{-2})	Parasites[c] (m^{-2})	Parasite biomass[c] (g m^{-2})
C1	4	358	464–1116	217–377		
C2	16	320	137–1050	0–358	35–586	94–534
E1	6	213	391–773	140–381	18–63	35–214
E2	6	498	239–920	42–499	16–156	70–491
E3	6	756	308–1163	83–645	32–273	217–765
E4	2	812	726–1348	460–878		

For more detailed information, see Manschadi et al. (2001) and Grenz et al. (2005). Trial numbers: see Table 1.
[a] Data used in the evaluation (cv. ILB 1814 and Aquadulce).
[b] Received between sowing and harvest of first-sown crops.
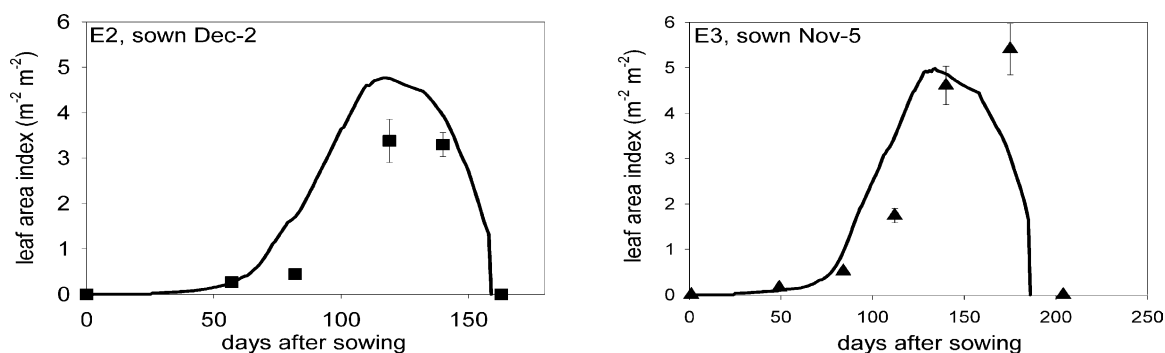[c] Ranges of treatment means.

Fig. 4. Course of simulated (curves) and measured (symbols, ±1S.E.) leaf area index of faba bean in different seasons and at different locations. Symbol meanings: see Table 1.

of evaluation experiments, cultivar ILB 1814 was replaced by the Spanish cultivar Aquadulce (Table 1). Both genotypes share similar phenological and morphological characteristics, thus one parameterisation was used to simulate both.

2.3. Model application

We used APSIM-Parasite with historical weather records (1979–2000) from Balcali and Tel Hadya (Syria, 36°N 37°E) to assess effects of delayed sowing, a traditional control measure against the parasite, and *O. crenata* infestation level on faba bean yield. Balcali has a humid Mediterranean climate, while Tel Hadya has a semi-arid Mediterranean-continental transition climate (Fig. 2). Solar radiation data for Balcali were completed by data generated by the Climgen program (Nelson, 2003). Soil parameters for Balcali and crop parameters were the same as during evaluation. Soil parameters for Tel Hadya were adopted from Moeller (2004). Seven sowing dates from October to January, representing the first and second halves of months, respectively, were tested. Crops growing in non-infested fields and fields infested with 100 *O. crenata* seeds kg^{-1} soil at 0–15 cm depth were simulated. For sensitivity analysis of crop response to parasite infestation, further seed-bank levels from 10 to 1000 seeds kg^{-1} soil were added. In
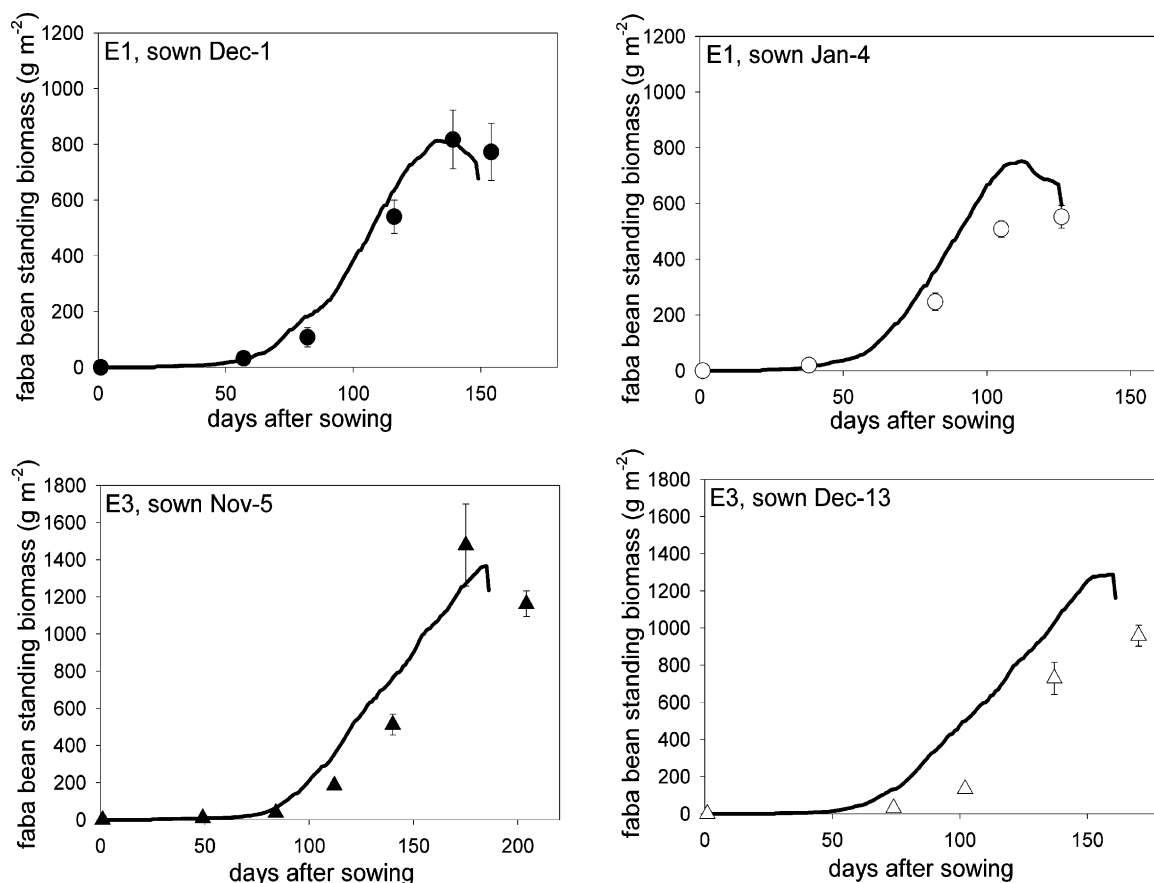

Fig. 5. Course of simulated (curves) and measured (symbols) standing biomass of noninfected faba bean as affected by sowing date in different seasons. Symbol meanings as in Fig. 4. Full and hollow symbols represent early and late-sown crops, respectively.
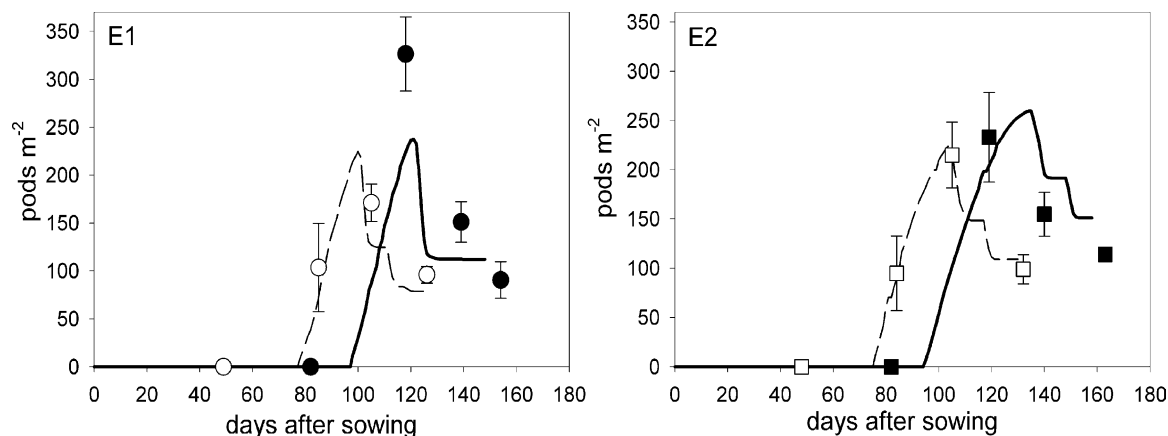
Fig. 6. Course of simulated (curves) and measured (symbols) pod number of noninfected faba bean as affected by sowing date at different locations. Symbol meanings as in Figs. 4 and 5.

all simulations, faba bean cultivar ILB 1814 was sown to 5 cm depth at 20 plants m^{-2}. At crop sowing, 20 kg N ha^{-1} (as urea) were incorporated to 10 cm depth. A starter irrigation of 30 mm was applied at sowing to ensure timely germination and comparability of treatment results. Statistical analysis of simulated data was performed using SigmaPlot^{TM} (SPSS Inc., 2000) and MINITAB^{TM} (MiniTab Inc., 2000).

3. Results and discussion

3.1. Model evaluation

An overview of experimental results is presented in Table 2. Faba bean emergence was reproduced well, except for early predicted emergence of early sown crops exposed to water stress and ground frosts. These conditions may have been beyond the range for which APSIM-Fababean is calibrated. Flowering was consistently predicted several days too early. This bias can be explained by deviant definitions of flowering: according to Knott (1990), whose key was used to rate crop phenology in the field, flowering is reached when 75% of plants have opened at least one flower, while APSIM employs a threshold value of 50% (APSRU, 1999). Post-flowering development was simulated accurately, and a comparison of model performance with and without activation of post-flowering drought stress effects on faba bean development illustrated the functionality of this feature. The period from faba bean emergence, when the first *O. crenata* seeds can have been stimulated to germinate (Linke, 1987), until parasite emergence was reproduced accurately (Fig. 3).

Simulations of leaf number, leaf dry weight and stem dry weight were mostly within the error of the measured data. Predicted leaf expansion and senescence often proceeded too fast, possibly compounded by positive feedback via biomass accumulation and partitioning to leaves: rapid leaf area expansion resulted in rapid crop growth and vice versa. Shape and magnitude of faba bean biomass accumulation were well simulated. However, there was a tendency to overpredict the onset of the exponential growth phase, possibly related to an overestimation of early leaf area development (Figs. 4 and 5). Predicted course of pod number and dry weight in non-infected crops were in good accordance with observed values (Fig. 6).

While root depth increase was reproduced well, root length density in 0–15 cm soil depth, a variable positively linked with parasite number, was often overpredicted. Consequentially, *O. crenata* number tended to be overestimated, particularly in treatments infested with 200 *O. crenata* seeds kg^{-1} soil. Nevertheless, simulations of parasite number mostly corresponded well
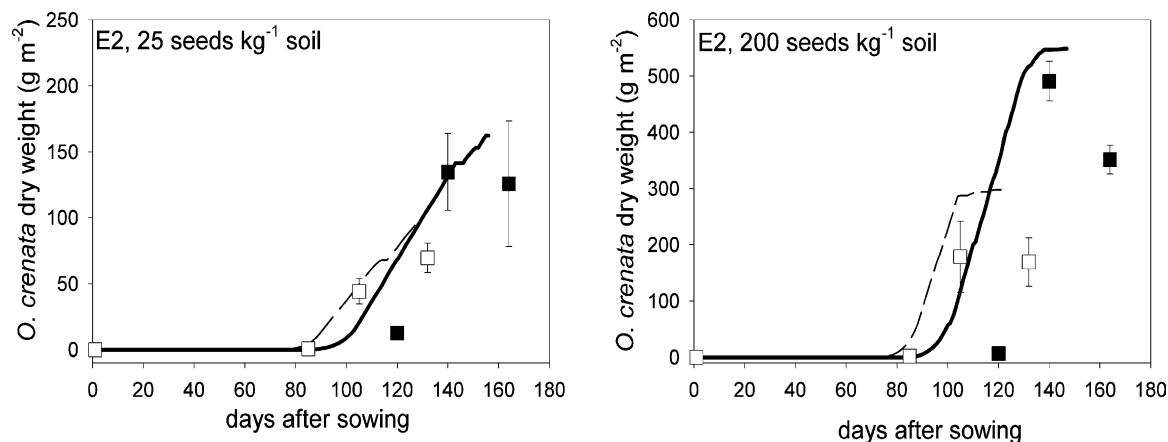

Fig. 7. Course of simulated (curves) and measured (symbols) *O. crenata* dry weight as affected by infestation level. Symbol meanings as in Figs. 4 and 5.
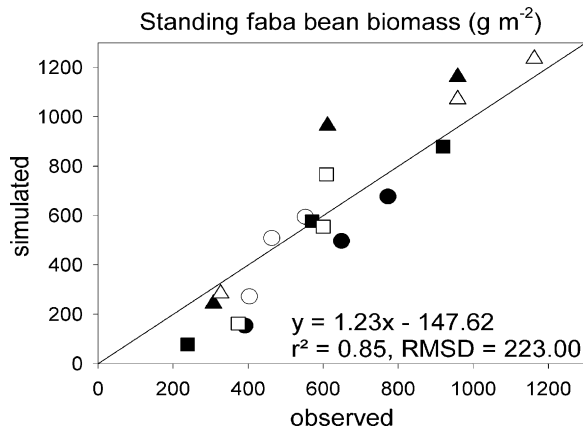
Fig. 8. Linear regression of simulated vs. observed faba bean standing dry weight at physiological maturity. Symbol meanings as in Fig. 3.

Fig. 9. Linear regression of simulated vs. observed faba bean pod dry weight at physiological maturity. Symbol meanings as in Fig. 3.

with field observations. Observed course and extent of *O. cre-nata* biomass accumulation were well reproduced (Fig. 7), given the difficulties associated with field determination of this parameter: parasite growth and decomposition occur at rates that render capturing the shape and maximum of the growth function very difficult. Reductions of parasite biomass caused by decomposition are not accounted for in the model, thus overpredictions of this variable during the final development stages were to be
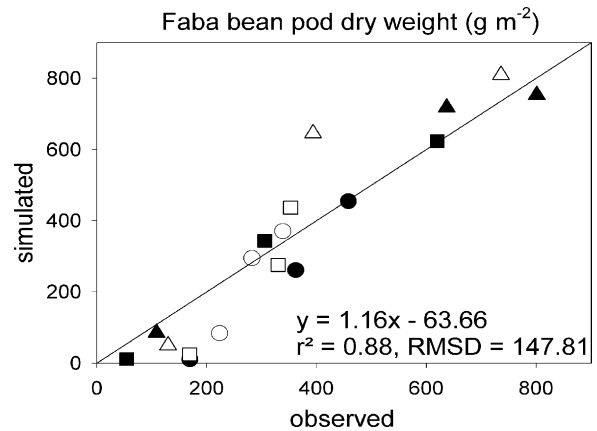
expected. Linear regression of observed versus simulated maximum *O. crenata* dry weight yielded an r^2 of 0.78 (RMSD: 99.82 g m^{-2}).

Simulated dry weight of parasite-infected crops at maturity was reasonably close to experimental results (Fig. 8). Pod yield was reproduced well at seedbank levels of 0 and 25 *O. crenata* seeds kg^{-1} soil, but underpredicted at 200 *O. crenata* seeds kg^{-1} soil (Fig. 9). Mean yield loss at this infestation level was
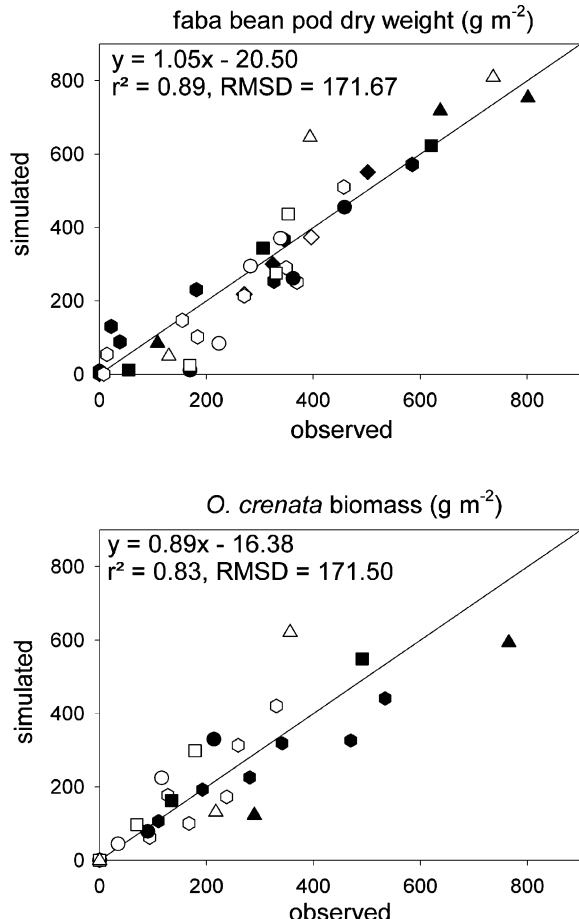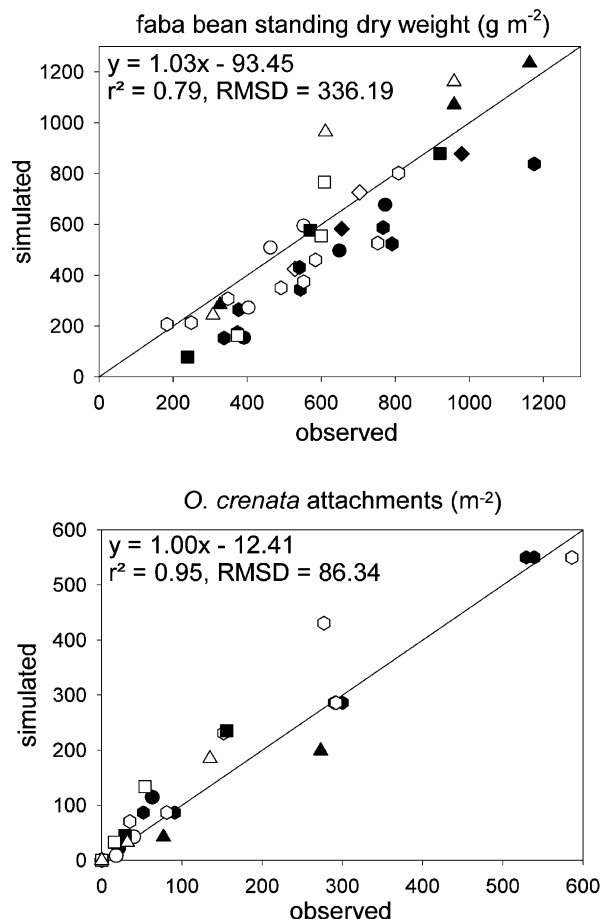

Fig. 10. Linear regressions of simulated vs. observed maximum faba bean standing and pod dry weight at harvest, as well as maximum *O. crenata* number and dry weight for the complete set of calibration and evaluation trials. Symbol meanings as in Fig. 3.
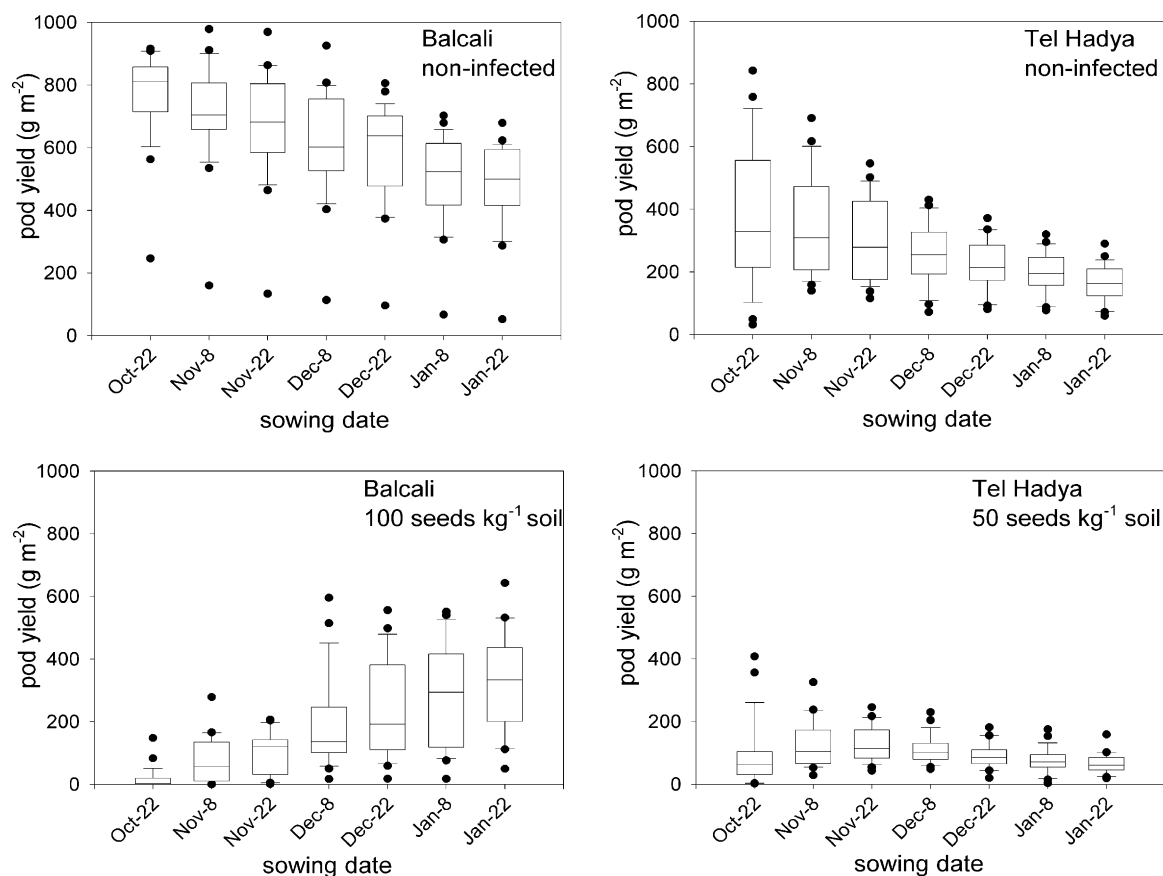
Fig. 11. Box–Whisker plots showing effects of sowing date on simulated faba bean pod yield without and with infestation by *O. crenata* at Balcali and Tel Hadya. Boxes comprise second and third quartiles, lines show median, whiskers mark 10% and 90% quantiles, dots symbolise outliers beyond 10% and 90%.

74% in the field, but 88% in the simulations. Linear regression showed variations in simulated parasite number to explain 90% (r^2) of yield loss variations in infected crops. Simulated parasite number at given seedbank density in turn is determined by host root length density. When simulated root length density in 0–15 cm depth was adjusted to field-observed values by using trial-specific exponents of the vertical root distribution function, the r^2 of the observed versus simulated parasite num-

ber increased from 0.69 to 0.97. We infer that overestimation of parasite number and underestimation of yield mostly resulted from inaccuracies of simulated vertical root distribution. Since all of the variables concerned are difficult to quantify, some deviation must be attributed to experimental error: sampling frequency was not sufficient to fully capture the dynamics of biomass accumulation and decay of faba bean roots and *O. crenata*. Soil sampling did not cover the complete root system, and
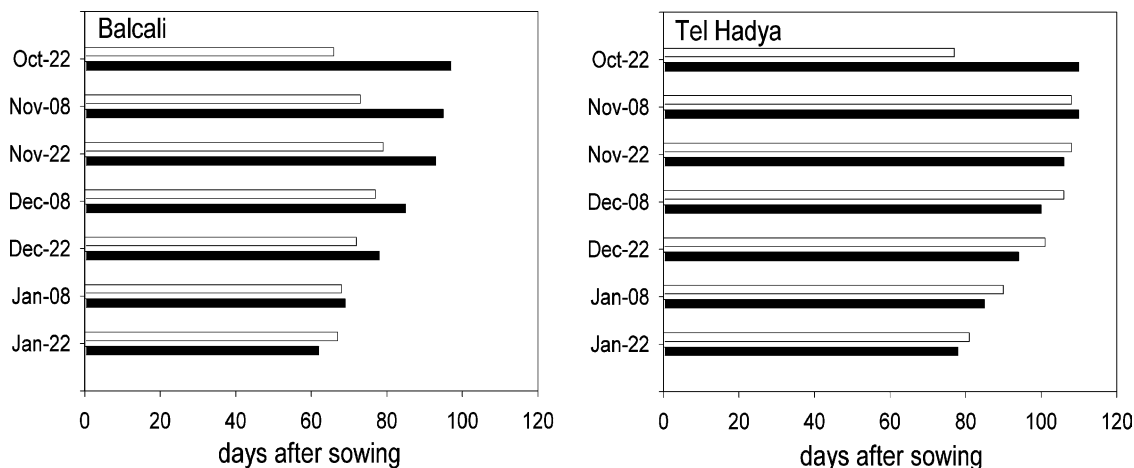

Fig. 12. Predicted duration of periods from faba bean sowing until flowering (black bars) and until first occurrence of *O. crenata* tubercles (white bars), respectively, as affected by sowing date and location.

a higher number of replicates would have been desirable for root-related parameters.

A combined analysis of all data used in model development and evaluation gave a good performance of the APSIM-Fababean and -Parasite modules. Linear regressions of simulated versus observed faba bean biomass and pod yield at harvest, as well as of maximum *O. crenata* number and biomass all yielded high r^2 values (Fig. 10). There was no serious bias, as all regression lines were close to the 1:1 line through the origin. APSIM showed a good capability to reproduce reductions of parasite number and increases of faba bean pod number and yield associated with delayed sowing of the host crop, which is an important touchstone for the practical relevance of model recommendations.

3.2. Model application

An Anderson–Darling test for normality showed simulated faba bean biomass and yields to follow non-normal distributions, thus yield averages were calculated as medians and a Mann–Whitney *U*-test was used to pairwise check treatments for significant differences. The examination of model-predicted phenology suggested that APSIM-Fababean does not account for frost damage to flowers, which might cause inaccuracies. At both locations, flowering was predicted to start in January or February for most crops sown in late October and November. Frost, which can cause yield penalties in faba bean when coinciding with flowering (ICARDA, 1987), affects about one-third of January and February days at Tel Hadya. Simulations of early sown crops must be interpreted with this in mind. Model predictions of *O. crenata* growth and development were realistic.

At Balcali, non-infected faba bean dry weight at harvest ranged from 1,346 g m^{-2} (standard error: 48.4 g m^{-2}) for crops sown on 22 October to 923 g m^{-2} (51.3) for the sowing date 22 January. At Tel Hadya, a maximum of 647 g m^{-2} (86.4) and a minimum of 411 g m^{-2} (28.8) corresponded to the same sowing dates. Simulations of pod yield in non-infected crops followed similar tendencies. The main determinant of crop biomass and yield was the amount of rainfall received, which was higher at Balcali than at Tel Hadya and in early-sown than in late-sown crops. Delaying sowing by 4 weeks gave significant yield reductions for all sowing dates at Balcali and all but the first sowing date at Tel Hadya. At an infestation level of 100 *O. crenata* seeds kg^{-1} soil, sowing faba bean 2 weeks later mostly increased yields significantly at Balcali. At Tel Hadya, effects of delayed sowing were not significant due to the simulated low overall yield level. At an infestation level of 50 *O. crenata* seeds kg^{-1} soil, delaying sowing until 22 November significantly improved yield at Tel Hadya (Fig. 11).

Delayed sowing prompted faster development of faba bean, mainly due to effects of daylength, temperature and drought stress. Parasites, whose development rate is affected neither by daylength nor by water stress, reacted to a much lesser extent. Hence, delayed sowing allowed faba bean to develop faster compared to *O. crenata* (Fig. 12). This translated into a competitive advantage of pods against parasites resulting in reduced pod
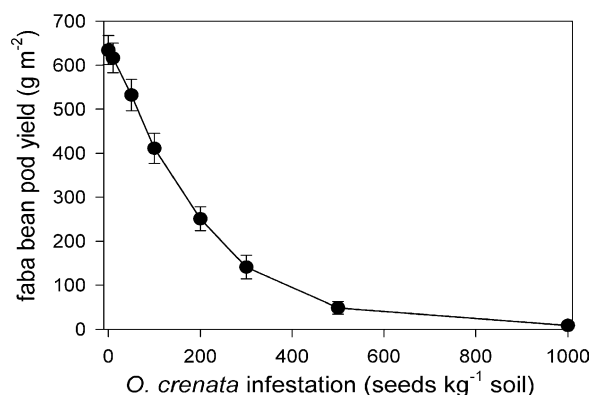

Fig. 13. Simulated pod yield of faba bean grown at Balcali as affected by *O. crenata* infestation. Results from simulations of 20 single seasons driven by historical weather data.

abortion. Similar mechanisms have been observed in field experiments (Grenz et al., 2005).

A sensitivity analysis of faba bean sown on 15 November at Balcali including infestation levels from 10 to 1000 *O. crenata* seeds kg^{-1} soil showed simulated pod yield to decrease hyperbolically with increasing parasite infestation (Fig. 13). A similar hyperbolic curve was derived by Bernhard et al. (1998, on pea). Infestation with 150 viable *O. crenata* seeds kg^{-1} soil reduced simulated yield by half. This is reasonably close to results of Linke et al. (1991), who found 50% yield losses in faba bean infested with 200 *O. crenata* seeds kg^{-1} soil, including non-viable seeds.

4. Conclusion

The configuration of the APSIM employed in this study showed a good ability to reproduce development, growth and interactions of faba bean and *O. crenata* as affected by environment and management. Effects of air and soil temperature, moisture supply and sowing date on host–parasite competition were realistically simulated. Effects of parasite infestation level were mostly well simulated. The model reproduced mechanisms likely to play a major role in the response of host—*O. crenata* associations to delayed sowing, in particular faster development of the host relative to the parasite (ICARDA, 1986, 1987; Sauerborn, 1989; Grenz et al., 2005).

Limitations of APSIM were partly related to inaccuracies in the simulation of root partitioning and vertical root distribution. The resulting error carried through to simulations of *O. crenata* number and yield formation in infected crops. It was demonstrated that improved simulation of vertical root distribution leads to more accurate predictions of *O. crenata* number. Collecting more extensive data on root growth dynamics could facilitate the implementation of more mechanistic root algorithms in APSIM-Legume. The present approach seems to lack the flexibility needed to precisely reproduce root growth as affected by soil properties and water or nutrient stress. In the model application, faba bean flowering was repeatedly predicted at times when flowers would likely be damaged by frost (ICARDA, 1987). Since frost damage is not considered in APSIM-Legume,

overestimations of pod number and yield may occur. Further research is required to collect quantitative information on frost-induced flower abortion in faba bean.

The present version of APSIM-Parasite is a potentially useful discussion support tool that can improve our understanding of the host-parasite system and help growers and extensionists explore tactical options for *O. crenata* control. However, the seedbank is a major determinant of yield losses caused by root parasites, and its containment at low levels is the key to long term control. Therefore, to further the development of strategical control approaches, the existing competition model should be combined with algorithms predicting parasite seed production and soil seedbank dynamics as affected by pedoclimatic conditions.

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