

Use of Ecophysiological Models for Crop-Weed Interference: Relations Amongst Weed Density, Relative Time of Weed Emergence, Relative Leaf Area, and Yield Loss¹

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Abstract. The performance of a mechanistic simulation model of crop-weed competition was evaluated with data on the effects of weed density, relative time of weed emergence, and environmental conditions on crop yield for three different crop-weed combinations. Reductions in crop yields due to weed competition were simulated accurately for all experiments, except for one case in which severe water stress combined with weed competition altered crop morphological development (height and leaf area). The mechanistic model was then used to assess the potential and constraints of two empirical models of crop-weed competition, one based upon weed density and relative time of emergence, and the other on relative leaf area. The empirical model describing the relationship between relative leaf area of the weeds shortly after crop emergence and yield loss appeared to have several advantages for management applications, whereas the mechanistic model is more suited for research purposes. **Additional index words.** Simulation, interference, *Zea mays* L., *Echinochloa crus-galli* (L.) Beauv. #³ ECHCG, *Beta vulgaris* L., *Chenopodium album* L. #³ CHEAL, *Lycopersicon esculentum* L., *Solanum tyocanthum* Dun. #³ SOLPT.

INTRODUCTION

Weed management programs often require quantitative estimates of effects of weeds on crop yield. Thresholds for action, which can be used to decide whether or not to control weeds, can be derived from regression equations which quantify yield loss as a function of level of weed infestation shortly after crop emergence.

A number of empirical models have been developed which describe the response of crop yield to weed density (2, 10, 14), and relative time of emergence of the weeds with respect to the crop (3, 4). These models have certain limitations. Weed density alone may not be a good predictor of crop yield if weeds vary greatly in size and/or relative time of emergence. Relative time of weed emergence with respect to the crop is difficult to estimate when weeds emerge in discrete flushes. To overcome these limitations, Kropff and

Spitters (7) recently introduced an empirical model that relates crop yield loss to the relative leaf area of the weeds with respect to the crop, estimated at a particular time after crop emergence. Empirical models generally provide a good description of the experimental data but cannot be extrapolated to other conditions (2, 8, 15).

Another approach has been introduced by Spitters (11, 12) and Spitters and Aerts (13). They developed a dynamic, weather-based simulation model, derived from existing ecophysiological models of crop growth, in which competition for light and water is simulated explicitly at the process level (9, 12, 17). Ecophysiological models may be used to obtain more insight into competition processes through detailed analysis of experimental data. After thorough validation of a simulation model over a wide range of conditions, it may also be simplified to generate robust descriptive models. Simulation models of crop-weed competition have been developed recently for production situations in which light, water, and/or nitrogen limit crop growth (5, 6, 12, 13).

In this paper, a simulation model was parameterized and validated with experimental data on the effects of weed density, date of weed emergence, and environmental conditions on crop yield for three crop-weed combinations: tomato and eastern black nightshade, corn and barnyardgrass, and sugarbeet and lambsquarters. The simulation model was then used to evaluate the potential and constraints of two descriptive models. Both mechanistic and descriptive approaches will be discussed with respect to their scientific and practical utility.

MATERIALS AND METHODS

The simulation model. The structure of the simulation model has been described in detail previously (12, 13). The model simulates growth of the crop and weeds from emergence through crop maturity as a function of radiation, temperature, water availability, and species characteristics with a time step of 1 d. Interactions are simulated by distributing the growth-limiting resources of light and water over the competing species. The amount of resources acquired by a species determines its growth rate. Nitrogen and other nutrients are assumed to be available in ample supply, and the effects of insects and diseases on crop and weed growth are neglected. In all experiments analyzed in this study, these assumptions had been met by careful fertilization and insect and disease control where needed. Interactions other than competition for resources, such as allelopathy, are not accounted for in the model.

The daily growth rates of each species (in kg dry matter ha⁻¹ day⁻¹) are calculated from daily rates of CO₂

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³Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Revised 1989. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.

assimilation and growth and maintenance respiration. The canopy is divided into a number of horizontal layers, and the proportion of leaf area of each species in that layer is determined from the height and leaf area distribution of that species. Rates of CO₂ assimilation are calculated for each layer, at several times during the day, based on the amount of light absorbed by each species and the photosynthetic rate of individual leaves, and are then integrated over the canopy and over the day. Assimilates are converted into dry matter, after subtracting growth and maintenance respiration, and distributed to the various organs as a function of developmental stage. Height and phenological development of each species are simulated as a function of accumulated degree days. A soil-water balance submodel permits simulation of the effect of water shortages on crop-weed competition. Processes that determine soil moisture content in the root zone are transpiration of the canopy, drainage, rainfall, and soil evaporation. When the amount of soil moisture declines to a critical level, rates of transpiration and photosynthesis are reduced as a function of soil moisture content and evaporative demand.

Physiological data used to parameterize the model for each crop and weed species were derived from the literature or independent experiments [1, 5, 8, 16, and Weaver (unpublished)]. Simulations were initialized with starting plant weight and leaf area at the time of emergence or transplanting. Daily weather data (maximum and minimum temperatures, total global radiation, and rainfall) recorded at each site were input to the model, as were weed densities and dates of crop and weed emergence for the different experiments. Empirical models. Two empirical, or descriptive models were fitted to both simulated and observed data. The model of Cousens et al. (3) relates crop yield loss to both weed density and relative time of weed emergence:

$$Y_L = \frac{bD}{e^{cT} + bD/a}$$

in which Y_L is percent yield loss, D is weed density, T is relative time of weed emergence, and a , b , and c are nonlinear regression coefficients. The model of Kropff and Spitters (7) relates crop yield loss to relative leaf area of the weeds with respect to the crop:

$$Y_L = \frac{qL_w}{1 + (q - 1)L_w}$$

in which Y_L is the relative yield loss, L_w is the relative leaf area of the weeds (leaf area index of the weeds divided by the total leaf area index of the crop and the weeds), and q (the "relative damage coefficient") is the single model parameter to be estimated.

Data used to test the models. Data on effects of nightshade density on tomato yields and a complete account of experimental methods were originally published in Weaver et al. (15). Transplanted and field-seeded 'H2653' tomatoes were grown on a sandy loam soil at the Agriculture Canada Research Station, Harrow, Ontario in 1984 and 1985, at a

density of 16 700 plants ha⁻¹. In late March, plants were started in the greenhouse and transplanted to the field May 15, 1984 and May 13, 1985. Seeded tomatoes were sown May 16, 1984 and May 13, 1985. Weed densities were established by thinning natural populations of eastern black nightshade to 0, 0.25, 0.5, 1, 2, 4, 8, 16, or 32 plants m⁻².

Data on the effects of barnyardgrass densities on corn yield were published in Kropff et al. (8). 'LG11' corn was grown on a sandy soil at Wageningen, The Netherlands, at a population of 110 000 plants ha⁻¹, in 1982 and 1983. In 1982 corn emerged May 15, and in 1983 June 5. Barnyardgrass densities were established by thinning natural populations to 0, 100, 200, and 300 plants m⁻² in 1982, whereas in 1983 naturally established densities were used. In 1982, the weeds emerged 5 d after the crop and in 1983 the weeds emerged 2 d before the crop.

Data on the effects of lambsquarters density and relative time of emergence on sugarbeet yields were originally published by Kropff (5). Field experiments were conducted in 1984, 1985, and 1986 on a sandy loam soil at Droevendaal Experiment Station at Wageningen, The Netherlands, at a sugarbeet density of 110 000 plants ha⁻¹. In 1984 naturally emerged lambsquarters plants were thinned to 0, 5.5, or 22 plants m⁻². Both the weeds and the crop emerged on April 27. In 1985 and 1986 the weeds were seeded by hand, after pretreatment with gibberellic acid and potassium nitrate to simulate germination, and thinned to 0, 5.5 (1985), or 10 (1986) plants m⁻². In 1985 sugarbeets emerged May 9 and the weeds May 19. In 1986 the crop emerged May 4 and the weeds May 25 and June 3 in two treatments differing only in the date of weed emergence.

Model analyses. The ability of the model to accurately simulate the effect of weed density on crop yields was tested by regressing observed against simulated yield losses over all weed densities and years for each crop. Ideally, the intercept should not be significantly different from 0, the slope should not be significantly different from 1.0, and the coefficient of determination should be high. The simulation model was used to generate hypothetical data, over a wide range of weed densities and relative times of emergence, which were then fitted to the two empirical models. These simulation runs were conducted separately for three different weed heights, so that the effect of weed height on the parameters of the empirical models could be assessed.

RESULTS AND DISCUSSION

Performance of the simulation model. Simulation runs were conducted initially for each crop under weed-free conditions. There was generally good agreement between simulated and observed crop yields in the absence of weed competition in each of the 5 yr, despite different locations and weather conditions (Table 1). Most simulated crop yields fell within the limits of the error terms of the corresponding observed yields. Simulation runs were then conducted for each crop-weed combination over the range of weed densities tested in the field experiments.

The model accurately simulated yield losses of seeded tomatoes over the entire range of eastern black nightshade

Table 1. Observed and simulated yields of weed-free crops^a.

Crop	Year	Yield (kg ha ⁻¹)	
		Observed yield ^b	Simulated yield
Tomato (seeded)	1984	3 172 ± 222	3 009
Tomato (seeded)	1985	2 704 ± 260	3 290
Tomato (transplanted)	1984	2 736 ± 164	2 990
Tomato (transplanted)	1985	4 189 ± 330	4 312
Corn	1982	13 110 ± 1940	13 901
Corn	1983	8 440 ± 210	8 459
Sugarbeet	1984	14 900 ± 1397	14 870
Sugarbeet	1985	23 100 ± 1233	20 644
Sugarbeet	1986	20 400 ± 687	20 450

^aYields of tomato, corn, and sugarbeet represent fruit, grain, and root dry weight, respectively.

^bMeans ± standard errors.

densities in both years, but predicted a greater yield reduction than observed in the field for transplanted tomatoes at weed densities greater than 10 plants m⁻² in 1984 (Figure 1, Table 2). The parameter sets of species characteristics used for the simulations of seeded and transplanted tomatoes were identical except for starting position of the crop. Results of the simulations clearly demonstrate that the large difference in yield losses between seeded and transplanted tomatoes at equal weed densities is due primarily to the difference in relative starting position of the weeds and the crop.

The model simulated corn yield losses from barnyardgrass competition well in 1982 but greatly underestimated crop yield losses at all weed densities in 1983 (Figure 2). Crop height and leaf area were also overestimated by the model in 1983 (data not shown). There was a severe drought during this year (8). Simulation results were improved when observed crop and weed heights were input to the model (Figure 2). However, simulations that predicted yield losses similar to those observed in the field were obtained only when the observed growth in leaf area of the crop and weeds at each weed density were introduced to the model. This suggests that the model does not adequately account for the effects of extreme water shortage on corn morphological development. Corn yield under weed-free conditions was

Table 2. Summary of regression analyses of observed against simulated yield losses for each crop over all years and weed densities.

Crop	df	Intercept ^a	Slope ^b	R ²	P
Tomato (seeded)	17	-0.3	0.99	0.99	0.001
Tomato (transplanted)	17	4.8*	0.62*	0.79	0.001
Sugarbeet	4	-6.4	1.1	0.98	0.001
Corn	8	2.4	3.1*	0.74	0.003
Corn ^c	8	2.4	1.0	0.96	0.001

^aIntercept values significantly different from 0 are indicated by *.

^bSlope values significantly different from 1.0 are indicated by *.

^cObserved leaf areas and heights input to simulation runs.

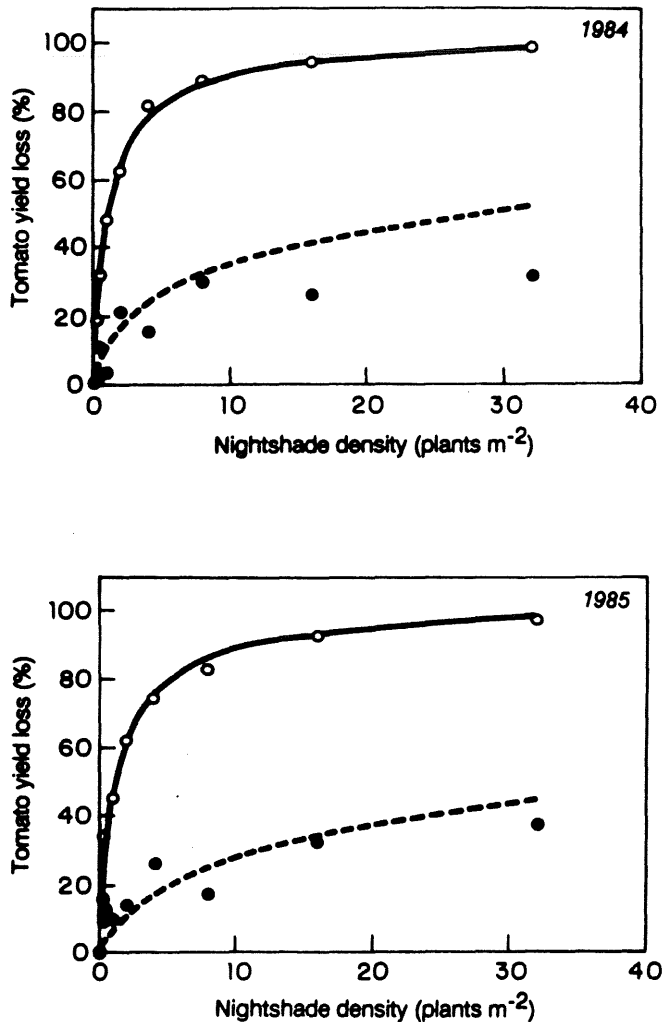


Figure 1. Observed and simulated (lines) yield losses of seeded tomatoes (○) and transplanted tomatoes (●) due to different densities of eastern black nightshade in 1984 and 1985.

accurately simulated during this year (Table 1), but the combination of drought and barnyardgrass competition severely reduced corn stem elongation and leaf area development.

Observed sugarbeet yield losses due to competition from lambsquarters were highly variable over weed densities ranging from 5.5 to 22 plants m⁻² and relative times of weed emergence from 0 to 30 d over 3 yr (Table 3). Kropff (5) had previously shown through model analysis that variation in sugarbeet yield losses in these experiments was due mainly to differences in the period between crop and weed emergence rather than to differences in weed density. There was good agreement between simulated and observed yield losses. Empirical models. The simulation model for sugarbeet-lambsquarters competition fit the experimental data within the range of densities and relative times of weed emergence

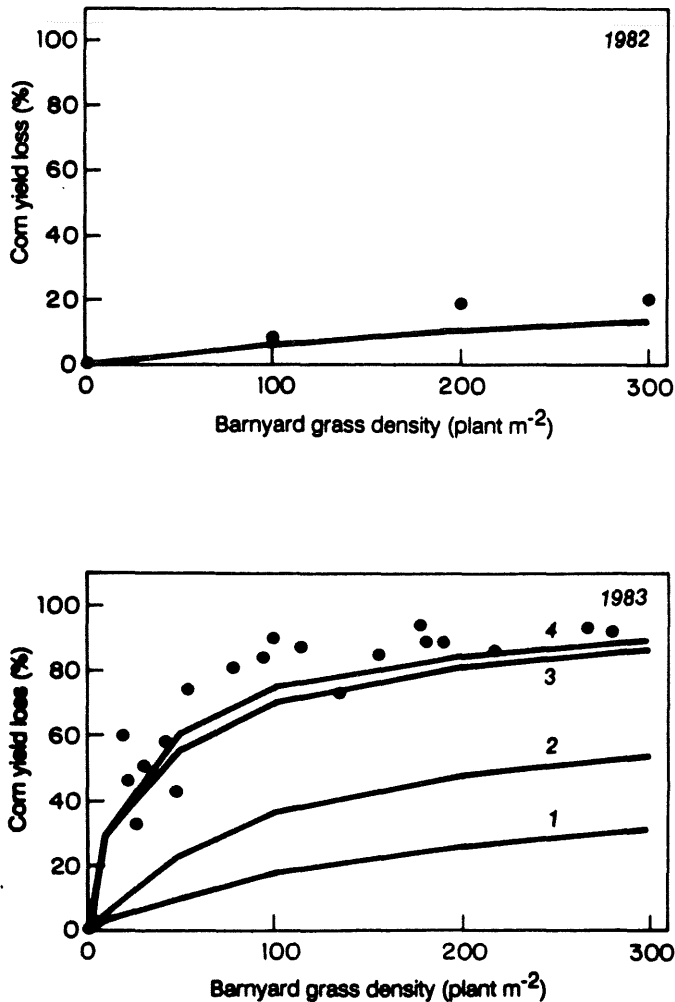


Figure 2. Observed (●) and simulated (lines) yield losses of corn as a result of competition with barnyardgrass at different densities in 1982 and 1983. Simulation results for the 1983 experiment are presented as: simulated leaf area and height (1), simulated with observed height (2) or leaf area (3) as input, simulated with both observed leaf area and height as input (4).

tested in the field experiments, and so was used to generate hypothetical data over a wider range of weed densities and times of emergence, which were then fit to the hyperbolic model of Cousens et al. (3) (Figure 3). Weed densities used in the simulation runs were 5.5, 11, 22, 44, and 88 plants m⁻², while weed times of emergence varied from 20 d before to 45 d after crop emergence. Average weather conditions (over 30 yr) for Wageningen were used in the simulation runs, and it was assumed that water was in ample supply. The mechanistic model indicated that relative height of the weed compared to the crop has a strong influence on competition for light and therefore on the magnitude of crop yield losses. The simulation runs were conducted separately for three different maximum weed heights, while keeping crop height and other factors constant. Results of the simulation runs demonstrate the strong sensitivity of crop yield to both the

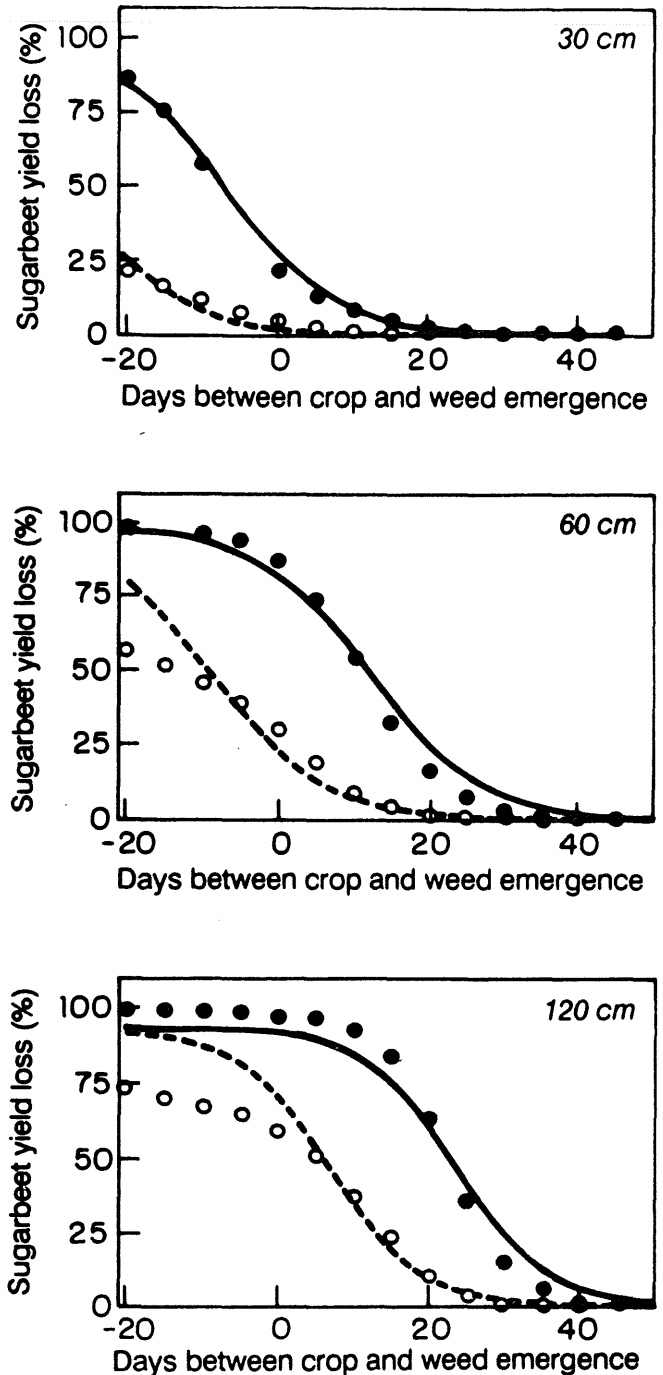


Figure 3. Simulated yield losses in sugarbeet at lambsquarters densities of 5.5 plants m⁻² (○) and 88 plants m⁻² (●) for a wide range of periods between crop and weed emergence. Maximum height of the weeds was 120, 60, or 30 cm; maximum height of the crop was 60 cm. Lines give the result of fitting the simulated data with the regression model of Cousens et al. (3).

relative time of weed emergence and the relative height of the weed with respect to the crop (Figure 3).

A reasonably good fit to the simulated data was obtained with the descriptive model based upon density and relative time of emergence, except when the weeds emerged far in

Table 3. Observed and simulated yield losses of sugarbeet due to lambsquarters competition at different weed densities and times of weed emergence.

Year	Weed density	Weed emergence	Observed yield loss	Simulated yield loss
	plants m ⁻²	days	%	
1984	5.5	0	79 ± 6	77
1984	22	0	93 ± 1	88
1985	5.5	10	37 ± 6	30
1986	9.1	21	7 ± 1	15
1986	9.7	30	-6 ± 5	3

advance of the crop (Figure 3). It should be noted that this descriptive model assumes a constant maximum yield loss, regardless of weed density, as T becomes large and negative, which may not be realistic. While such situations seldom arise in annual crops under conventional tillage, this discrepancy may be of more concern under no-till or minimum tillage where weeds escape control by burn-down herbicides. The fit of the descriptive model resulted in parallel curves which were shifted horizontally. The parameter that varied the most with weed height was b , which is the percent yield loss per weed at low densities when T is zero, i.e. when the crop and weed emerge on the same day (Table 4).

Simulated data for sugarbeet-lambsquarters competition were also fit to the model of Kropff and Spitters (7), again using three different maximum weed heights (Table 4). This one-parameter model was able to account for over 90% of the variation in crop yield losses due to differences in weed density and relative time of emergence. The strong sensitivity of the relationship between Y_L and L_w to the maximum height of the weeds relative to that of the crop is clearly demonstrated. Furthermore, the value of q is dependent upon the particular point in time that L_w is estimated. If relative growth rates of crops and weeds differ, the relative leaf area of the weeds changes with time. Therefore, the value of q will be a function of the amount of time (or thermal time) between crop emergence and the moment of observation (7).

Data from the experiments with tomatoes and eastern black nightshade were previously fitted to a hyperbolic model based on weed density alone (2), with parameters determined separately for each year and method of crop establishment,

e.g. seeded or transplanted (15). The estimated parameters for the damage function in tomatoes differed markedly between seeded and transplanted tomatoes with the curve for seeded tomatoes having a greater initial slope and a higher maximum yield loss than that for transplanted tomatoes. The extended hyperbolic model (3), based on both weed density and relative time of emergence, could not be used to derive a common curve for both seeded and transplanted tomatoes, because time of emergence of the transplanted tomatoes could not be estimated.

The model of Kropff and Spitters (7) provided a way to quantify the effects of eastern black nightshade on yield losses of both seeded and transplanted tomatoes. Observed leaf area data were not available from the tomato experiments to evaluate this model. However, the simulation model performed reasonably well over a wide range of weed densities for both seeded and transplanted tomatoes (Figure 1), and so simulated leaf areas of the crop and the weed were used to calculate L_w . Relative leaf area was determined at approximately 200 degree-days (base temperature = 10 C) after seeding or transplanting. The close fit of this model to the data (Figure 4) suggests that the effects of both weed density and the relative time of weed emergence, or starting position, can be characterized by only one variable, the relative leaf area of the weeds compared to the crop (L_w).

The empirical model based upon relative leaf area has several advantages over that based upon weed density and relative time of emergence: leaf area index of the weed and the crop need to be observed only at one point in time, whereas estimating the relative time of weed emergence requires daily observations; a one-parameter model is easier to fit and interpret than a three-parameter model; and the model can be readily extended to competitive situations with multiple weed species (7). However, relative leaf area of the crop and the weeds (L_w) must be measured accurately, and must always be determined at the same time after emergence unless the relative growth rates in leaf area of both the crop and the weed have been previously determined (7). The parameters of both empirical models must be determined over a wide range of weather conditions and soil types if these models are to be useful for general management purposes.

Neither empirical model will contribute to an understanding of the mechanisms of competition between crops and weeds in the way that a simulation model will. Mechanistic models can be useful in the analysis of experimental data and

Table 4. Estimated parameter values and standard errors using the regression models of Cousens et al. (3) and Kropff and Spitters (7) to fit simulated data on the effect of lambsquarters competition on sugarbeet yield losses with three different maximum weed heights.

Weed height	df	Model I				Model II	
		a	b	c	R ²	q	R ²
cm							
30	51	98.9 ± 5.0	0.44 ± 0.02	0.136 ± 0.003	0.98	16.04 ± 0.91	0.91
60	51	98.2 ± 7.7	5.55 ± 0.35	0.132 ± 0.005	0.97	0.82 ± 0.02	0.99
120	51	93.1 ± 15.2	53.88 ± 8.41	0.167 ± 0.008	0.96	0.10 ± 0.01	0.97

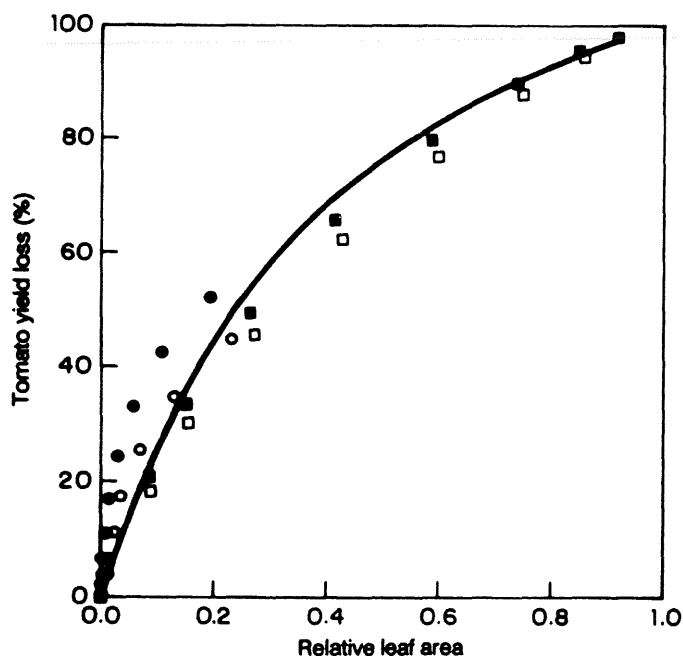


Figure 4. Yield losses of seeded and transplanted tomatoes (■, ● and □, ○ in 1984 and 1985, respectively) as a function of simulated relative leaf area of eastern black nightshade at approximately 200 degree-days (base temperature = 10 C) after seeding or transplanting. Nightshade densities ranged from 0 to 32 plants m^{-2} . The line is the result of fitting the data to the model of Kropff and Spitters (7) ($q = 3.19$, $df = 35$, $R^2 = .96$).

to obtain insight into the process of crop-weed competition. These models require a great deal of information on the physiological characteristics of the crop and each weed species, and a great deal of time to develop and validate. They may be most helpful when they fail to simulate the data correctly (e.g., in the corn/barnyardgrass experiment) and thereby point to areas where further research is needed. Once a model has been validated over a wide range of environmental conditions, it can also be used to generate data for hypothetical experiments which can then be tested in the field. Here we have shown how a simulation model may be used to evaluate the potential of simple descriptive models, and to investigate the effect of plant attributes, such as height, on their parameter values.

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