

Modelling the effects of weeds on crop production

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Summary: Résumé: Zusammenfassung

In most quantitative studies on interplant competition, static regression models are used to describe experimental data. However, the generality of these models is limited. More mechanistic models for interplant competition, which simulate growth and production of species in mixtures on the basis of the underlying physiological processes, have been developed in the past decade. Recently, simulation models for competition between species for light and water were improved and a detailed version was developed for sugarbeet and fat hen (*Chenopodium album* L.). The model was validated with data sets of five field experiments, in which the effect of fat hen on sugarbeet production was analysed. About 98% of the variation in yield loss between the experiments (which ranged from -6 to 96%) could be explained with the model. Further analysis with the model showed that the period between crop and weed emergence was the main factor causing differences in yield loss between the experiments. Sensitivity analysis showed a strong interaction between the effect of the variables weed density and the period between crop and weed emergence on yield reduction. Different quantitative approaches to crop-weed competition are discussed in view of their practical applicability. Simulations of experiments, where both the weed density and the period between crop and weed emergence were varied over a wide range, showed a close relation between relative leaf cover of the weeds shortly after crop emergence and yield loss. This relation indicates that relative leaf cover of the weeds accounts for both the effect of weed density and the period between crop and weed emergence. This relation has the potential to be

developed into a powerful tool for weed-control advisory systems.

Modélisation des effets des adventices sur les cultures

Dans la plupart des études sur la compétition en plantes des modèles de régression statique sont utilisés pour décrire les données expérimentales. Cependant la valeur générale de ces modèles est limitée. Des modèles plus sophistiqués pour la compétition interplantes qui simulent la croissance et la production des espèces sur la base des mécanismes physiologiques, ont été développés au cours de la dernière décennie. Récemment, des modèles simulant la compétition interespèces pour la lumière et l'eau ont été améliorés et une version détaillée a été améliorée pour les betteraves et le chénopode blanc (*Chenopodium album* L.). Le modèle a été établi à partir des données de 5 essais de plein champ dans lesquels l'effet des chénopodes sur la production betteravière avait été analysé. Environ 98% de la variation des baisses de rendement entre les essais (qui vont de 6 à 96%) peut être expliquée par le modèle. Des analyses ultérieures avec le modèle ont montré que le temps entre la levée de la culture et celle des mauvaises herbes était la facteur principal influant sur les différences de baisses de rendement entre les essais. Des analyses fines ont montré une grande interaction entre les effets sur le rendement de densités d'adventices variables et le temps entre la levée de la culture et celle des mauvaises herbes. Différentes approches quantitatives de la compétition culture/adventices sont discutées en regard de leur possibilité pratique de mise en application. Des expérimentations en simulation où la densité en adventices et le temps entre les levées de la culture et des adventices variaient dans de grandes proportions, ont souligné une étroite relation entre le pourcentage de surface foliaire d'adventices juste après de la culture et les pertes de rendement. Cette relation représente un outil potentiel à développer pour les systèmes de conseil en désherbage.

Modellierung der Wirkung von Unkräutern auf die Pflanzenproduktion

In vielen quantitativen Untersuchungen zur Konkurrenz zwischen Pflanzen werden statische Regressionsmodelle zur Beschreibung der Ergebnisse benutzt. Darüber hinaus wurden auch mehr mechanistische Modelle entwickelt, die die Biomasseproduktion von Pflanzenarten in Mischbeständen auf der Grundlage physiologischer Prozesse simulieren. Kürzlich wurde ein Modell zur Konkurrenz zwischen Zuckerrüben und Weissem Gänsefuss (*Chenopodium album* L.) um Licht und Wasser entwickelt. Das Modell wurde mit Daten aus 5 Feldversuchen, bei denen die Ertragsverluste zwischen -6 und 96% lagen, validiert. Die Variabilität zwischen den Versuchen konnte zu etwa 98% mit dem Modell erklärt werden. Weitere mit dem Modell vorgenommene Analysen zeigten, dass die zeitliche Differenz zwischen dem Auflaufen der Kulturpflanze und dem des Unkrauts die Hauptursache für die unterschiedlichen Ertragsverluste zwischen den Versuchen war. Verschiedene Ansätze zur Beschreibung der Konkurrenz zwischen Kulturpflanzen und Unkräutern werden im Hinblick auf ihre praktische Verwendbarkeit diskutiert. Simulationen unter Einbeziehung grosser Spannweiten in der Unkrautdicke und der Periode zwischen Kulturpflanzen- und Unkrautauflauf ergaben eine enge Beziehung zwischen der relativen Unkrautblattfläche kurz nach dem Auflaufen der Kulturpflanze und dem Ertragsverlust. Diese Beziehung besagt, dass mit der relativen Unkrautblattfläche sowohl die Wirkung der Unkrautdicke als auch die des zeitlich versetzten Auflaufens erklärt werden können. Diese Zusammenhänge sind geeignet, als Grundlage für die Beratung zu dienen. Sie sollten daher weiterentwickelt werden.

Introduction

Basic requirements for decision making in weed control are good models for crop loss assessment, which can be based upon observations of the weed infestation early in the growing season. The major cause for yield reduction by weeds is competition with the crop for the growth-limiting resources of light, water and nutrients. Models for interplant competition have been developed at different levels of complexity.

In most studies of quantitative aspects of competition, regression models are used to describe competition effects empirically. Most of these regression models are static: a description is given of competition effects at a certain moment. The widely used hyperbolic yield density equation for the description of yield loss in relation to weed density is an example of this category of regression models: a description is supplied of the depression in crop yield at a given weed infestation at a given moment in the growing season. Examples of this approach are produced by Spitters (1983) and Cousens (1985).

Although the hyperbolic yield-density equation fits very well with data of additive experiments where only the weed density is varied, model parameters may vary strongly among experiments, due to the effect of other factors on competition processes. One of the most important factors causing this variation is the date of weed emergence relative to the crop (Kropff *et al.*, 1984; Cousens *et al.*, 1987).

Some workers introduced an additional variable in the hyperbolic yield-density equation to account for the effect of differences in the period between crop and weed emergence (Håkansson, 1983; Cousens *et al.*, 1987; Spitters & Aerts, 1983) suggested that it would be more appropriate to characterize the weed infestation with the estimated leaf area of the weeds relative to the leaf area of the crop, early in the growing season.

Besides these static regression models for assessment of yield loss at a given weed infestation, a few regression models with a dynamic character have been developed. They describe the time-course of competition with a set of logistic equations or extended hyperbolic equations. The most advanced approach is described by Spitters & van den Berg (1982), which accounts for differences in relative times of emergence and for the effects of plant height.

However, the general applicability of these descriptive regression models is limited because they only describe the effects observed in field experiments.

A new type of model for crop-weed competition was introduced in 1983 by Spitters & Aerts, mechanistic dynamic simulation models in which competition effects are explained from the underlying processes. The basis of the approach is the distribution of the growth-determining and limiting resources of light, water and nutrients over the species. From the amount of resources (light,

water and/or nutrients) acquired by the competing species, and the efficiency of the species in using these resources, the formation of dry matter by the species is computed. These models may be useful to gain a more thorough insight in the crop-weed system and the backgrounds of competition. The advantage of this approach is that the model, if thoroughly validated, can be used to analyse competition effects in untried situations, since the model is valid for a large range of environmental conditions.

Simulation models for crop-weed competition have been developed for potential production situations and for production situations where water and/or nitrogen are limiting crop growth (Spitters & Aerts, 1983; Spitters, 1984).

In this paper an overview will be given of some recent developments in crop-weed competition modelling. A short description will be given of the simulation model, followed by an evaluation of the model with experimental data. Finally the approach will be discussed in relation to practical applications.

Simulation models for crop-weed competition

In simulation models for crop-weed competition, two or more crop-growth models are coupled and parameterized for the species concerned. The principles of the crop-growth model will be discussed first.

Simulation of crop growth

The model used in this study simulates growth of crop and weeds in two production situations. In the first (potential) production situation crop growth is determined only by the incoming light, temperature and some species characteristics; water, nitrogen, and other nutrients are available in ample supply and the crop is assumed to be free of pests and diseases. In the second production situation crop growth is limited by water shortage for a part of the growing season. A schematic representation of the model is given in Fig. 1.

In the potential production situation, the instantaneous CO_2 assimilation rate of the canopy is calculated per leaf layer from the amount of radiation absorbed by that leaf layer, which is calculated in a submodel for the profiles of absorbed radiation in canopies, and the photo-

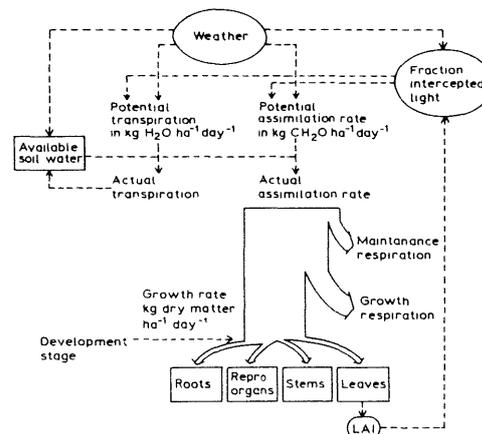


Fig. 1 A simple scheme of the crop growth model.

synthesis-light response of individual leaves. Daily gross CO_2 assimilation rate of the canopy is calculated by integration of these instantaneous CO_2 assimilation rates per leaf layer over the height of the canopy and over the day. After the subtraction of respiration costs for maintenance and after conversion of glucose into structural dry matter, the daily growth rate is obtained in $\text{kg dry matter ha}^{-1} \text{ day}^{-1}$. Depending on the developmental stage of the crop, the dry matter produced is distributed over the organs of that crop.

In order to simulate the effect of water shortage on crop growth, a soil water balance is incorporated in the model. The processes that determine the soil moisture content in the rooted zone are the transpiration of the canopy, drainage, infiltration of water and soil evaporation. When the amount of soil moisture reaches a critical level, the reduced actual transpiration is calculated as a function of soil moisture content and the evaporative demand. In the case of water shortage the potential CO_2 assimilation rate will be reduced with the same factor as the potential transpiration rate.

Recently the procedure to simulate leaf area development was changed considerably. Until now, leaf area development was simulated on the basis of the simulated leaf dry weight with an empirical parameter: the specific leaf area (SLA in $\text{m}^2 \text{ leaf kg}^{-1} \text{ dry matter leaf}$). In this approach it is assumed that leaf area development is source limited: leaf formation and expansion is deter-

mined by the amount of carbohydrates produced in photosynthesis. In early growth stages, when crop (and weed) plants are growing exponentially, the models appeared to be very sensitive to the value of the SLA, as a result of a positive feedback loop between dry matter production, leaf area development and light absorption. Especially in competition models, where the starting position of the species determines their competitive strength, this approach led to unrealistic simulation results, making it necessary to start the model a couple of weeks after emergence (Spitters, 1984).

However, it can be concluded from morphological studies that leaf area development early in the growing season in field situations is not limited by carbohydrate supply, but is driven mainly by temperature. Therefore, leaf area development in this period is simulated on the basis of an experimentally derived temperature-dependent, relative growth rate of leaf area. When the canopy closes, leaf area development is calculated from the dry matter increment of the leaves and an experimentally determined specific leaf area, which is a function of the developmental stage.

Simulation of crop-weed competition

The distribution of radiation over the species is simulated as follows: (i) the amount of absorbed radiation is calculated for the species together; (ii) the amount of radiation absorbed by a species in a certain canopy layer is calculated from its share in effective leaf area (the leaf area weighted with the extinction coefficient for light (k)):

$$f_{abs_i} = \frac{k_i LAI_i}{\sum k LAI}$$

where f_{abs_i} is the fraction of absorbed radiation by species i , and LAI_i is the Leaf Area Index of species i in the leaf layer (m^2 leaf m^{-2} ground). Integration of the CO_2 assimilation of the leaf layers per species over canopy height, and over the day, gives the daily CO_2 assimilation rate of the species. The same procedure is followed in the calculation of potential transpiration. Growth reduction is calculated for both species separately depending upon evaporative demand (potential transpiration) and soil moisture content. Plant height is simulated with an empirically determined function of developmental stage.

A full description of the model by Spitters & Kropff is in preparation.

Model performance

Preceding studies

Most parts of the model have been evaluated and tested thoroughly (Penning de Vries & van Laar, 1982) and different versions of the competition model were tested with data of competition experiments with maize, yellow mustard and barnyard grass (Spitters & Aerts, 1983, Kropff *et al.*, 1984, Spitters, 1984). In these studies, the extreme difference in the effect of barnyard grass on maize production between two successive field experiments was only partly explained with the model. This was probably due to the extreme effect of the weeds on crop growth in one of the experiments in which severe drought stress influenced the competitive interactions. Irreversible effects of drought stress, like leaf death or the dying off of whole plants, were observed for maize plants in plots with higher weed densities. Extreme stress effects on physiological processes were not included in the model.

Recent studies with sugarbeet and fat hen

In the next study the model was parameterized for sugarbeet and fat hen and was used to analyse the data from five field experiments (Kropff *et al.*, unpublished results). The experiments were conducted over 3 years at the same site in Wageningen. Weed densities ranged from 5.5 to 22 plants m^{-2} and leaf emergence relative to the crop ranged from 0 to 30 days. The time-course of crop and weed growth was followed by frequent harvesting.

Experimental specific model inputs are the measured daily weather variables from a nearby station (maximum and minimum temperature, total global radiation, rainfall, humidity and wind speed), weed density, and dates of crop and weed emergence for the different experiments. Data on species characteristics were derived from literature, my own experiments and were partly based upon the first three field experiments with sugarbeet and fat hen. A detailed description of the parameterization of the model by Spitters & Kropff is in preparation. Soil parameters, like the soil moisture content at permanent wilting point, field capacity and rooting depth, were derived in the first experiment. In order to analyse the explanatory power of the model, the same set of

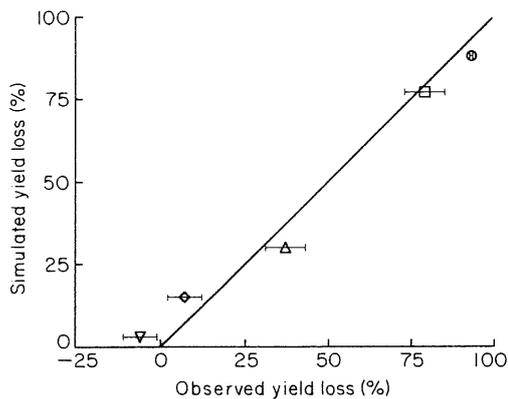


Fig. 2 Observed and simulated yield losses for five sugarbeet-fat hen competition experiments. Standard errors of the observed data are plotted.

species-specific parameter values was used in the simulation of the five experiments.

Simulation results (M.J. Kropff *et al.*, unpublished data) are summarized in Fig. 2, where the relation between simulated and observed yield loss at final harvest is plotted. This figure shows a close relationship between simulated and observed yield losses, which ranged from -6 to 96%. Since the model explains 98% of the variation between the experiments, the model was used to analyse the contribution of the different factors to differences in yield loss between the experiments. Model analysis (by changing the values of the variables step by step) showed that the variation accounted for by differences in weed density between the experiments was 13%, whereas differences in the period between crop and weed emergence explained 96% of the variation in yield loss between the experiments. The introduction of observed weather hardly improved the simulation results. Thus, it was concluded that in these experiments, differences in yield loss were mainly due to differences in the date of weed emergence relative to the crop. Further analysis, however, showed that temperature can be of great importance when the weeds emerge considerably later than the crop. At lower temperatures (like in the first experiment where the weeds emerged at the same day as the crop) the advantage of the crop is, of course, reduced since leaf area production is slower. It was concluded that the period between crop and weed emergence should be expressed in a developmental unit instead of days (i.e. degree days).

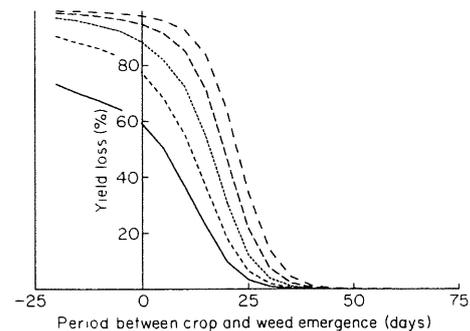


Fig. 3 Simulated yield losses of sugarbeet at different weed densities of fat hen (—) 5.5 plants m^{-2} , (---) 11 plants m^{-2} , (···) 22 plants m^{-2} , (-·-) 44 plants m^{-2} , (—) 88 plants m^{-2} .

Sensitivity analysis showed that the extreme sensitivity of model output to parameters for leaf area development (Spitters, 1984) was strongly reduced with the new method for simulation of leaf area development. However, morphological development (plant height and leaf area) appeared to be the most important factor determining competition effects. A full description of this work by Kropff *et al.* is in preparation.

Applications

Damage relationships

The effect of different weed densities and periods between crop and weed emergence on yield loss was analysed with the model using average weather and the species characteristics of sugarbeet and fat hen. The simulation results are presented in Fig. 3. This figure clearly shows an S-shaped relation between yield loss and the period between crop and weed emergence. Yield loss was most sensitive when the weeds emerged around 10–20 days after the crop, depending on weed density.

An alternative damage relationship could be the relation between yield loss and relative leaf area of the weeds with respect to the crop, as observed shortly after crop emergence. In order to analyse the possibilities of such a relationship, we simulated sugarbeet production at different fat hen infestations consisting of many combinations of weed densities (ranging from 5.5 to 88

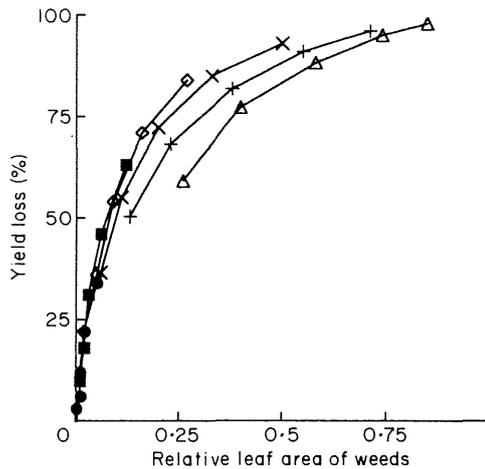


Fig. 4 Simulated yield loss of sugarbeet related to relative leaf area of the weeds (fat hen) 30 days after crop emergence. Data obtained from simulated experiments where weed density and the period between crop and weed emergence were varied. Data from simulated experiments with the same dates of emergence are connected (—).

plants m^{-2}) and periods between crop and weed emergence (ranging from 0 to 35 days).

Simulated yield losses are plotted versus the relative leaf area of the weeds with respect to total leaf area, 30 days after crop emergence, in Fig. 4. This figure shows a close relationship between the relative leaf area and yield loss, which can be described with a hyperbolic equation. In this specific competition situation with sugarbeets and fat hen, strong yield reductions can be expected even when there are hardly any weeds present 30 days after crop emergence. The variation in yield loss at a given relative leaf area is due to the effect of differences in the vegetative period of the weeds: early emerged weeds die off during maturity.

These results indicate that the use of the variable relative leaf area of the weeds shortly after crop emergence is promising for the development of new models to describe damage relationships, since quite a good relation is found for a wide range of competition situations. However, it should be noted that this relation for this specific competition situation is almost useless for advisory systems, since the effect of fat hen on sugarbeet production is very great, even when the leaf cover of fat hen is too low for easy assessment. For less competitive weed species this relation can serve as a tool in yield-loss assess-

ment, because the parameter used here covers the effect of both the variables of plant density and the period between crop and weed emergence.

Discussion

Models for crop-loss assessments, on the basis of observations on the weed infestation early in the growing season, are essential for decision making in weed control. In most available supervised weed control advisory systems the weed infestation is characterized by the densities of the different weed species. In this approach it is assumed that weed density is the main factor influencing yield loss due to competition. In current advisory systems a linear relation between weed density and yield loss is often used, which is, of course, only valid at very low weed densities. However, other factors than weed density, like the relative time of weed emergence, appear to be of primary importance in competition situations.

More detailed models (ranging from the hyperbolic yield density equation to the most detailed dynamic simulation models) have the advantage of larger generality, which may lead to more accurate extrapolations to other situations. The more complex mechanistic models may be especially useful for scientific research, since they provide much insight in the competition processes. However, empirical static models seem to be more suitable for practical application, since they are relatively easy to parameterize.

Another important criterion in the use of models for crop-loss assessment is the practical feasibility of making the observations that are needed to apply a model. The hyperbolic yield density equation, with an extension to account for differences in time of emergence, needs observations on crop and weed emergence and plant numbers m^{-2} . As is shown in Fig. 4, yield loss is very sensitive to small differences in the period between crop and weed emergence. This implies that very accurate data on dates of emergence and densities are required for reliable forecasting on the basis of such a model. However, estimating dates of weed emergence is almost impossible on a practical scale, since daily observations are needed.

A more promising static model may be a mathematical equation to describe the relation between yield loss and the relative leaf area of the weeds with respect to the crop, monitored a

couple of weeks after crop emergence. Theoretical data obtained with the model indicate that both the effect of weed density and the relative time of weed emergence can be characterized by only one variable: the relative leaf cover, which is relatively easy to estimate in practical situations. However, it should be noted that errors in estimations of leaf cover can be large, which implies that the sensitivity of yield loss to the relative leaf cover has to be small. The parameters for different species will differ strongly and should be estimated for different groups of species in a certain crop. Since available control methods restrict the possibilities for post-emergence control (especially in sugarbeet crops), it is important to analyse the minimum period between crop emergence and observation date, which is needed for reliable prediction of the yield loss.

This study clearly illustrates the possibilities of the simulation approach in weed research, which can be summarized as follows: (i) the simulation model provides a tool for analysis of complex field experiments on crop-weed competition, which leads to more insight in the effect of weed characteristics on competitive strength of the weeds, in the course of time; (ii) when validated, the model can be used to perform imaginary experiments to generate new insight in damage relationships or to evaluate the practical useful-

ness of simple empirical models before doing cost- and labour-intensive field experimental work.

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