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**Crop-weed interactions and weed population dynamics:
current knowledge and new research targets**

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Summary

Quantitative knowledge on weed population dynamics and crop-weed interactions is required to design preventive measures, to develop long-term and short-term strategies for weed management, to assist in decision making to determine if, when, where and how weeds should be controlled, and to identify new opportunities for weed control and increase the precision of weed control. Significant improvements have been made with respect to the quantitative understanding of crop-weed interactions. Simulation models helped to improve insight into the crop-weed system and can be used for various purposes like the development of simple predictive yield-loss models, threshold weed infestation levels for weed control or the design of competitive plant types. Simple models based on the relative leaf area better describe yield losses by competition from weeds that emerge in flushes than density models, but the predictive value of these relative leaf area models still needs to be improved before they can be applied in weed management. The density of a weed population varies over time and space. For strategic weed management activities, quantitative insight into the dynamics and spatial patterns of weed populations is required. Several approaches have been developed and can be used for strategic weed management. New research targets can be found in the development of integrated weed management systems based on prevention, improved decision making with minimum risk and precision weed control in space and time.

Introduction

Increased concern about environmental side effects of herbicides, the development of herbicide resistance in weeds and the necessity to reduce cost of inputs have resulted in greater pressure on farmers to reduce the use of herbicides. As a result, there has been an increasing interest in the development of integrated weed management systems based on the use of additional methods for weed control (like bioherbicides), breeding for increased competitive ability of the crop, improved general crop management practices and the rationalisation of herbicide use. Emphasis should be based on the management of weed populations, taking actions based on knowledge of the level of weed infestation, the effect of husbandry practices and information on options for controlling the weeds in a cost-effective way. The development of such systems requires improvements with respect to i. prevention, ii. decision making and iii. weed control technology (Kropff 1996).

Prevention involves any aspect of management that favours the crop relative to the weeds. Decision making consists of strategic (long term) decisions, tactic decisions (for a season) and operational decisions in the field to determine if, when, where and how weeds should be controlled. Improvements in these components involves quantitative insight into both crop-weed interactions and the dynamics of weed populations. Because of the complexity of the processes and the long term aspects in population dynamics, models are required to obtain such quantitative insight and to make the knowledge operational. This paper reviews the state of the art with respect to quantitative knowledge on crop-weed interactions and weed population dynamics and discusses options to use this knowledge in weed management systems and where to focus future research emphasis.

Crop-weed interactions

Two types of models for crop-weed interactions have been developed: (i) eco-physiological crop growth models that simulate competition for the resources between species and (ii) descriptive regression models with a few parameters that can be determined by fitting the model to field data.

Eco-physiological models for crop weed-interactions

Competition is a dynamic process that can be understood from the distribution of the growth-determining (light) or -limiting (water and nutrients) resources over the competing species and the efficiency with which each species uses the resources. Eco-physiological models that simulate the physiological, morphological and phenological processes provide insight into competition effects. Various competition models have been developed (review by Kropff & Van Laar 1993). The eco-physiological model INTERCOM described by Kropff & Van Laar (1993) consists of a number of coupled crop growth models equal to the number of competing species. Under favourable growth conditions, light is the main factor determining the growth rate of the crop and its associated weeds. Site-specific input requirements of INTERCOM include geographical latitude, standard daily weather data, soil physical properties, dates of crop and weed emergence, and weed density. This eco-physiological competition model has been tested with data from competition experiments with several crop-weed combinations (see for a review Kropff & Van Laar 1993). The results of these studies indicate that interplant competition for light and water can be well understood from the underlying physiological processes. Several approaches to introduce spatial variability in the models is underway for e.g. row crops (Schneider *et al.*, submitted). The main gaps in knowledge are related to phenotypic plasticity of weeds with respect to morphological development.

Applications of these models can be found in the development of new simple predictive models for yield loss due to weeds, the analysis of the impact of sub-lethal control measures, the design of new plant types for weed suppression and risk analysis for the development of weed management strategies.

Descriptive models for crop weed-interactions

The most widely used regression model to describe effects of competition at a certain moment is the hyperbolic yield-loss weed density model (Cousens 1985):

$$Y_L = \frac{aN_w}{1 + \frac{a}{m}N_w} \quad (1)$$

where Y_L gives the yield loss, N_w is the weed density, a describes the yield loss caused by adding the first weed per m^2 and m the maximum yield loss. This hyperbolic yield-density equation fits well to data from experiments where only the weed density is varied (Cousens 1985). However, the parameters a and m may vary strongly among experiments due to the effect of other factors on competition processes (Kropff & Van Laar 1993). Because both weed density and the period

between crop and weed emergence strongly determine the competitive relationship between crop and weeds (Cousens *et al.* 1987), more robust prediction of yield loss on the basis of early observations should be based on these two factors.

A simple descriptive regression model for early prediction of crop losses by weed competition introduced by Kropff & Spitters (1991) and extended by Kropff *et al.* (1995) was derived from the eco-physiological model INTERCOM (Kropff & Van Laar 1993). The model relates yield loss to relative weed leaf area (L_w expressed as weed leaf area /crop+weed leaf area) shortly after crop emergence, using the 'relative damage coefficient' q as the main model parameter next to the maximum yield loss m :

$$Y_L = \frac{q L_w}{1 + \left(\frac{q}{m} - 1\right) L_w} \quad (2)$$

Because leaf area accounts for density and age of the weeds, this regression model accounts for the effect of weed density and the effect of the time of weed emergence (Kropff & Spitters 1991). The relative leaf area model was tested in various crops (Kropff and Spitters 1991, Lotz *et al.* 1996). Lotz *et al.* (1996) evaluated the approach over a wide geographic region and found that the descriptive value of the model is good, but that the current predictive ability is still insufficient for practical use in weed management. Techniques to estimate relative leaf areas of weeds in crops by photography and image analysis (Lutman 1992) or by measuring infra-red reflectance (Lotz *et al.* 1994) are very promising. These techniques, however, still need to be improved and implemented in tractor mounted equipment for fast and reliable use for practical decision making.

Weed population dynamics

The current state of the art related to weed population dynamics was reviewed by Cousens & Mortimer (1995) and briefly by Kropff *et al.* (1996). Models have been developed to integrate the knowledge on life-cycle processes. The main processes involved are germination and emergence of seedlings from seeds in the seed bank in the soil, establishment and growth of the weed plants, seed production, seed shedding and seed mortality in the soil. Competition plays an important role in establishment and growth and therefore strongly affects the population dynamics of weeds. Comprehensive models that are based on physiological principles are available for parts of the life cycle: plant growth and competition (as discussed) and germination and emergence (L.M. Vleeshouwers, in prep.). In contrast, processes like seed shedding, seed dispersal and predation of seeds are poorly understood. The different mechanisms of dispersal have been discussed in detail by Cousens & Mortimer (1995). Because most weed seeds remain very close to the plant (Harper 1977), weed patterns in fields do not change dramatically in time (Wilson & Brain 1991) which may be a basis for precision agricultural practices.

Not all models are aimed at understanding and integrating detailed knowledge. Another objective is to predict future weed infestations. Models for forecasting need to be robust. They generally exhibit a better predictive capability when they contain only a few parameter. The various complex processes in the life-cycle are then blended into a few lumped parameters like a germination rate, a reproduction rate and a mortality rate. Forecasting future infestations is bound up with very large error margins, irrespective of our understanding of weed population biology, since some key factors like future weather conditions are unknown.

The most detailed models that encompass the whole life-cycle have been developed for species like *Avena fatua* L. (Cousens *et al.* 1986), *Alopecurus myosuroides* Huds. (Doyle *et al.* 1986) and *Galium aparine* L. (Van der Weide & Van Groenendael 1990). Apart from the level of detail at which the life-cycle is studied, three different modelling approaches to integrate individuals into a population can be distinguished (Durrett & Levin 1994, Kropff *et al.* 1996): (i) the density

based models, (ii) the density based models that take spatial gradients in density into account and (iii) the individual based models which also account for spatial processes. Individual based models are the most comprehensive, but the complexity is not always required. The density based model can be very useful to roughly explore options for long term weed management strategies. The individual based models can be very helpful to explain how patchiness arises (Wallinga 1995a) and to identify opportunities for site specific weed management (Wallinga 1995b).

New research targets

As mentioned in the introduction, three aspects can be distinguished with respect to the improvement of weed management systems (Kropff 1996): prevention, decision making, and control technology. New research targets can be found in all three areas.

Prevention

The first aspect to improve weed management involves any aspect of management that favours the crop relative to the weeds. In traditional agricultural systems, where hand-weeding was practised intensively, cropping systems were designed to reduce weed problems as much as possible. For example, varieties were selected that suppressed weeds. However, today, varieties are only selected with respect to yielding ability and product quality. In rice systems, for example, increased concern about herbicide use induced studies toward the competitiveness of rice varieties. An eco-physiological simulation model for interplant competition was used to identify traits that determine the competitive ability of a crop (Kropff & Van Laar 1993). Detailed studies on trade-offs between different traits (like competitiveness versus yielding ability or sensitivity to diseases) have to be conducted to make this option feasible. New research targets lie in the interface of competition and weed population dynamics. Weed management strategies have to be based on a long term strategy (Kropff *et al.* 1996). Therefore, weed competitiveness is only of interest if weed seed production is significantly reduced as well. In a preliminary analysis with the model of Firbank & Watkinson (1986) it was found that the critical kill rate (the kill rate at which the population of weeds does not increase in the next year and is kept at a low density) only responds strongly when *Agrostemma githago* L. biomass is reduced by more than 60% as a result of increased competitive ability of the crop (Fig. 1). These model results should be tested experimentally. The traits mentioned here could be identified or even modified in the future using biotechnology tools.

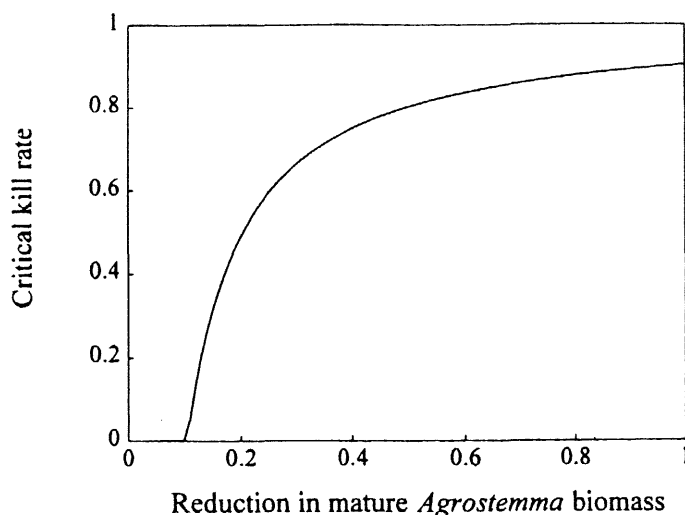


Figure 1. Relation between critical kill rate of *Agrostemma githago* and competitive ability of the crop against *A. githago*, based on the model of Firbank & Watkinson (1986).

Decision Making:

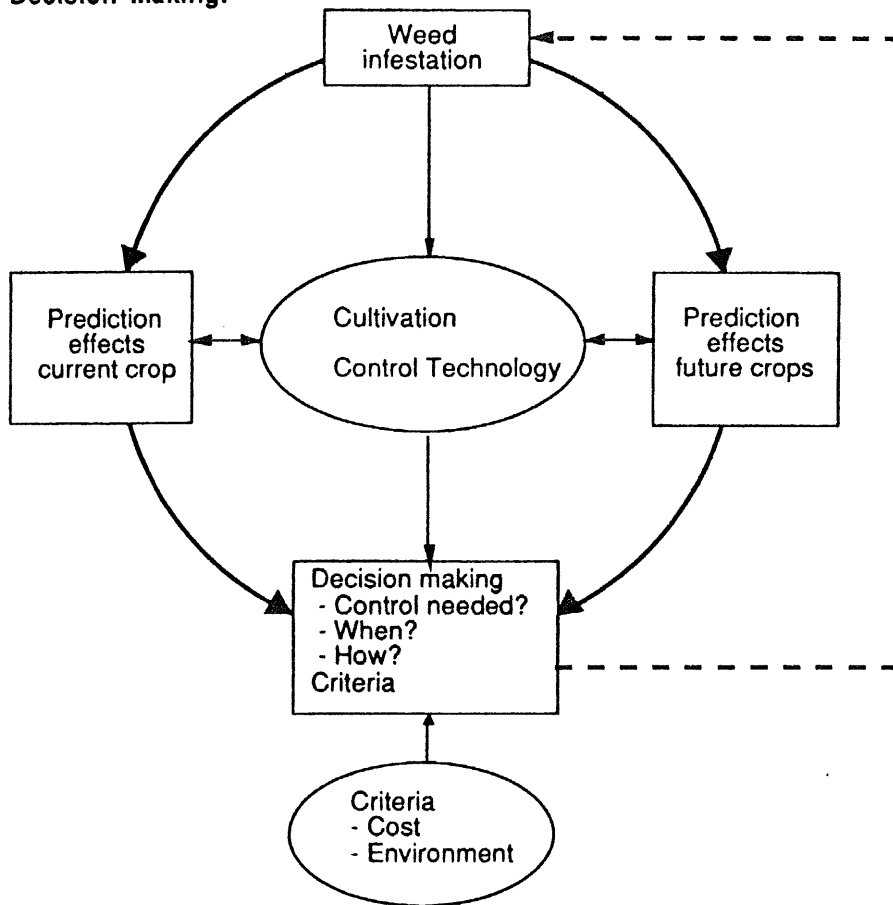


Figure 2. Schematic representation of the decision making process in weed management.

The ability to suppress weeds is just one of the options in relation to prevention. Other options include: timing of cultural measures, stale seed beds, adaptation of the rotation and nutrient management system, crop density, allelopathic varieties etc. For all these options, systems ecological insight in the life cycle of weeds and crop weed interactions is required.

Decision making

The second aspect is the improvement of the decision making process which consists of strategic (long term) decisions, tactic decisions (for a season) and operational decisions in the field. It involves long-term and short-term strategies for weed management, to assist in decision making to determine if, when, where and how weeds should be controlled.

The decision-making process for tactical and operational decisions in a weed management system based on post-emergence observations is illustrated in Fig. 2. To allow rational decision making, the severity of weed infestation shortly after crop emergence should be estimated. Criteria must be defined (i.e. the objectives and planning horizon of the farmer) to enable economic decision making. Severity of the weed infestation has to be estimated in order to predict crop yield loss and weed population density at the end of the growing season along with quantification of costs, efficacy and side effects of possible control measures. The relative leaf area-yield loss regression model would offer an option as it accounts for the effect of weed densities, different flushes of weeds and the period between crop and weed emergence. However, it is still not easy to determine relative leaf areas of weeds in the field. Moreover, the effect of other factors, such as transplanting shock or

severe water stress, is not accounted for, because the regression models do not account for underlying processes. Further development and testing of the relative leaf area approach will be required in the future.

Is control needed?

Several weed control advisory systems have been developed that use threshold densities for weed control or that focus on the need for and optimisation of herbicide dosage (if and how questions). The threshold is the level of weed infestation which can be tolerated based on specified criteria (generally based on economic objectives). Different concepts for thresholds for tactical (within season) and strategic (long-term) decision-making in weed management have been developed. Predictions of yield loss in the current season and future seasons can be used to decide whether and how the weeds should be controlled using defined criteria such as maximisation of profits and minimisation of environmental effects. Such approaches to weed management have scarcely been tested (c.f. Cousens 1987). A solid comparison of single year and multiple year threshold weed infestation levels is required for further development of these systems. Population predictions will never be accurate as future conditions cannot be predicted accurately, but risk analyses and scenario studies would be a good step toward rational decision making systems.

When is control needed?

The timing of weed control is very important in integrated weed management. With mechanical control, the timing often determines the selectivity between crop and weeds for harrowing. Another example is found in work underway to predict the minimum lethal herbicide dosage based on the development stage of the weeds (Ketel *et al.* 1996). Based on fundamental knowledge of herbicide effects at the chloroplast level (for photosynthesis inhibitors) the minimum lethal herbicide dose can be calculated for each development stage. It appears that the minimum lethal herbicide dose relates exponentially to the biomass of the weeds, indicating the opportunities for saving herbicide because the advised dosage is based on large plants as a safely net for weed control. Further improvements can be made based on insight in the effect of environmental factors on herbicide efficacy.

Where should weeds be controlled?

Much is expected from site specific weed management techniques that make use of the fact that the spatial pattern of annual and perennial weeds is typically aggregated. The aggregated pattern creates the potential for spraying only the weed patches, thereby reducing the amount of herbicide applied (Mortensen *et al.* 1993; Wallinga 1995a). Engineering approaches have tried to develop a technology to support such a weed control (Miller *et al.* 1995, Felton 1995). The potential reduction in herbicide use was estimated, and as 9% up to 97% for cereal fields in England infested by *Elymus repens* (L.) Gould (Rew *et al.* 1996). The use of a patch spraying machine reduced herbicide use by 9% up to 60 % in a fallow season, and 50 % to 80 % in post-harvest application on Canadian prairies (Blackshaw 1996). The estimated reduction in herbicide use varied with weed infestation level and spatial pattern of weeds (Rew *et al.* 1996). New research targets lie in the field of technology development related to weed recognition by tools like image analysis and optical systems in combination with precision spraying technology or mechanical cutting technology.

Method of control

Ideally, integrated weed management systems should be based on the use of mechanical and biological control first and using herbicides for correction. For decision support systems a pragmatic approach was generally adopted like systems that focus on herbicide selection and the optimization of herbicide dosage have been quite successful (Fischer & Lee 1981; Pandey & Medd 1991, Rydahl 1995). Future options lay in the development of self learning systems which develop site specific management options based on knowledge and information built up at the specific site (farm).

Control technology development

There are many ways in which control technology can be improved ranging from precision mechanical weed management tools to precision herbicide treatments. The work mentioned before based on the minimum lethal herbicide dose, patch spraying equipment, new techniques for mechanical control, preferably based on optical detection for site specific management. The identification of new potential break points in the life cycle of weeds that may lead to the identification of new control technologies is a major target for the future. An example is the separation of the effects of weeds in current and future crops. Often weeds do not cause yield loss in a current crop. In such situations, we need new technology to avoid or reduce weed seed production (Medd & Ridings 1989). The approach to use biological insight for technology development is a major challenge for the future.

Conclusion

For the development of weed management systems which are effective at minimum cost, safe for the environment and adaptable to individual situations, an integrated weed management approach has to be developed in analogy to the strategies developed for integrated pest management. Options to improve weed management systems with a minimum herbicide use exist in all its components: prevention, decision making and control technology. Future research should focus both on technology development as well as on prevention and strategic decision making. Quantitative insight in weed ecology and crop weed interactions is essential for that purpose and further increase of eco-physiological insight in these processes integrated in models should be one of the main targets for future weed ecological research.

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