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Approaches used in the prediction of weed population dynamics

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ABSTRACT

The design and evaluation of weed management systems, including systems based on herbicide resistant crops, requires quantitative insight into the population dynamics of weeds. It may help to identify risks and changes in weed vegetation development and may be useful for the determination of new control techniques that disrupt the life cycle of resistant weeds at some point in time. Such insight may also be useful to develop management technologies and to develop strategies for weed management. The complexity and the long-term nature of weed population dynamics make the use of models essential. Different modelling approaches have been developed and are described briefly. Opportunities for applying these techniques to improve weed management systems, including systems based on herbicide resistant crops, and requirements for further research are discussed.

INTRODUCTION

Traditionally, most management practices in agricultural systems were focused on the reduction of weed infestations. Experience-knowledge related to the population dynamics of weeds often formed the basis of these management practices which is clear from sayings found back in many different cultures such as "one years' seeding, seven years' weeding". With the introduction of herbicides, the need to focus general crop management on the long-term reduction of weed problems diminished. Today, weeds are relatively easy and cheap to control by herbicides in many crops, though this situation is changing. Increased concern about environmental side effects of herbicides (resulting in a ban on major herbicides in e.g. Europe in the coming years), the development of herbicide resistance in weeds and the necessity to reduce the cost of inputs, have resulted in greater pressure on farmers to reduce the use of herbicides. This caused an increased interest in the development of integrated weed management systems (IWM). Rather than trying to eradicate weeds from a field, emphasis is on the management of weed populations (Cousens, 1987).

Three aspects of IWM systems can be distinguished: decision-making, prevention and weed control technology (Kropff *et al.*, 1997). If only the short-term perspective is considered, decision making mainly involves operational decisions on if, when, where and how weeds should be controlled. In order to answer this type of question quantitative insight into crop-weed interactions is highly relevant. If weed problems are examined on a longer-term perspective, the first step in the decision making process deals with strategic decisions, which set the framework for tactical and operational decisions. Apart from the effect of the weeds in the present crop, the potential consequences for future crops are accounted for. For such considerations knowledge on the dynamics of weed populations in space and time becomes pertinent. Irrespective of the time dimension of the analysis, it is clear that attempts to reduce the present dependency on herbicides should focus on prevention. This can be based on cultural measures that favour the crop or through the use of more competitive varieties, on the development of better curative control techniques and on better long- and short-term decision making. This becomes even more important when precision farming techniques facilitate site and development stage specific weed control. Quantitative insight into both crop-weed interactions and the dynamics of weed populations in space and in time forms the basis for such explorations of opportunities to improve weed management.

A novel approach in weed management involves the use of transgenic herbicide resistant (HR) crops that enable the use of broad-spectrum herbicides like glyphosate and glufosinate. There is a considerable debate over whether this will result in a reduced level of herbicide use, and a concern over what the long-term implications for farming systems may be. It is well recognised that this will lead to new weed problems such as changing weed populations and the development of (partial) resistance. To evaluate the impact of such herbicide resistant crops on weed populations and the risks involved, thorough quantitative insight is required into the behaviour of weeds, the effects of the weeds in agroecosystems, and the efficacy of weed control technologies. This involves comprehensive understanding of the dynamics of weed populations across growing seasons. 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.

Modelling approaches for weed population dynamics and crop-weed interactions were reviewed by Cousens & Mortimer (1995), Kropff & Van Laar (1993) and Kropff *et al.* (1996). This paper discusses the methods available to help develop a quantitative understanding of the population dynamics of weeds and the opportunities to use this knowledge for the evaluation of weed management strategies including the use of herbicide tolerant crops.

PROCESSES DETERMINING THE LIFE CYCLE OF WEEDS

The main processes determining the life cycle of weeds are: germination and emergence of seedlings from seeds; establishment and growth of the weed plants; seed production; seed shedding and seed mortality in the soil. Competition plays a major role in different stages of the life cycle and therefore strongly affects the population dynamics of weeds. For perennial or clonal weeds, additional processes of importance are formation of underground structures and regrowth from associated buds. The dissemination, invasion and spread of weeds are very important for the population dynamics of weeds in real farming systems. This is determined by spread by natural processes but also by the distribution of weed seeds by farmers' equipment.

Seed bank dynamics

The weed seed bank is determined by inflow from newly produced seeds and outflow due to germination and mortality of seeds in the soil. Mortality often follows germination when the seedling cannot reach the surface because of the seed depth or the mechanical impedance of the soil. Predation of weed seeds, however, is also a very important factor determining the reduction of viable seeds in the soil. Harper (1977) developed a conceptual framework for the dynamics of seed banks. Weed seeds can remain viable in the soil for very long periods, with strong implications for management strategies. A key process determining the germination ability of seeds is dormancy, which can be defined by the range of environmental conditions under which the seeds can germinate. The dormancy status of seeds in the field is changing continuously. Karssen (1982) developed a conceptual model in which the dormancy status is defined as the width of the temperature range in which seeds can germinate. In summer annuals, dormancy is broken by low winter temperature and induced by high summer temperatures, whereas the opposite is found in winter annuals. Approaches to modelling dormancy have been developed by Bouwmeester & Karssen (1992) and Vleeshouwers & Bouwmeester (1993). Attempts to quantify germination and emergence in the field are rare (Forcella, 1993; Vleeshouwers, 1997). The main limitation for accurate prediction of emergence in the field seems to be an accurate prediction of dormancy (Vleeshouwers, 1987).

In spite of the vast amount of work on germination and dormancy it is still difficult to realistically predict seed bank dynamics and in particular field germination and emergence of weeds. This may result from limited availability of data from field studies, especially complete data sets where all relevant environmental data have been monitored. It also may be due to the complexity of processes in the soil related to seed bank dynamics (like predation) which cannot easily be monitored. As the dynamics of the seed bank forms the essential link between weed populations in subsequent years, much greater emphasis is needed on studies of seed bank dynamics that focus on mechanisms.

Weed establishment and growth in competition with the crop

One of the significant areas of recent research in weed biology has been the interaction between the crop and the weeds. However, most work has been restricted to a descriptive quantification of crop loss due to weeds. In these studies weed species, weed densities, dates of weed emergence and environments differ (but are not recorded), resulting in a vast amount of data showing wide ranges of yield losses; such data can hardly be interpreted, nor used for the improvement of weed management. Concepts like damage thresholds and the critical period for weed control have been developed, but are not used intensively because of the importance of long-term aspects related to the population dynamics. Farmers are "risk averters" to weeds, and not just "profit maximisers". Detailed understanding of the effect of the crop on the weeds is crucial for understanding the life strategies of weeds. Eco-physiological competition models like INTERCOM (Kropff & Van Laar, 1993) provide such an understanding. In these models the growth of all competing species is simulated, based on morphological, physiological and phenological processes in relation to environmental biotic and abiotic factors. Eco-physiological characteristics of weeds have been determined for key weed species, including *Chenopodium album* L., *Stellaria media* L. *Avena fatua* L., and *Echinochloa crus-galli* (L.) Beauv. The models have demonstrated a strong capability to quantitatively understand crop-weed interactions in different environments and competition situations (Kropff & Van Laar, 1993). Studies on the competitive relations of crop cultivars demonstrated the ability of the models to quantitatively explain varietal differences in competitive ability (Bastiaans *et al.,* 1997). The main gaps in knowledge are related to morphological development and especially the phenotypic plasticity of weeds with respect to these morphological features. Kropff & Van Laar (1993), for example, demonstrated the impressive plasticity of *C. album* with respect to height development in different competition situations.

Weed seed production

Competition by neighbouring plants strongly determines the production of seeds by weed plants. Increased competition results in reductions of biomass, seed biomass and the number of seeds per plant. Hence early-emerging weeds, under a more favourable competitive situation can produce many more seeds than late-emerging weeds. For annual weeds simple relationships between total biomass of vegetative parts and reproduction have been reported (e.g. Thompson *et al*., 1991). However, recent results (Bastiaans, unpublished) with *Chenopodium album* L. and *Echinochloa crus-galli* L. in different competition situations show that this relationship is not the same for all weed cohorts. Late-emerging weeds have a lower reproductive effort; a very important aspect for population dynamics. If the relationships are known, the mechanistic simulation models for crop-weed competition offer a powerful tool to predict weed reproduction over a variety of environments. In such circumstances different cohorts of weeds have to be distinguished. Field studies should be initiated to enable the implementation of weed reproduction in models for crop-weed interactions. This indicates the important change that is needed in competition studies: instead of studying the effect of the weeds on the crop we need to study the effect of the crop on the weed and especially its effect on weed seed production. That is a key process determining the weed population dynamics.

Seed dispersal

The dispersal of seeds determines the inflow of weed seeds in the system on a spatial scale. Invasion of weeds is important at different scales ranging from continent, country, region, community, and farm to field level. Besides natural dispersal processes, man has had a major impact on the spread of weeds at all different scales. Cousens & Mortimer (1995) have reviewed the different mechanisms of dispersal. They concluded that apart from wind dispersal few quantitative studies have been conducted on these mechanisms. Most weed seeds remain very close to the parent plant (Harper, 1977), and field weed patterns may not change dramatically in time (Wilson & Brain, 1991); this may be a basis for precision agricultural practices. Wallinga (1998) demonstrated that the formation of relatively stable patches of weeds as found in field situations, can be explained by relatively simple population dynamical models that are spatially explicit.

MODELLING POPULATION DYNAMICS

To obtain an integrated insight into life cycle processes mathematical models are indispensable. The state of the art in modelling life-cycle processes was described by Cousens & Mortimer (1995). Comprehensive models that are based on physiological principles are only available for some parts of the life cycle including plant growth and competition (Kropff & Van Laar, 1993), germination and emergence (Vleeshouwers & Bouwmeester, 1993). In contrast, processes like seed shedding, seed dispersal and predation of seeds are poorly understood. The most detailed models that encompass the whole life cycle have been developed for *Avena fatua* L. (Cousens *et al.*, 1986), *Alopecurus myosuroides* Huds. (Doyle *et al.*, 1986) and *Galium aparine* L. (Van der Weide & Van Groenendael, 1990; Wallinga, 1998).

The basic structure used in most models was described by Spitters (1989). In this model, *St* indicates the density of weed seeds in the soil, where the subscript denotes the year when density is observed. Each year a portion *m* of the seeds is removed by natural mortality of seeds, while germination and emergence of seeds remove a portion *g*. The emerged plants will reproduce on average *z* viable seeds that return to the seed bank. The effect of weed plant density on *z* is introduced by a rectangular hyperbola:

$$z = \frac{a}{1 + \frac{a}{b} g(1-r)S_t} \qquad (1)$$

where *a* is the production of viable seeds per plant at low weed densities and *b* is the maximum seed production per unit area at high weed densities. Weed control is introduced by multiplying the density of emerged weeds by (1-*r*), where *r* is the fraction of weed seedlings killed by weed control. Integration of these life-cycle processes into one equation that generates the weed population dynamics in terms of density of weed seeds in the soil gives:

$$S_{t+1} = (1-g-m)S_t + z(1-r)gS_t \qquad (2)$$

This equation shows how the weed density in the previous year determines the density of seeds in the soil, based on species characteristics, and on the intensity of weed control. In this simple case the model can be written as one equation and solved analytically, but when processes are described in more detail, numerical integration techniques have to be used.

Besides understanding and integrating detailed knowledge, these models can also be used to predict future weed infestations. Models for forecasting need to be robust, and they generally exhibit a better predictive capability when they contain only a few parameters, even if there is a sound understanding of underlying processes. Forecasting future infestations using models may be subject to very large error margins, because of the nature of the process (exponential growth until density effects occur) and because some key factors like future weather conditions cannot be predicted.

Three conceptually different approaches have been developed to predict population dynamics from the life-cycle processes, and these variations may lead to different results (Durrett & Levin, 1994). Three different modelling approaches for integrating individuals into a population can be distinguished (Wallinga, 1998): (i) density based models, (ii) density based models that take spatial processes into account and (iii) individual based models which also account for spatial processes.

Most frequently the density of weeds is used as the key variable. From the density in a given year, the rate of change in density and the density in the next year are derived. An important assumption underlying this approach is that each weed perceives a similar environment and that the system is homogeneous. Due to the conceptual clarity in modelling temporal changes in density this approach is widely used, ranging from exponential growth to bounded growth (Firbank & Watkinson, 1986).

Weed dispersal can be included into the model by explicitly introducing the spatial dimension in the model by dividing an area into small units; this results in so-called cellular automaton models. Versions of this type of model have been employed to simulate spread of weeds (e.g. Maxwell & Ghersa, 1992). The key variable in this modelling approach again is weed density. To overcome problems real values have to be truncated to integer values at low densities. Another problem is that in the course of time spatial gradients will either move or flatten out, and so for any particular site this approach reduces with time to the previously mentioned approach of modelling only density.

In the third approach weed density is not included as a basic variable in the model, but the configuration of weeds over space is taken. This modelling approach includes model types like the individual based model (cf. Pacala & Silander, 1985) and cellular automaton models (cf. Silvertown *et al.*, 1992). This type of model makes it possible to study the interaction between dynamics and patchiness in weeds. Wallinga (1995) analysed the development of patchiness of weeds at realistic low densities using such an individual based spatial model. Using simulation studies, this study demonstrated that patchiness occurs naturally at low weed densities whereas homogeneous situations are found at higher densities. Whenever patchiness occurs, the mean density of weeds per unit area gives misleading estimates of average yield loss and reproduction rates of weeds because of the nonlinear relation between weed density and yield loss (Brain & Cousens, 1990; Kropff *et al.*, 1993). Hence disregarding spatial distribution of weeds will result in a systematic overestimation of population growth rates (Wallinga, 1995).

Of the modelling approaches, individual based models are the most comprehensive, but complete models based on individuals and including spatial aspects are hardly available and difficult to parameterise. Therefore, the most simple and applicable approach has to be selected for a specific application. The non-spatial density-based models can be very useful to roughly explore options for long term weed management strategies, spatial processes need to be taken into account to study effects of weed invasions and to identify opportunities for site specific weed management. A major difference between the population dynamics of plants in general and weeds is that man explicitly interferes in weed population dynamics, thus models for weed population dynamics have an additional control variable. That factor has major implications for population behaviour.

EXPLORATION OF LONG-TERM WEED MANAGEMENT STRATEGIES

A major application of the population dynamics models is to explore the optimal control that fits the needs of the farmer and to evaluate scenarios for different control strategies such as the use of preventive measures, the use of thresholds, a critical kill rate or the use of HT crops.

Prevention through increased crop competitive ability and weed populations.

Kropff *et al.* (1997) determined whether the introduction of cultivars with an increased competitive ability would reduce the seed production of weeds (in this case *Agrostemma githago* L. in wheat). In a preliminary analysis it was found that the critical kill rate to maintain the population of weeds at a low density was very sensitive to competition by the crop. Large differences in competitive ability between genotypes have been demonstrated (e.g. for rice by Kropff & Van Laar, 1993). Especially the seed production of late-emerging weeds or weeds that survive control measures can be strongly reduced by using competitive varieties. In addition this component could be used in herbicide resistant crops to reduce population development of relatively insensitive weeds. Effects of other preventive measures also can be evaluated using the models.

Frequency of herbicide-application and thresholds

In simulation studies, the frequency of herbicide-application required to manage weeds in continuously grown cereals was found to be needed only once every second year with a yield loss of less than 5% (Spitters, 1989). The only disadvantage of this control strategy would be that a failure of weed control in one year bears the danger of having to take cumbersome and more expensive measures against large infestations in future crops.

Wallinga (1998) used the density-based model to determine the influence of the threshold level on the frequency of herbicide applications. The simulations resulted in an oscillation of weed density in a periodic fashion around the threshold, with a frequency that seemed to be independent of the threshold value. He concluded that the weed control threshold as a tool to base control frequency on economic considerations loses meaning when it is applied to the long term. These are very important findings to take into account when applying these approaches in herbicide resistant crops for the late-emerging weeds and surviving weeds.

Critical kill rate

The long-term density of weeds responds sensitively to the kill rate, and only for a very narrow range of kill rates is a stable low density obtained. Control strategies need not only be imposed, they can also be extracted from the population dynamics model by optimisation of control using, for example, dynamic programming. Pandey & Medd (1991) employed this technique and showed that for control of *Avena fatua* optimal decision rules lead to higher densities compared with long-term decision rules. In a stationary situation the long-term effect of a strategy can be evaluated. In the model mentioned the critical kill rate $\bar{r}$ can be expressed by (Wallinga, 1998; Kropff *et al.*, 1996):

$$r_c = 1 - \frac{g+m}{ag} \qquad (3)$$

where population dynamic characteristics are captured in the parameters a (the production of viable seeds per plant at low densities), b (the maximum production of viable seeds per unit area at high densities), m (the relative amount of seeds removed annually due to mortality), and g (the relative amount of seeds that germinate and emerge). In this equation, r_C denotes the critical kill rate, which is required to maintain the weed population at a low density. Any weed management strategy that does not aim for eradication and that avoids high yield losses must have a kill rate that approximates to this critical kill rate. At very high kill rates, as $r > r_C$, the weed population will die out eventually, unless there is a continuous import of weed seeds. When this import is virtually absent, it is also feasible to keep weeds stationary at a zero density, which must be the result of an eradication programme. This shows that an optimal control strategy leads in the long-term to the maintenance of a positive density (containment) or, as a particular case, to striving for a zero density (eradication).

Evaluation of systems based on herbicide resistant transgenic crops

The approaches discussed can be used to evaluate the impact of the introduction of transgenic HR crops in combination with broad spectrum herbicides and can help to quantify the risks of this weed management approach, such as:

- The possible development of herbicide resistant weeds as a result of large scale intensive use of single herbicides (Darmency, 1996), through mutation and selection. Recently this has been observed for glyphosate in *Lolium rigidum* in Australia or through backcrossing between crop and weed. Mikkelsen *et al.* (1996) showed that backcrossing can lead to herbicide resistant weeds in two generations following treatment of *Brassica campestris* with glufosinate. Models for the population dynamics combined with population genetic models could help in identifying the risk for the development of herbicide resistant weeds in different scenarios.
- The change of species composition because of the new opportunities for less sensitive weeds. Models for the population dynamics of weeds can be used to identify the need for additional measures based on population management.
- Volunteer plants of the HR crop in successive crops in which these herbicides are used for control such as the use of glyphosate to control volunteer potatoes (Squire *et al.*, 1997).
- Opportunities for site specific weed control in herbicide resistant crops (for the major herbicide or for additional herbicides for escaping weeds)

Population dynamics in complex field situations

The models discussed deal with a continuously grown single annual crop species and with one weed species that can manifest a rapid population growth and that can cause severe yield losses. In order to encompass crop rotations, the duration of the rotation might be considered as a time step, rather than one year for a continuously grown crop. This does not, however, cause any essential changes in the approaches outlined above. Several studies have been directed at modelling population dynamics over crop rotations (e.g. Mortensen *et al.*, 1993). Multiple weed populations with different characteristics form a more difficult topic and several studies have tried to address this problem (Gressel & Segel, 1978; Mortimer *et al.*, 1990), but this is an area where further work is required.

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 analogous to the strategies developed for integrated pest management (IPM). Such systems should focus on the development of an environment that favours the crop relative to the weeds. If HR crops are used as part of the system, changing problems related to weed management have to be identified at an early stage. This requires more quantitative knowledge of weed population dynamics and crop weed interactions. Sound modelling frameworks for these processes have been developed and can be used to improve weed management systems and to evaluate all the advantages and disadvantages of the introduction of HR crops. However, introduction of these crops is taking place rapidly, before we have even attempted to predict their implications.

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