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Weed population dynamics

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Summary

For the development of improved weed management systems with a reduced dependency on herbicides, quantitative insight in the population dynamics of weeds and interactions between crop and weeds is needed. Such insight may help to identify opportunities for new control techniques that break the life cycle of weeds at some point in time, to develop management technologies and to develop strategies for weed management. The complexity of the matter and the long-term character of weed population dynamics makes the use of models necessary. Different modelling approaches have been developed and are described briefly. Opportunities to use the available knowledge and models to improve weed management and research needs for that purpose are discussed.

Introduction

Knowledge of the biology of plants is the basis for all weed management systems. In traditional agricultural systems, in which herbicides were not used, most management practices were focused on the reduction of weed problems. This was mainly based on experience-knowledge related to the population dynamics of weeds. The importance of weeds in traditional systems appears from the vast amount of sayings like "one years' seeding equals seven years' weeding". With the introduction of herbicides, the need to focus general crop management on the reduction of weed problems in the long term diminished. In many crops, weeds are relatively easy and cheap to control by herbicides. However, that is changing. There is an increasing pressure on farmers to reduce the use of herbicides. Besides the necessity to reduce cost of inputs, other factors contribute to this trend like the widespread concern about environmental side effects of herbicides which has resulted in a ban of several herbicides in some countries, the development of herbicide resistance in important weed species and the increasing cost to develop new herbicides.

As a result, there has been an increasing interest in the development of strategies for integrated weed management 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 rationalization of herbicide use. In this strategy emphasis is 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. Three main categories of weed management strategies were distinguished by Cousens (1987):

(i) Eradication, where all effort is focused on the elimination of the weeds. Only for a few very "noxious" weeds like *Avena fatua* L. and *Cyperus esculentus* L. eradication programs have been used in the Netherlands. These programs are expensive though they may well be cost-effective on a long term (Murdoch, 1988; Medd *et al.*, these proceedings).

(ii) Prophylaxis, where crop loss by weeds is minimized each year (generally by using pre-emergence herbicides)

(iii) Containment, where the weed population is kept at a specified low level.

For the development of weed management systems that focus on containment, 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 both crop-weed interactions within the growing season and the dynamics of weed populations across growing seasons. The current state of the art related to quantitative understanding of weed population dynamics and crop weed interactions was reviewed by Cousens & Mortimer (1995) and Kropff & Van Laar (1993).

Most research effort in the past decades has been focused on the improvement of weed control technologies, mainly herbicides. That may have been a major reason leading to the conclusion Norris (1992) drew from an extensive survey. He stated that apart from weed biological research related to herbicides, not many examples can be given in which weed biological research was used to improve weed management. Because of the complexity of the system, quantitative systems approaches are required to bridge the gap between knowledge at the process or physiological and individual level and management at the population level.

In this paper we review the state of the art with respect to quantitative understanding of the population dynamics of weeds, opportunities to use this knowledge for the improvement of weed management and challenges for future research.

The life cycle of weeds

The life cycle of annual weeds and the main processes involved are illustrated in a simplified form in Figure 1. The main processes 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 a major role in different stages of the life cycle and therefore strongly affects the population dynamics of weeds. For perennial weeds or clonal weed species, additional processes of importance are formation of underground structures and regrowth from buds on these structures. The dissemination, invasion and spread of weeds is not indicated in the scheme, but is of relevance for the population dynamics of weeds in real farming systems. Besides natural processes of spread, the spread of weed seeds by farmers' equipment is significant as well.

Seed bank dynamics

The dynamics of the seed bank is determined by inflow from newly produced seeds and outflow due to germination and emergence and mortality of seeds in the soil. Mortality often follows germination when the seedling cannot reach the surface because of the depth of the seed or the mechanical impedence of the soil. However, predation of weed seeds is assumed to be a very important factor determining the reduction of viable seeds in the soil as well. A conceptual framework for the dynamics of seed banks was developed by Harper (1977). Weed seeds can remain viable in the soil for very long periods, which has strong implications for management strategies. One of the key processes determining the germinability of seeds is dormancy. The dormancy status can be defined by the range of environmental conditions under which the seeds can germinate. Primary dormancy is the dormancy found in freshly shed seed and secondary dormancy is induced when seeds do not germinate after the release of primary dormancy (Karssen, 1982). In the field, the dormancy status of seeds 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. This "window of opportunity" changes throughout the season and is mainly regulated by soil temperature. 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 model dormancy have been developed by Bouwmeester & Karssen (1992) and Vleeshouwers & Bouwmeester (1993). Attempts to quantify germination and emergence in the field, which includes the process of seedling growth from the location of the seed to the surface, are rare. The main limitation for accurate prediction of emergence in the field seems to be an accurate prediction of dormancy (Vleeshouwers, personal communication).

It can be concluded that in spite of the vast amount of work on germination and dormancy, yet there are no studies that show the possibility to realistically predict the seed bank dynamics and in particular field germination and emergence of weeds. On the one hand this may be the result from limited availability of data from field studies, especially complete data sets where all relevant environmental data were monitored. On the other hand, the complexity of processes in the soil related to seed bank dynamics (like predation) which cannot easily be monitored has also limited progress. As the seed bank dynamics forms the essential link between weed populations in subsequent years, much greater emphasis is needed on seed bank dynamics studies.

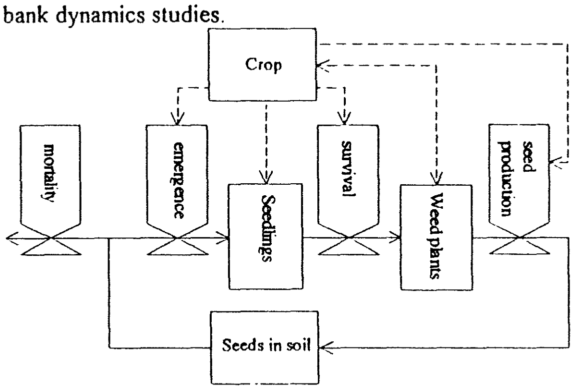

Fig. 1. Schematic representation of population dynamics of weeds. Drawn lines indicate the life cycle of weeds, broken lines indicate processes where crop and weeds interact.

Establishment and growth of weeds in competition with the crop

Although crop-weed competition has been the main area of research in weed biology in the past decades, most work has been restricted to a descriptive quantification of crop loss by weeds (Norris, 1992). In these studies weed species, weed densities, dates of weed emergence and environments have been varied, resulting in a vast amount of data showing wide ranges of yield losses which 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. Detailed understanding of the effect of the crop on the weeds is crucial for understanding the life strategies of weeds. Recently developed eco-physiological competition models like INTERCOM (Kropff & Van Laar, 1993) provide such 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 some key weed species like *Chenopodium album* L., *Stellaria media* L. and *Echinochloa crus-galli* (L.) Beauv. The main gaps in knowledge are related to morphological development and especially the phenotypic plasticity of weeds with respect to these morphological features which are essential for understanding weed growth in competition situations. Kropff & Van Laar (1993) for example studied the plasticity of *C. album* with respect to height development in relation to dry matter growth which was varied by growing the weeds in different competition situations. *C. album* demonstrated an impressive capacity to overtop the crop (sugarbeet) in spite of an unfavourable starting position due to late weed emergence.

Weed seed production

The production of seeds by weed plants is strongly determined by the competition situation. With increasing competitive pressure by neighbouring plants, the biomass per plant will be reduced and thereby the seed biomass and the number of seeds per plant. That implies that early emerging weeds, that face 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 exist. Samson & Werk (1986) developed a simple model based on a linear relationship between absolute reproductive biomass and vegetative biomass per plant. Thompson *et al.* (1991) demonstrated that in five species of agricultural weeds this linear relationship could be used. Given the validity of this simple relationship, the aforementioned mechanistic simulation models for crop-weed competition offer a powerful tool to predict weed reproduction over a variety of environments; especially, when these environments differ in level of competition. Field studies should be initiated to determine the applicability of practical implementation of weed reproduction in models for crop-weed interactions

Spatial dynamics of weeds

Invasion of weeds is important at different scales ranging from continent, country, region, community, farm to field level. Besides natural processes, man has a major impact on the spread of weeds at all different scales. The different mechanisms of dispersal have been discussed in detail by Cousens & Mortimer (1995) and Rew & Cussans (1995), who concluded that apart from wind dispersal hardly any quantitative studies have been conducted on these mechanisms. 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 (Johnson *et al.*, 1995).

Modelling population dynamics

Models can be helpful to integrate the knowledge on life-cycle processes. The current state of the art in modelling life-cycle processes was described by Doyle (1991) and Cousens & Mortimer (1995). Comprehensive models that are based on physiological principles are only available for parts of the life cycle: plant growth and competition (Kropff & Van Laar, 1993) and 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 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). The common basic features of these models are illustrated by the model described in Appendix 1 and illustrated in Fig. 1.

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, and they generally exhibit a better predictive capability when they contain only a few parameters, even if there is complete understanding of underlying processes (cf. Ludwig & Walters 1985). 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.

Apart from the level of detail at which the life-cycle is studied, it is important to realise that there are various ways to retrieve population dynamics from the life-cycle processes, and these various ways may lead to different results (Durrett & Levin, 1994). Three different modelling approaches to integrate individuals into a population can be distinguished: (i) the density based models, (ii) the density based models that take spatial processes into account and (iii) the individual based models which also account for spatial processes.

The modelling approach that is most frequently used takes density of weeds as a key variable. From the current value of the density, the rate of change in density and new values for the density are derived. A tacit assumption underlying this approach is that each weed perceives a similar environment and that the system is homogeneous. The consequence of this assumption is an impossibility to encode dispersal of weed seeds into this type of models. Yet due to the conceptual clarity in modelling temporal changes in density this approach is widely used, ranging from exponential growth (Selman 1970) to bounded growth (Firbank & Watkinson 1986). The model described in Figure 1 and appendix 1 also follows this modelling approach, hence parameters that describe dispersal of weeds are lacking.

A rather obvious way of including dispersal of weeds is to include space into the model and allow for spatial gradients in density, which results in so-called reaction-diffusion models. Discrete versions of this type of models have been employed to simulate spread of weeds (Auld & Coote, 1980; Ballaré *et al.*, 1987; Maxwell & Ghersa, 1992). The key variable in this modelling approach again is the weed density. Since density is interpreted as a real variable it is easy to generate artefacts like 0.001 plant on one square meter. This problem can be overcome by truncating low densities to integer values (Schippers *et al.*, 1993; González-Andujar & Perry, 1995). 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 of modelling density and dispersal reduces in the course of time to the previous mentioned approach of modelling density only.

One step further is to abandon weed density as a basic variable in the model, and proceed with the configuration of weeds over space. This modelling approach includes model types like the individual based model (cf. Pacala & Silander, 1985) and cellular automaton models (cf. Barkham & Hance, 1982; Silvertown *et al.*, 1992). This type of models makes it possible to study the interaction between dynamics and patchiness in weeds. Wallinga (1995b) analysed the development of patchiness of weeds at realistic low densities using such an individual based spatial model. This study demonstrated with simulation studies that patchiness occurs naturally at low weed densities whereas homogeneous situations are found at higher densities. This phenomenon could not be simulated using the existing density based models of weed population dynamic. Whenever patchiness occurs, the mean density of weeds per unit area gives misleading estimates of average yield loss and reproduction rate of weeds because of the nonlinear relation between density and yield loss or weed (Van Groenendael, 1988; Kropff *et al.*, 1993). Hence disregarding spatial distribution of weeds will result in a systematic overestimation of population growth rates (Wallinga, 1995b).

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 parameterize. Therefore, the most simple and applicable approach has to be selected for a specific application. The density based model can be very useful to roughly explore options for long term weed management strategies, the spatial processes need to be taken into account to study effects of weed invasions, whereas the individual based models can be very helpful to identify opportunities for site specific weed management.

Application of population dynamic models to improve weed management

So far, our reflections on modelling weed population dynamics are valid for modelling plant population dynamics in general (see Pacala, 1989). The major difference between plants and weeds is that man explicitly interferes in weed population dynamics, thus models for weed population dynamics have a control variable as an additional whereas models of plant population dynamics do not. The question is how to set this control, and how to find the optimal control that fits the needs of the farmer.

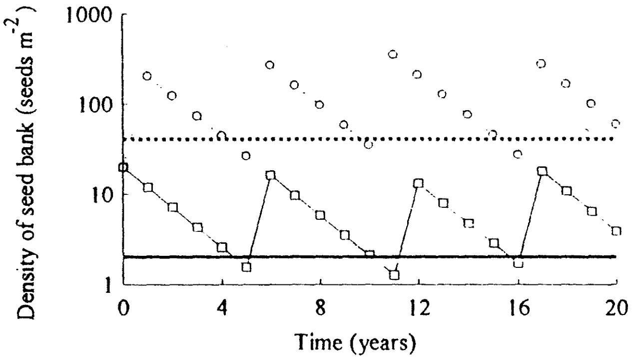

Fig. 2. Idealised effects of control thresholds on density of weed seeds in the soil, and on control frequency. Population dynamics are simulated using equation A4. Circles and broken lines indicate density of weed seeds in the soil managed according to a threshold of 40 seeds per m^2, squares and drawn lines indicate density of weed seeds in the soil managed according to a threshold of 2 seeds per m^2. Initial density is set at 20 seeds per m^2. Disregarding the initial effects in the first year, weeds are controlled in 16 out of 19 years for both thresholds in this simulation.

The simplest way is to implement various control strategies, calculate the effects with a model and than compare the results. For instance, the effects of different kill rates were calculated by Firbank & Watkinson (1986). Their results show that long-term density appears to respond sensitively to kill rate, and only for a very narrow range of kill rates a stable low density is obtained. Another way to implement a strategy is to impose a threshold density, and for densities above the threshold weeds are controlled, and for densities below the threshold weeds are not controlled. This approach is illustrated by simulations with the model described in Appendix 1 (Fig. 2). The density oscillates in a periodic fashion around the threshold, and the approximate frequency of oscillations does not seem to depend on the threshold value. Studies that have used this approach revealed that economic benefits for various threshold values depend on initial densities and on the number of years over which economic benefits are calculated, with a tendency that a longer period favours lower threshold values (Cousens, 1987; Vleeshouwers & Streibig, 1988). These results suggest that the frequency of herbicide applications does not depend on the threshold level which is applied.

Control strategies need not only be imposed, they can also be extracted from the population dynamics model by optimisation of control. An optimisation technique that can be used for this purpose is dynamic programming (e.g. Fisher & Lee, 1981). Pandey & Medd (1991) employed this technique and showed that for control of *Avena fatua* optimal decision rules lead to stationary densities, where optimal myopic decision rules lead to higher densities as compared to long-term decision rules. The consideration that optimal control lead to stationary situations leads to a simpler approach: if we are interested in the long-term effect of a strategy and not in any initial transient effect, we can take a look at the stationary situations only. This idea is worked out by Pandey *et al.* (1993) to calculate benefits of research for improved weed management. In the model described in the appendix (equation A4), the stationary situations are found by imposing a constant positive density of seeds in the soil $S_{t+1} = S_t = \bar{S}$. The result is a relation between stationary seed bank density $\bar{S}$ and stationary kill rate $\bar{r}$:

$$\bar{S} = \frac{b}{g+m} - \frac{b}{ag(1-\bar{r})} \quad \text{for } 0 \le \bar{r} \le r_c \quad \text{with } r_c = 1 - \frac{g+m}{ag} \qquad (1a)$$

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 annually removed 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 the kill rate 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 affect a kill rate that approximates 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. This hints at another stationary solution for the model (as in equation A4):

$$\bar{S} = 0 \qquad (1b)$$

and this zero density of weeds must be the result of an eradication program. Now we have derived that an optimal control strategy leads on a long-term to the maintenance of a positive density (containment) or, as a particular case, to striving for a zero density (eradication). Note that the strategy of always applying herbicides at the prescribed dose (prophylaxis) does not follow from this discussion.

The interest in organic farming systems is increasing. The weed management strategy in such systems might be different from systems in which herbicides are used. In ecological farming weed control is done by harrowing and hand weeding (Rasmussen & Ascard, 1995). Here, we will make a short digression to analyse the differences in strategy needed. We will employ the model described in appendix 1, with parameter values that are representative of a situation where *G. aparine* has infested a field where winter wheat is grown continuously under Dutch conditions (Wallinga, unpublished results). We are interested only in long-term effects of control, so we can regard stationary situations where control compensates for potential increase in weed population size. As a reference for hand weeding we take a whole-field application of the herbicide fluroxypyr. The return on weed control by a herbicide comprises the cost of control and the actual yield. The cost of control is about constant on an area base. The actual yield is closely related to the number of weeds that survive control. For feasible weed densities the number of surviving weeds is very low, rendering an about constant yield and an about constant return on weed control for various weed densities (Fig. 3). The return on weed control by hand weeding comprises the cost of control and the actual yield. The cost of control consists here of a fixed amount for inspection of the field and a variable amount for picking the plants. This variable amount of costs is proportional to the number of weed plants on the field. As a consequence, annual costs of control decrease rapidly when lower densities are maintained. Again, the yield is about constant hence the return on weed control increases rapidly when lower densities are maintained (Fig. 3). This simple calculation illustrates that for whole-field application of herbicides the weed density hardly effects the long-term economics of control, whereas for weeding by hand the weed density proves to be very important. On a long-term, hand weeding is only feasible when low weed densities are aimed for. This strategy is used by organic farmers in the Netherlands, who apply this strategy selectively for weeds that do not invade form the outside very strongly.

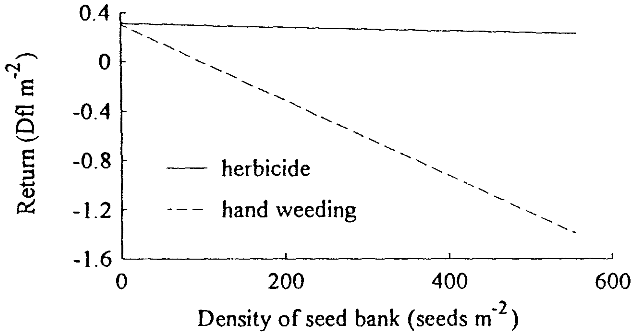

Fig. 3. Long-term annual return on weed control, calculated as economic crop yield minus costs of weed control. The control rate set to maintain the weed density that is indicated on the abscissa.

So far, the analyses dealt 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 however not 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; Lindquist *et al.*, 1995). Multiple weed populations with different characteristics form a more difficult topic, several studies have tried to get a grip on this problem (Gressel & Segel, 1978; Mortimer *et al.*, 1990).

Future

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 (IPM). Such systems should focus on the development of an environment that favours the crop relative to the weeds. That requires more quantitative knowledge of weed population dynamics and crop weed interactions. Sound modelling frameworks for these processes have been developed, but have yet hardly been used to improve weed management systems. By focusing weed biology research on clearly defined problems, the development of IPM may take a major leap in the coming decade.

Some clearly defined problems, where quantitative knowledge on weed biology can be applied, seem feasible.

(i) The identification of new potential break points in the life cycle of weeds that may lead to the identification of new control technologies. The use of systems approaches can encourage weed ecologists to produce challenging questions for weed technologists. 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 (cf. Lotz *et al.*, 1990). In such situations, we need new technology to avoid or reduce weed seed production (Medd & Ridings, 1989, Pandey *et al.*, 1993, Kempenaar *et al.*, 1995). Biological knowledge and insights could be used to develop technologies that enables interference with the development of plants. An idea could be to prevent flowering in short-day plants (weeds) when days become shorter by interrupting the night period using light flashes (Kropff & Van Laar, 1993).

(ii) The development of site specific management techniques in which only patches of weeds are controlled. A question here is how intensive weed patterns would have to be sampled to facilitate precision agriculture. The use of spatial statistics has opened perspectives in this area (Donald, 1994; Cardina *et al.*, 1995), yet such a purely descriptive approach is a far cry from biological understanding of weed patterns. The localised application of herbicides begs the question how population dynamics are affected and what the long-term viability of this technique will be (Johnson *et al.*, 1995). Here, the study of weed dispersal (Cousens & Mortimer, 1995) and individual based modelling techniques (Wallinga, 1995a) can be of help to improve weed management.

(iii) The development of strategies for weed control based on long term dynamics of weeds. Suitable strategies for weed control will in most cases be containment strategies. Research on realization of such a containment strategy easily gets side-stracked into a study of the relationship between a threshold weed density and long-term control rate (see Fig. 2). Another approach is to calculate the required kill rate to maintain a low density (cf. equation 1a) and how such a kill rate can be realized.

From this list of challenges it may be clear that, although modelling efforts in weed science have concentrated primarily on crop-weed competition and population dynamics with few links to other critical areas like invasion, rate of spread, effectiveness and economics of weed control (Doyle, 1991), the future challenge for modelling in weed science will be the development and integration of the different components.

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Appendix 1. A basic model for the population dynamics of weeds

The basic structure of the model is given in Figure 1. The model as used here is equal to the one presented by Spitters (1989), although the notation differs. In this model, the density of weed seeds in the soil is indicated by S_t, 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, and a portion g is removed by germination and emergence of seeds. In absence of weed control, the emerged plants will reproduce on average z viable seeds that return to the seed bank. Thus in absence of weed control, the following equation is obtained:

$$S_{t+1} = (1-g-m)S_t + zgS_t \qquad \text{(A1)}.$$

Weed control is introduced by replacing density of emerged weeds gS_t by the density of weed plants that survived weed control (P_t)

$$P_t = g(1-r)S_t \qquad \text{(A2)}$$

where r is the fraction of weed seedlings killed by weed control. The effect of weed plant density on the average reproduction per plant z is introduced in the model by the commonly used rectangular hyperbola (review by Kropff & Van Laar, 1993):

$$z = \frac{a}{1+\frac{a}{b}P_t} \qquad \text{(A3)}$$

where a is the production of viable seeds per plant at low weed densities, b is the maximum seed production per unit area at high weed densities. These three equations are combined to integrate the life-cycle processes into one equation that generates the weed population dynamics in terms of density of weeds in the soil:

$$S_{t+1} = (1-g-m)S_t + \frac{a}{1+\frac{a}{b}(1-r)gS_t}(1-r)gS_t \qquad \text{(A4)}$$

This equation shows how the density of seeds in the soil depends on the density in the previous year, on the population dynamic characteristics of the species, and on the intensity of weed control. In this simple case the model can be written as one equation and solved analytically (equation 1a and 1b), but when processes are described in more detail, numerical integration techniques have to be used.