ADVANCES IN WEED-CROP ECOPHYSIOLOGICAL RESEARCH AND THEIR CONTRIBUTIONS TOWARDS ATTAINING SUSTAINABILITY IN AGRICULTURAL PRODUCTION SYSTEMS

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Summary: Sustainability in agricultural production systems demands for weed management with a reduced dependency on herbicides. This can only be realised if suitable alternative weed management options, be it preventive measures or curative weed control techniques, are available. Insight in processes related to crop-weed interactions and weed population dynamics might help in the development of preventive measures and to identify new opportunities for weed control. Furthermore this insight can be used to improve operational and tactical decision making and to design and explore long-term strategies for weed management. The complexity of the processes involved in crop-weed interactions and the long-term character of weed population dynamics hints at the use of simulation models. In this paper the state of the art of weed-crop ecophysiological knowledge is briefly described and its contribution to the development of sustainable agricultural production systems by improving present-day weed management systems is discussed.

Keywords: management strategies, computer simulation, weed-crop interactions

INTRODUCTION

In most agricultural systems, weed management has been one of the major issues determining the design of cropping systems, especially before herbicides became available. The use and application of herbicides was one of the main factors enabling intensification of agriculture in developed countries in the past decades. More recently, the availability of herbicides has been coupled to intensification of agriculture in developing countries as well. A well-described example is the recent area expansion of direct seeded rice in Asian countries; a technology not widely practised before the late seventies largely because of weed control problems and now becoming a major system in Asian tiger economies, like Malaysia and Korea, where labour shortage is pressing.

However, 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. This has led to the need for the development of strategies for integrated weed management (IWM). Rather than trying to eradicate weeds from a field, emphasis is on the management of weed populations. The development of such weed management systems requires thorough quantitative insight into the behaviour of weeds in agroecosystems and their effects.

In Fig. 1 a simplified scheme for the relations between weed problems and weed management options, which broadly can be classified into preventive and curative measures, is presented. If only the short-term perspective is considered, decision making mainly involves operational decisions on if, when, where and how weeds should be controlled. For this type of questions quantitative insight into crop-weed interactions is highly relevant, when another threshold than 0 is used. 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, through for instance 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 enable us to control weeds site specifically and development stage specifically. 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. 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 insight in crop-weed interactions and weed population dynamics and discusses possibilities to use this knowledge to design improved weed management systems that add to the development of more sustainable agricultural production systems.

Integrating ecophysiological understanding of crop weed-interactions: Competition is a dynamic process that encompasses the capture and utilisation of shared resources (i.e. light, water, nutrients) by the crop and its associated weeds. In case of crop-weed competition, focus is on the effect of resource capture by weeds on crop growth and production. Those resources of which supply cannot meet demand are of major interest, as they determine the attainable yield of the crop. If weeds capture such resources, crop growth will be reduced resulting in yield loss. Quantitative understanding of crop-weed interactions seems a solid basis for the improvement of weed management systems in different ways. Ecophysiological models that simulate the uptake and use efficiency of resources by the competing species provide insight into the outcome and the dynamics of competition and may aid in seeking options to manipulate competitive relations in agro-ecosystems.

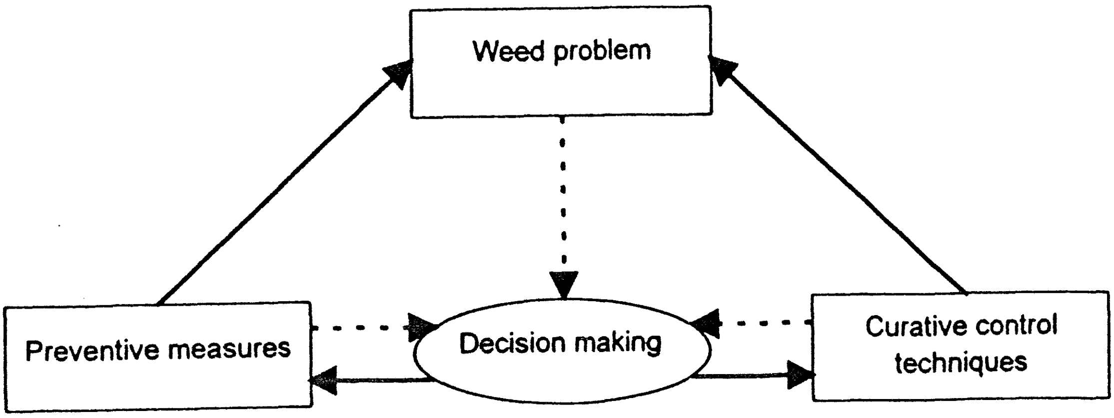

Figure 1. A simplified schematic representation of the relations between weed problem and options for weed control. Weed management can be enhanced through improved preventive or curative control measures or improved decision making. Broken lines represent flows of information, solid lines indicate operations.

Various competition models have been developed (15, 19, 20, 40, 49). The ecophysiological model INTERCOM described by Kropff and Van Laar (19) consists of a set of individual growth models (one for each competing species), that calculate the rates of growth and development for species based on environmental conditions (Fig. 2). The growth models are expanded to account for morphological processes that only affect growth in competition and coupled to account for the simultaneous absorption of available resources by the different species in a mixed vegetation. Under favourable conditions, light is the main factor determining the growth rate of the crop and its associated weeds. In INTERCOM, the quantity of photosynthetically active radiation absorbed in mixed canopies by each species is a function of the amount and vertical distribution of photosynthetic area within the canopy, and the light extinction coefficient of the species. A water balance for a free draining soil profile is attached to the model, tracking the available amount of soil moisture during the growing season. When available soil moisture drops below a critical level, transpiration and growth rates of each species are reduced. Since transpiration is driven by the absorbed amount of radiation and the vapour pressure deficit inside the canopy, competition for water is closely linked to aboveground competition for light. The more light a species absorbs, the more water is required for transpiration. Direct competition for water as a result of differences in rooting density is not accounted for. An extension of the model for simulation of competition for nitrogen has been described, but has not yet been implemented.

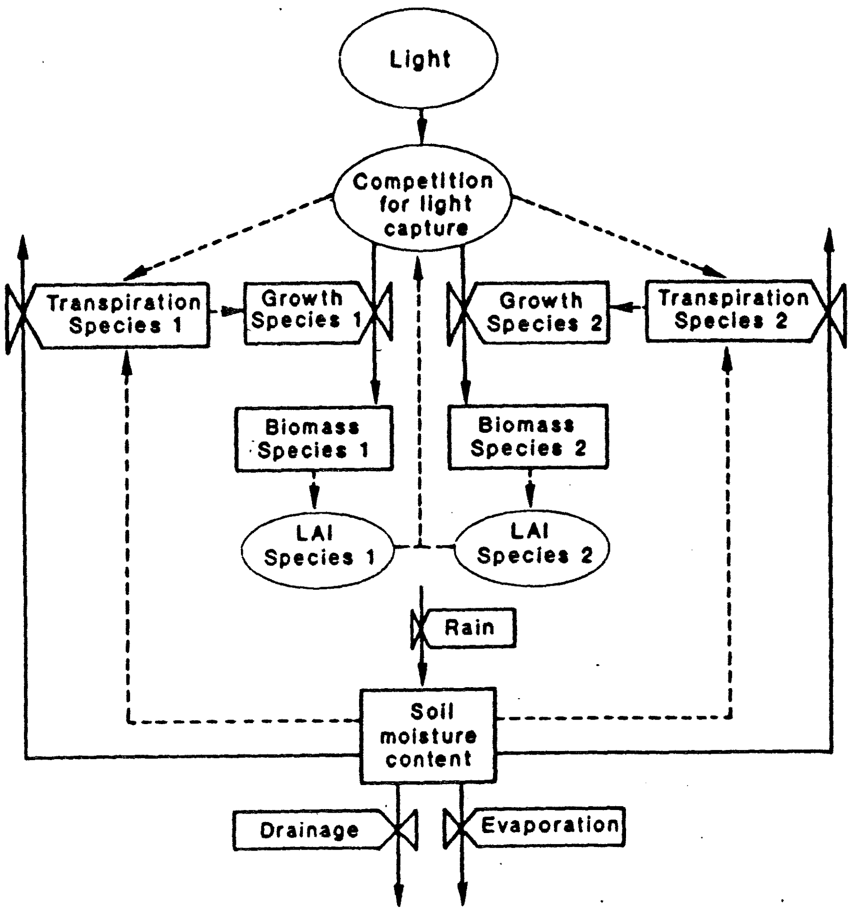

Figure 2. General structure of the eco-physiological model for interplant competition (INTERCOM) (19).

The ecophysiological competition model has been tested with data from competition experiments with maize (*Zea mays* L.) versus yellow mustard (*Sinapis arvensis* L.) and barnyard grass (*Echinochloa crus-galli* L.) (20, 38 40, 48), tomato (*Lycopersicon esculentum* L.) versus pigweed (*Amaranthus retroflexus* L.) and eastern black nightshade (*S. americana*) (21, 47), sugarbeet (*Beta vulgaris* L.) versus fat hen (*Chenopodium album* L.) (22) and rice versus *E. crus-galli* (19). 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 are underway for row crops and complex vegetations. 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 (19) 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 by minimising its specific stem length.

Applications of these models can be found in the analysis and extrapolation of experimental data, the analysis of the impact of sub-lethal control measures (like low-dosages of herbicides and bio-herbicides), risk analysis for the development of weed management strategies, the development of new simple predictive models for yield loss due to weeds and the design of new plant types for weed suppression. These last two applications are briefly discussed.

Development of new simple tools for early-season prediction of yield loss due to weeds: The most widely used regression model to describe effects of competition at a certain moment is the hyperbolic yield-loss weed density model (6):

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

where Y_L gives the yield loss, N_w is the weed density, a describes the yield loss per unit weed density as $N_w \rightarrow 0$ and m the maximum yield loss. This hyperbolic yield-density equation fits well to data from experiments where only weed density is varied (6, 20). However, parameters a and m are not constant for a specific crop-weed combination, but vary strongly from site to site and year to year. This instability is due to the effect of factors other than weed density on the competitive relationship between crop and weeds (19). Experimental results and analyses with the ecophysiological model identified the prominent role of the period between crop and weed emergence on the outcome of competition. This indicates that a more robust prediction of yield loss on the basis of early observations would only be feasible if this factor would be accounted for. For this purpose, some workers introduced an additional variable in the hyperbolic yield-density equation that represents the effect of differences in the period between crop and weed emergence (8). However, in practice weeds often emerge in successive flushes, making it difficult to apply a descriptive model that accounts for the effect of both weed density and the relative time of weed emergence: every flush has to be regarded as if it was a different weed species.

Supported by the analyses of the ecophysiological model for competition and based on the well-tested hyperbolic yield-density model, an alternative descriptive regression model for early prediction of crop losses by weed competition was derived (18; 23). This model relates yield loss to relative weed leaf area (L_w expressed as the share of the weed species in total (crop and 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:

$$Y_L = \frac{qL_w}{1 + (\frac{q}{m} - 1)L_w} \qquad (2)$$

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 relative time of weed emergence (18). The example in Fig. 3 clearly demonstrates the superiority of relative weed leaf area over plant density as an explanatory variable in descriptive yield loss models, especially if results from more than one site and year are simultaneously examined. However, a simple model like this, of course, can not explain the complexity of effects of environmental factors on yield loss by weeds. Lotz *et al.* (29) found that the relative leaf area model was superior to the density model but could not explain yield loss differences across sites exactly.

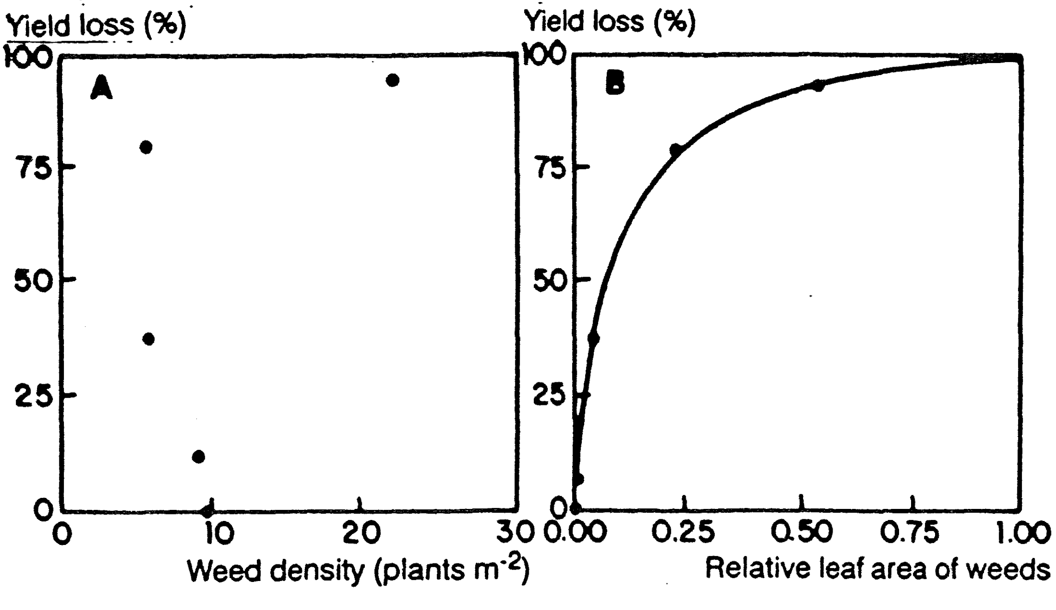

Figure 3. (A) Relationship between weed density and yield loss for five field experiments with sugar beet and C. album; (B) relationship between relative leaf cover of the weeds 30 days after sowing and yield loss for the same five experiments (19).

Designing cultivars that are more competitive against weeds: The development and introduction of crops or cultivars with an improved competitive ability might help reduce the present dependence on herbicides. Procedures for selecting genotypes with an improved competitive ability can be categorised into two main classes (26). One involves direct selection of genotypes in the presence of weeds. This type of selection can only be applied in the later stages of a breeding program when sufficient seed is available. Furthermore, experimental analysis of the competitive ability of a wide range of genotypes is very labour intensive and expensive (43). Indirect selection is an alternative in which selection is aimed at attributes, such as plant height, that are associated with competitive ability. Selection can thus be started early in the breeding program and can be carried out in the absence of weeds. Traits contributing to competitive ability need to be identified prior to the actual selection, and the contribution of different traits and their trade-off with yielding ability should be determined. This is where ecophysiological models for crop-weed interactions can contribute. Recently, the usefulness and limitations of ecophysiological competition models in designing more competitive cultivars were discussed, using rice as an example (4). Differences in competitive ability between two contrasting rice cultivars (IR8 and Mahsuri) were experimentally determined at the lowland research site of the International Rice Research Institute (IRRI) in Los Baños, Philippines. Mahsuri is a native cultivar that originates from Malaysia. It is a late-maturing, tall growing cultivar, with fast growth at early stages. IR8 is the first IRRI-bred semi-dwarf rice cultivar. It is a medium-maturing cultivar, with low stature and a high harvest index relative to Mahsuri. Both cultivars were grown in monoculture for quantification of various phenological, physiological and morphological traits, which were then translated into parameters that fit into INTERCOM. In monoculture IR8 had a lower shoot dry weight (-15%), but a higher grain yield (+36%) than Mahsuri. Growing the cultivars in competition with purple rice, which was used as a model-weed, and comparing the performance of cultivars in mixture and monoculture was used to determine the competitiveness of each cultivar. In mixture, dry matter production of IR8 was far more affected than the dry matter production of Mahsuri, demonstrating the higher competitive ability of the latter cultivar. The accurate simulation of competitive ability of both cultivars indicated that the observed differences in phenology, physiology and morphology between both cultivars were able to explain their differences in competitive ability (Fig. 4). An estimation of the contribution of various traits to overall competitive ability was made by analysing the experimental results with the help of INTERCOM. The importance of each trait was determined by constructing hypothetical isolines of IR8; for each isoline the original value of a single trait of IR8 was replaced by the value measured for Mahsuri. Model analysis revealed that the greater competitive ability of Mahsuri was mainly due to a greater relative leaf area growth rate early in the season and larger maximum plant height.

Competitive ability of rice has often been reported to be negatively correlated with yield potential and the presently used cultivars confirmed this finding; Mashuri, being the cultivar with the highest competitive ability, was lower yielding than IR8. INTERCOM was used to estimate the trade-off between competitive and yielding ability by quantifying the effect of single traits on both yielding (simulations in weed-free conditions) and competitive ability (simulations in weedy conditions). This approach demonstrated for instance that a more or less identical increase in the ability to suppress weeds could be obtained through an increase in either specific leaf area or light extinction coefficient. Under weed-free conditions, grain yield responded quite different to an increase in one of those traits. An increase in light extinction coefficient caused a poor light penetration and poor distribution of radiation within the canopy, resulting in a reduced radiation-use efficiency and accordingly in a decrease in simulated grain yield. An increase in SLA on the other hand, led to earlier canopy closer and accordingly to an increase in simulated grain yield. This example shows that trade-off between competitive and yielding ability differs per trait and moreover that the model is an appropriate tool for designing competitive, high-yielding ideotypes (4).

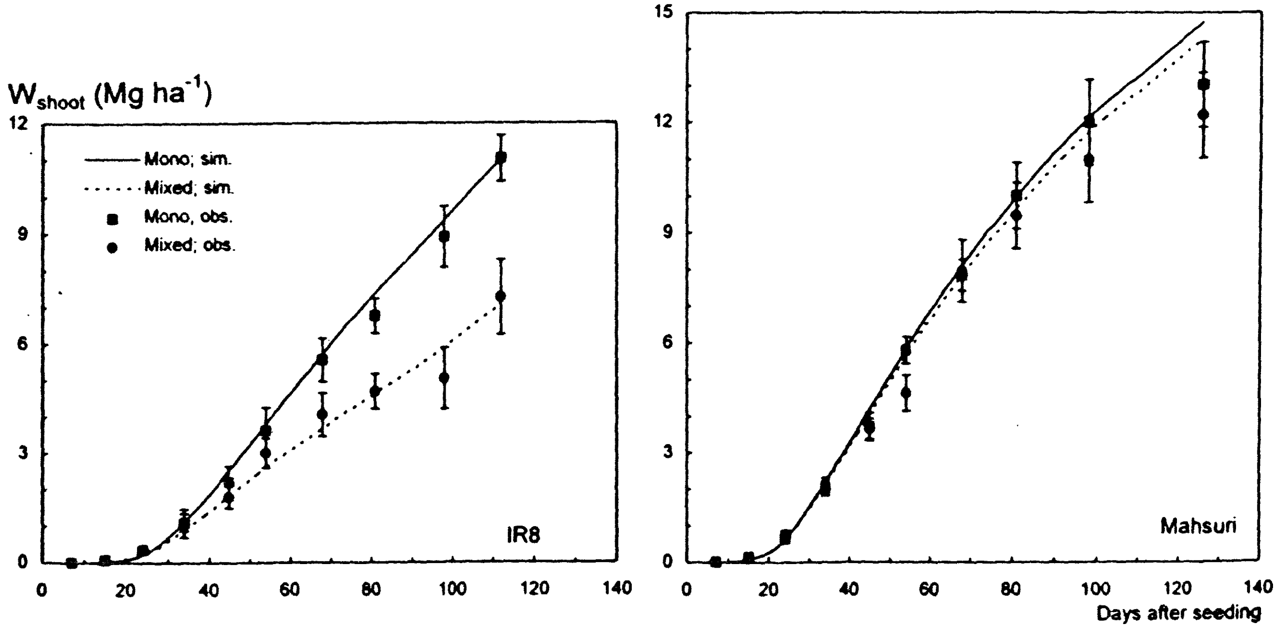

Figure 4. Observed and simulated shoot dry weight (W_{shoot}) of rice in monoculture or in mixture with purple rice for IR8 and Mahsuri rice. Vertical bars represent the standard errors of the mean. (4)

Weed population dynamics: The life cycle of annual weeds is schematically illustrated in Fig. 5. 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, dispersal, predation 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 regrowth from buds on underground structures and the formation of these structures. The dissemination, invasion and spread of weeds is not indicated in the scheme, but is of extreme 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 of great significance as well.

Models can be helpful to integrate the knowledge on life-cycle processes. The most detailed models that encompass the whole life-cycle have been developed for species like *Avena fatua* L. (7), *Alopecurus myosuroides* Huds. (12) and *Galium aparine* L. (41). Comprehensive models that are based on physiological principles are only available for parts of the life cycle: plant growth and competition (19) and germination and emergence (42). In contrast, processes like seed shedding, seed dispersal and predation of seeds are poorly understood.

The basic structure used in most models was described by Spitters (39) and Kropff et al. (24). 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. 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:

$$z = \frac{a}{1 + \frac{a}{b} g(1-r)S_t} \tag{3}$$

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 weeds in the soil gives (24):

$$S_{t+1} = (1-g-m)S_t + z(1-r)gS_t \tag{4}$$

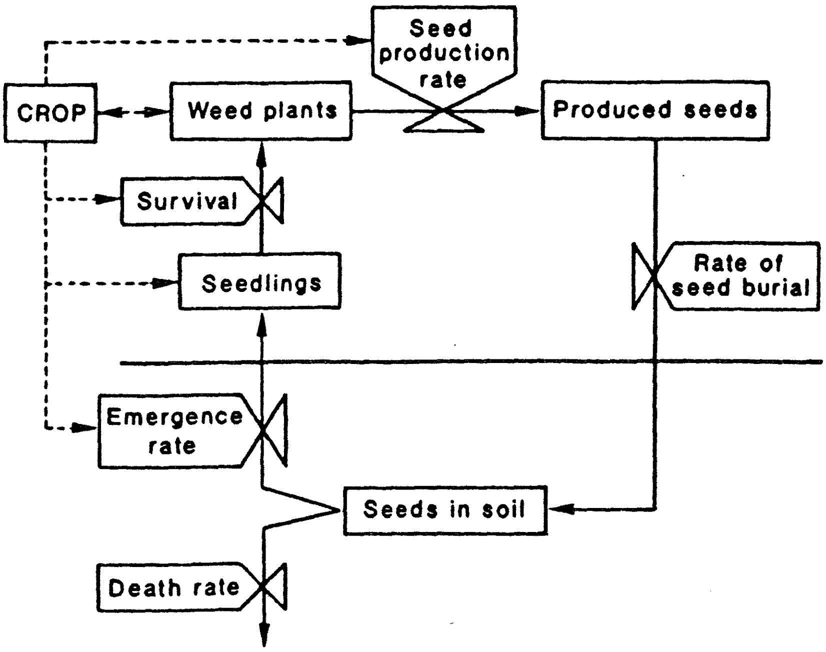

Figure 5. Schematic representation of population dynamics of weeds. Drawn lines indicate the life cycle of weeds, broken lines indicate processes where crop and weed interact (19).

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, but when processes are described in more detail, numerical integration techniques have to be used. Since density of weeds is taken as a key variable, these models are generally referred to as density based models. Due to the conceptual clarity in modelling temporal changes in density this approach is widely used, ranging from exponential growth (36) to bounded growth (13).

The major difference between population dynamics of weeds and other plants is that man explicitly interferes in weed population dynamics. Models for *weed* population dynamics thus have a control variable as an additional parameter (*r* in equation 4), whereas models of plant population dynamics do not. The aim for weed population dynamics models is to find the optimal control strategy that fits the needs of the farmer. The simplest way of using density based models for this purpose is to conduct scenario studies based on different control strategies. Such a simple approach helps to get a better notion of the consequences of various weed control strategies and to roughly explore options for long term weed management strategies. Some examples are given below.

Required seed-cleaning efficiency: Firbank & Watkinson (13) determined the effect of different weed control efficiencies on the long-term, or equilibrium weed density. Their results showed that the sensitivity of long-term density towards differences in control efficiency was strongly related to the level of control efficiency. In their model-system corncockle (*Agrostemma githago* L.) in spring wheat (*Triticum aestivum* L.) contaminated wheat seed was regarded as the only source of weed infestation and seed cleaning as the most important control strategy. Model calculations demonstrated that a seed-cleaning efficiency of less than 50% would hardly influence the long-term density. Efficiencies between 50-80% had a marginal effect, whereas an improvement in cleaning efficiency between 80-90% had a strong effect on the long-term weed density. Eradication would occur if cleaning efficiency would exceed 90%. These results demonstrate that the significance of an improvement in weed control technique is among others related to actual control efficiency.

Increased crop competitive ability for management of weed populations: Kropff *et al.* (25) used the model of Firbank & Watkinson (13) to determine whether the introduction of spring wheat cultivars with an increased competitive ability would reduce the seed production of *A. githago* and thus lower the need for high seed cleaning efficiencies. In a preliminary analysis it was found that the seed cleaning efficiency required to maintain the population of weeds at a low density (the critical seed cleaning efficiency) only decreased strongly when the reduction in *Agrostemma* biomass as a result of competition by the crop exceeded 60%. This means that an increased competitive ability only affects long term population development effectively when weeds are suppressed strongly. With the previously discussed example of rice it was shown that large differences in competitive ability between genotypes of cereals are present (4).

Frequency of herbicide-application: Spitters (39) used a similar model to determine the frequency of herbicide-application required to manage wild oat in continuously grown spring barley. For this purpose the population dynamical model was coupled to a simple descriptive model for yield loss. Calculations were based on a control efficiency of 95%, established through a post-emergence application of a herbicide. The simulations demonstrated that weeding wild oat once every second year restricted yield losses to about 5% or less. Such a control strategy would be economically attractive, since in cereals yield benefits of less than 5% in general do not outweigh the costs of herbicide application. 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. With annual control of wild oat in cereals a farmer would restrict the increase in weed seed population, avoiding the risk of serious weed problems in future crops. In this example the model thus helps to identify the consequences of various control strategies, offering farmers the opportunity to select the strategy that fits their attitude against risk. This analysis refers to situations were cereals are grown continuously. For cereals grown in rotation with other crops the situation is different, since weeds are often controlled in cereals to reduce problems in future crops, as cereals offer good opportunities for weed control.

Usefulness of damage thresholds: Wallinga and van Oijen (46) used the density based model to determine the influence of the threshold level on the frequency of herbicide applications. In a simulation study based on their analysis, threshold levels of 2 and 40 seeds per m^2 were imposed (24). A control measure was applied for densities above the threshold, whereas below the threshold weeds were left uncontrolled. The simulations resulted in an oscillation of weed density in a periodic fashion around the threshold, with a frequency that seemed to be independent on the threshold value. This result suggests that long-term application of a control threshold results in a control frequency that is independent of the threshold level. In the more detailed analysis, Wallinga and van Oijen (46) reached a similar outcome and 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.

Extensions of the density based approach: The previous examples all 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 however not cause any essential changes in the approaches outlined above. A few studies have been directed at modelling population dynamics over crop rotations (e.g. 27, 31). Several studies have tried to get a grip on the problem of multiple weed populations with different characteristics (16, 32). This appears to be very complex.

Another assumption underlying the previously described approach is that each weed perceives a similar environment and that the system is homogeneous in space. However, environments are heterogeneous and population development is heterogeneous, even in a homogeneous environment. 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 (1, 2, 30). The key variable in this modelling approach is the weed density as well. 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 (14, 35). Another problem is that in the course of time spatial gradients will eventually flatten out. Therefore it is hard to explain the observed patchiness of weeds by these models. A different approach is to abandon weed density as a basic variable in the model, and proceed with the actual configuration of weeds over space. This modelling approach includes model types like the individual based model (cf. 33) and cellular automaton models (cf. 3, 37). This type of models makes it possible to study the interaction between dynamics and patchiness in weeds. Wallinga (45) 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, even in homogeneous environments. Of the modelling approaches, individual based models are the most comprehensive, but as a result of their complexity they quickly run into computing problems.

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 (IPM). Options to improve weed management systems with a minimum herbicide use exist in all its components: prevention, decision making and control technology (Fig. 2). Future research should focus both on technology development as well as on prevention, and operational 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 as well as integration of this knowledge in manageable models should be one of the main targets for future weed ecological research.

By focusing weed biology research on clearly defined problems, weed research might give a major contribution to the development of more sustainable agricultural production systems 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 (28). In such situations, we need new technology to avoid or reduce weed seed production. 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 (19).

(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 (5, 10), 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 (17). Here, the study of weed dispersal (9) and individual based modelling techniques (44) 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 strategy, which is directed towards managing weed populations, rather than to eradicate. The approach to be used would be to calculate the required weeding efficiency to maintain a low density and how such a weeding efficiency can be realised.

From this list of problems it may be clear that, although ecophysiological research in weed science has 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 (11), the future challenge for weed science will be the development and integration of the different components.

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