4º PAINEL – MANEJO INTEGRADO DE PLANTAS DANINHAS

Ecophysiological models as a tool for developing integrated weed management

Lammert Bastiaans[1]
D.T. Baumann[2]
M.J. Kropff[1]

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 contribution of crop-weed competition models to the development of sustainable agriculture by improving present-day weed management systems is illustrated and discussed.

Introduction

Before the introduction of herbicides, weed management was one of the major factors determining the design of cropping systems in most agricultural systems. Crop management practices were adjusted such that crop-weed interactions were altered to the benefit of the crop. These cultural methods included some of the oldest weed control practices, such as transplanting of rice. The systematic use of herbicides had a major influence on the perception of the weed problem. Weeds came to be regarded as solvable side problems rather than being regarded as an important factor in

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[1] Crop and Weed Ecology Group, Department of Plant Sciences, Wageningen University and Research Centre, P.O. Box 430, 6700 AK Wageningen
[2] Swiss Federal Research Station for Fruit-Growing, Viticulture and Horticulture, P.O. Box 185, CH-8820 Wädenswil, Switzerland E-mail: lammert.bastiaans@wur.nl

the design of cropping systems. The introduction of herbicides has therefore been one of the major factors enabling intensification of agriculture. Currently, concerns on environmental side-effects of herbicides combined with fear for public health has resulted in the banning of several herbicides and an increasing pressure on farmers to reduce the use of chemical means. This has led to the need for development of strategies for integrated weed management (IWM). In line with this, increased interest has been devoted to non-chemical control strategies, which might be made more effective than in the past by combining the former holistic approach, with improved knowledge on the eco-physiology of crops and weeds.

Weed management aims at reducing the negative effect of weeds on crop production. Using the hyperbolic yield loss-weed density curve as a basis, Figure 1 outlines the various ways in which this can be achieved. Fig. 1a represents curative weed control, where weed seedlings are killed through for instance a herbicide treatment or a mechanical intervention. For prevention, three key mechanisms can be distinguished: a reduced recruitment of seedlings from the soil seed bank (1b); an alteration of crop-weed competitive relations to the benefit of the crop (1c); and a reduction of the weed seed bank (1d). This last option corresponds to a long-term strategy, realised by various interventions in all possible life cycle stages of the weed that ultimately result in a reduced input or increased output of seeds from the soil seed bank. The use of a cover-material, like mulches, might result in a reduced recruitment of seedlings, either through physical impediment or phyto-toxic (allelopathic) effects. An improved competitiveness of the crop can be realised in many different ways, like transplanting, the use of competitive cultivars, an increased sowing rate, and a more uniform spatial arrangement of the crop.

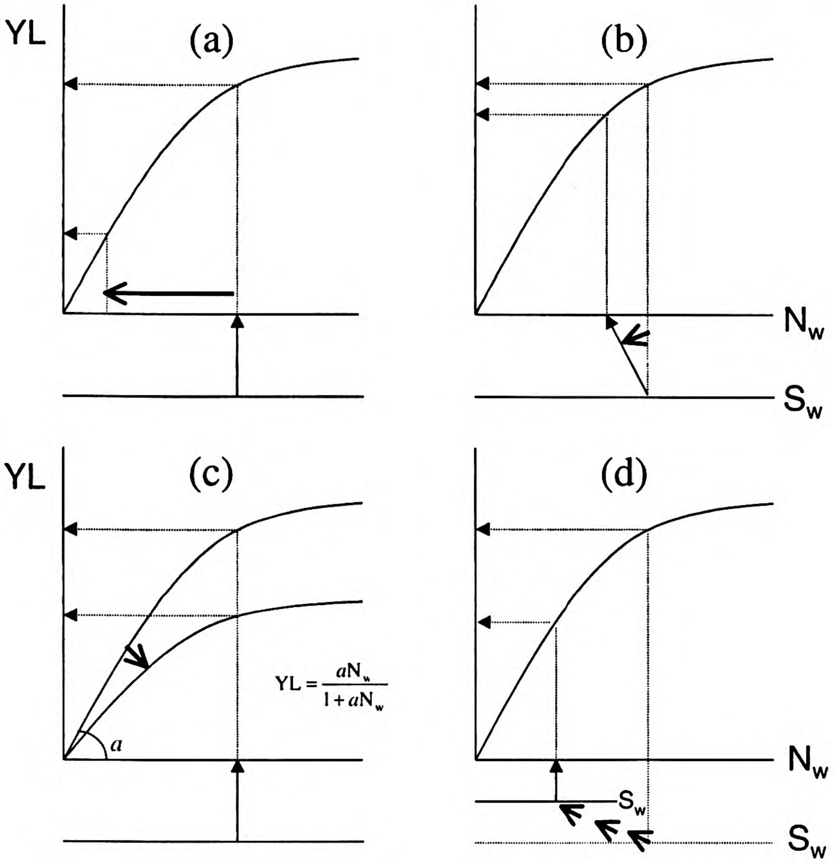

Figure 1. The hyperbolic yield loss-weed density relation used to illustrate various options for reducing yield loss due to weeds. (a) Killing or removalof weed plants; (b) reduced recruitment of weeds from the seed bank; (c) alteration of crop-weed competitive relations; (d) gradual reduction or depletion of the weed seed bank. Thick lines represent the major effect of a specific intervention (YL= relative yield loss due to weed competition; S_w = seed bank density; N_w = weed plant density).

In Fig. 2 a simplified scheme for the relations between weed problems and weed management options 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 zero 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 (i) prevention, on (ii) the development of better curative control techniques and on (iii) better long- and short-term decision making. This becomes even more important when precision farming techniques enable us to control weeds site 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.

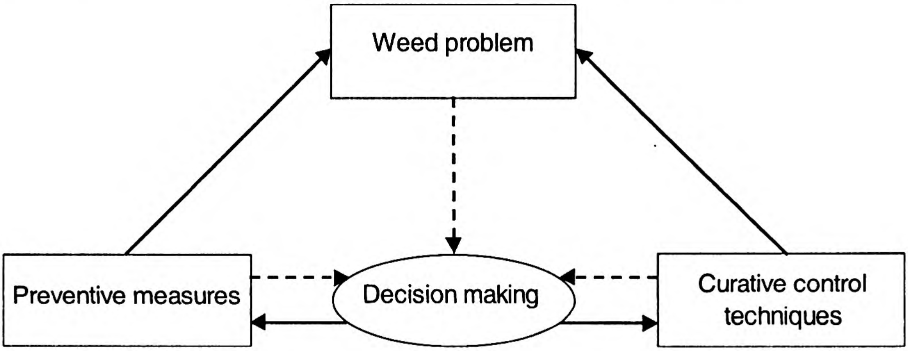

Figure 2. A simplified schematic representation of the relations between weed problem and options for weed control. Weed management can be enhanced through improved preventive and curative control measures or improved decision making. Broken lines represent flows of information, solid lines indicate operations.

This paper describes how models can be used to analyse crop-weed competitive relations and how these analyses might be used 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.

The ecophysiological crop-weed competition model INTERCOM, described by Kropff and Van Laar (1993) 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. 3). The growth models are expanded to account for morphological processes that are only relevant in competition situations 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.

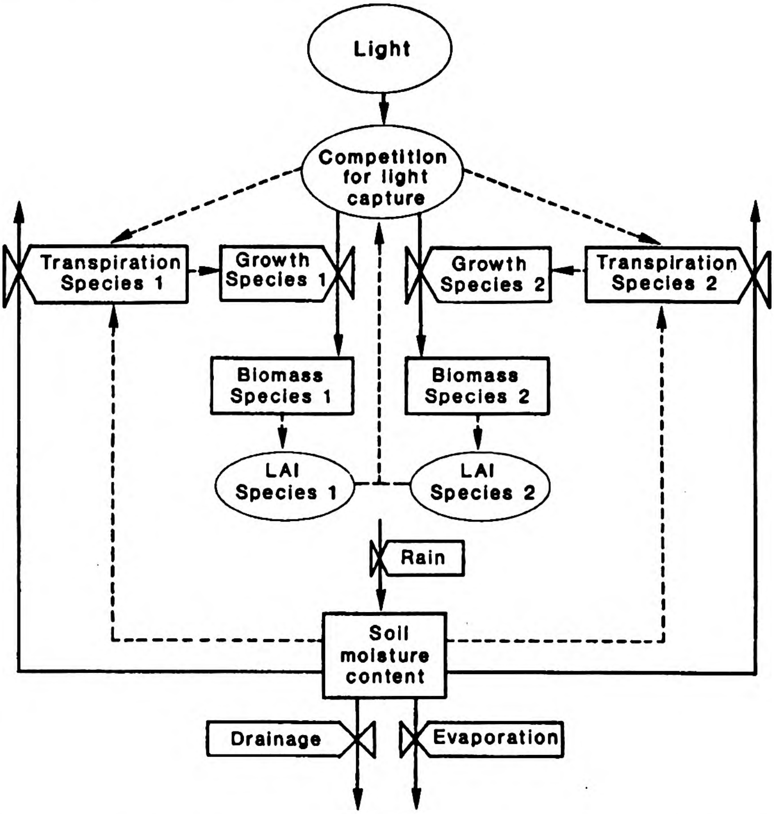

Figure 3. General structure of the eco-physiological model for interplant competition (INTERCOM).

The ecophysiological competition model has been tested with data from various competition experiments like maize (*Zea mays* L.) versus yellow mustard (*Sinapis arvensis* L.) and barnyard grass (*Echinochloa crus-galli* L.), tomato (*Lycopersicon esculentum* L.) versus pigweed (*Amaranthus retroflexus* L.) and eastern black nightshade (*S. americana*), sugarbeet (*Beta vulgaris* L.) versus fat hen (*Chenopodium album* L.) and rice versus *E. crus-galli*. The results of these studies indicate that interplant competition for light and water can be well understood from the underlying physiological processes. The main gaps in knowledge are related to morphological development and especially the phenotypic plasticity of weeds with respect to these morphological features (e.g. Cavero et al., 2000). *C. album* for example demonstrated an impressive capacity to overtop a sugarbeet crop in spite of an unfavourable starting position due to late weed emergence by minimising its specific stem length.

Applications of crop-weed competition models can be found in the analysis and extrapolation of experimental data. Other examples are the analysis of the impact of sub-lethal control measures (like low-dosages of herbicides and bio-herbicides), the development of new simple predictive models for yield loss due to weeds, the design of new plant types for weed suppression and optimisation of intercropping systems. Some of these applications will be briefly discussed.

Development of tools for early-season prediction of yield loss due to weeds.

The most widely used regression model to describe effects of weed competition on crop production is the hyperbolic yield-loss weed density model (Cousens, 1985):

$$Y_L = \frac{aN_w}{1 + \frac{a}{m} N_w} \tag{1}$$

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 represents the maximum yield loss. This hyperbolic yield-density equation fits well to data from experiments where only weed density is varied. 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. 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. 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 an 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 (Kropff & Spitters, 1991). 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:

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

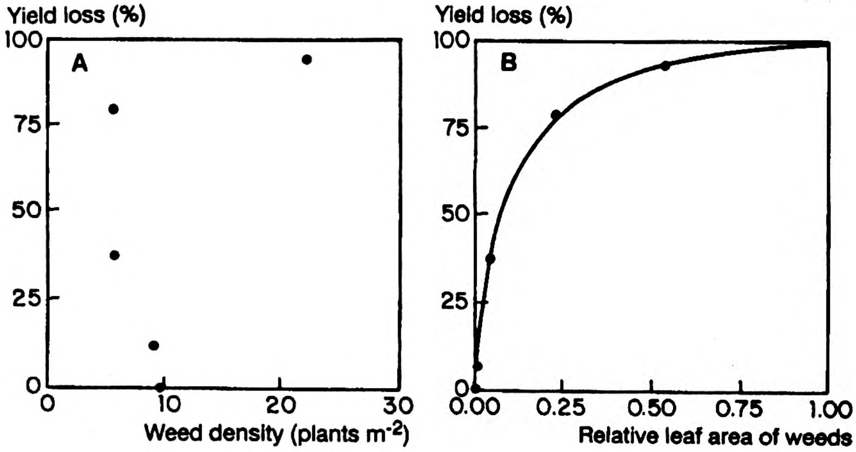

Figure 4. (A) Relationship between weed density and yield loss for five field experiments with sugar beet and *Chenopodium album*; (B) relationship between relative leaf cover of the weeds 30 days after sowing and yield loss for the same five experiments (Kropff and van Laar, 1993).

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. The example in Fig. 4 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.* (1996) found that the relative leaf area model was superior to the density model but could not explain yield loss differences across sites exactly.

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. 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. 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.

Bastiaans et al. (1997) discussed the usefulness and limitations of ecophysiological competition models in designing more competitive cultivars, using rice as an example. 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. 5). Analysing the experimental results with the help of INTERCOM resulted in an estimation of the contribution of various traits to overall competitive ability. 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 growth rate of leaf area early in the season and larger maximum plant height.

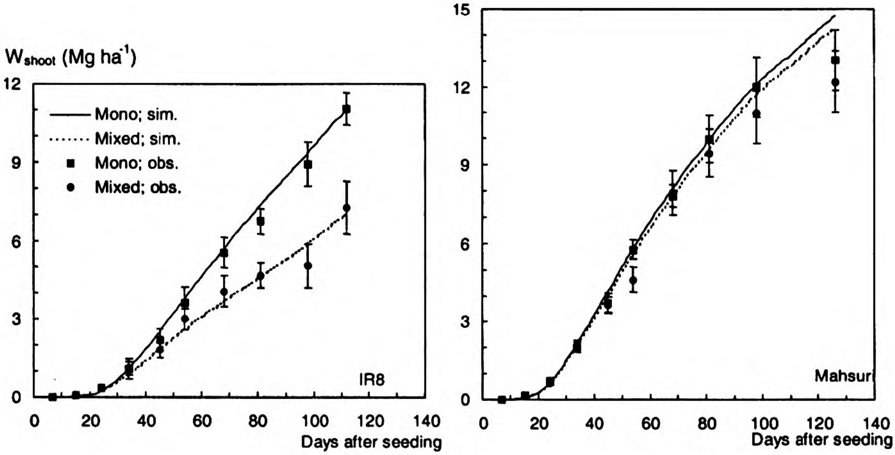

Figure 5. Observed and simulated shoot dry weight (W_{shoot}) of rice in monoculture or in mixture with purple rice for IR8 and Mahsuri rice. Vertical bars represent standard errors of the mean (Bastiaans et al., 1997).

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.

Cash crops as cover crop

Many field vegetables such as leek (*Allium porrum* L.) are weak competitors against weeds, causing high costs for labour intensive weed management practices. An intercropping system using celery (*Apium graveolens* L.) as a companion cash crop was developed to improve the weed suppression of leek (Baumann et al., 2000). In glasshouse and field experiments it was shown that the increased competition of light by the intercrop canopy compared to a leek monoculture significantly reduced the biomass and the seed production of late-emerging *Senecio vulgaris* L., an important annual weed in vegetable production (Baumann et al., 2001a). Analysis using an eco-physiological competition model showed that intra- and interspecific competition in the intercropping system was largely determined by the morphological characteristics of the species. Next a methodology was developed with the objective to utilise the competition model for the design of a leek-celery intercropping system with high potential for yield, quality and weed suppressive ability.

An adapted version of the eco-physiological competition model INTERCOM was used to simulate interplant competition between leek, celery and *S. vulgaris* in pure and mixed stands for various conditions and a wide range of crop densities and different relative times of weed emergence (Baumann et al., 2002). After calibration of the eco-physiological competition model with data from monocultures, simulations for the intercrop resulted in accurate predictions of leek and celery biomass and quality and *S. vulgaris* biomass. Moreover a high correlation between number of seeds and above-ground per plant dry weight of *S. vulgaris* was found (Baumann et al, 2001a).

With non-linear regression using a hyperbolic yield-density model (Spitters, 1983) it was shown that the relative competitive ability of leek versus late-emerging *S. vulgaris* was clearly lower than the relative competitive ability of celery. Increasing the proportion of celery in the crop mixture would thus result in an improved weed suppressive ability of the intercrop, but at the same time cause a severe reduction in the quality of leek. It was found that the stem diameter of leek appeared to be the limiting factor for crop quality in the optimisation process; celery plants of sufficient size could be produced at a much wider range of density combinations. By plotting the isoline for crop mixtures producing a leek-stem diameter of 20 mm a solution space indicating crop stands with acceptable quality was determined (Fig 6a). By combining isolines for financial yield with the quality isoline for leek the mixture with the highest financial yield was determined. For the intercropping system with 19 leek and 9.4 celery plants m^{-2}, indicated by the point where the isoline for financial yield touches the leek quality isoline (Arrow, Fig. 6b), the financial yield was 7% higher than for the highest yielding leek monoculture and 9% higher than the maximum financial yield of a celery monoculture. The effect of this cropping system on the reproductive potential of 50 *S. vulgaris* plants m^{-2}, emerging 40 days after crop establishment, is indicated by a third set of isolines (Fig 6c).

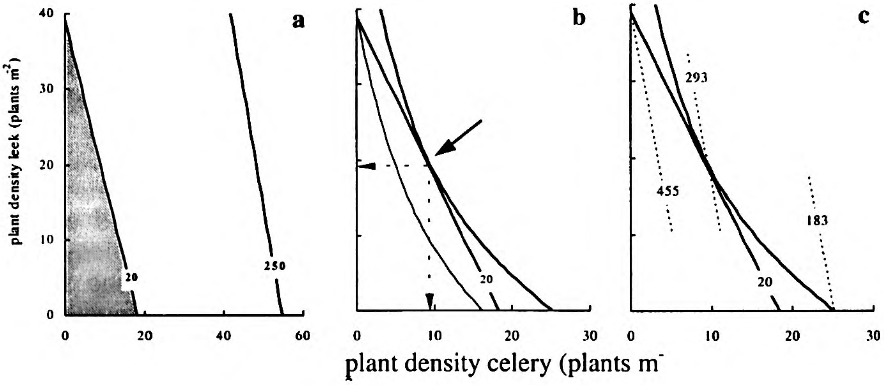

Figure 6. Isolines for crop stands producing (a) leek (minimum quality: 20 mm stem diamter) and celery (minimum celery quality: 250g fresh plant weight) with marketable quality; (b) maximum financial yield (arrow) and crop mixtures with financial yield similar to the highest yielding leek monoculture (thin line); and (c) combined isolines for minimum required leek quality, financial yield and seed production of *S. vulgaris* (seeds m^{-2}; dotted lines). The hatched area indicates the solution space for crop mixtures with marketable yield for both leek and celery.

Lower densities are usually planted in practice to ensure high plant quality and to enable efficient and labour-saving cultivation and harvesting processes. It was clearly shown that the intercropping system of leek and celery contributes to an improvement of the economical potential of a highly developed agricultural production system. At the same time the sustainability of the system was improved by reducing the need for labour and cost intensive weed control measures and environmental exposure to potentially harmful chemicals.

Long term-aspects and strategic decision making

Late-emerging weeds, though not very competitive, are likely to become a more important component in the long-term development of weed populations in future. Particularly in weed management systems that do not rely on herbicides, seed production of late-emerging weeds represents an important determinant in population development. Firstly, because mechanical weed control, often used as an alternative to chemical weed control, induces weed emergence flushes late in the season. Secondly, because in low-chemical input systems the density of the weed seed bank largely determines the amount of time, labour and money spent on weed control. A clear example comes from the Netherlands where an innovation project for arable and vegetable farming was conducted as a joint activity of the DLO-Institute for Agrobiology and Soil Fertility in Wageningen and 10 organic farms in the central clay area in the Netherlands. A multifunctional 6-year crop-rotation model was designed as a basis for achieving objectives related to various matters such as soil fertility and the environment, product quality, economics, and energy efficiency. The multifunctional crop rotation involved developing a well-balanced "team" of crops so that inputs necessary to maintain soil fertility and crop health could be minimised. With respect to weed management, an alternation of highly competitive mown crops (e.g. cereals) with less competitive lifted row crops (e.g. carrot, onion) was expected to have benefits for weed management in the row crops. Because of the alternation of crops, the cultivation method would change with each crop, achieving as complete a pressure as possible on the weeds. This, strengthened with the intrinsic competitive ability of the mown crops, was expected to suppress reproductive output and lead to low equilibrium densities of weeds.

Evaluation of this concept at the organic farms showed that weeds remained one of the major problems. For adequate management of the weeds, the hours of hand weeding varied between 490 and 3100 hours per farm, mainly spent in carrot and onion, whereas 500 hours per farm had been set as the target. A detailed survey revealed that a shift in weed flora composition had occurred on organic farms, and weeds such as *Stellaria media* (L.) Vice, and to a lesser extent *Poa annua* L. and *Capsella bursa-pastoris* (L.) Med., had become major constituents. Furthermore, the survey showed that the enormous amount of hand weeding in crops like onion and carrot was mainly caused by seed production of poorly competing, hardly detrimental, weeds down in the canopy of the preceding cereal crop. This example clearly illustrates that in cropping systems that do not rely on herbicides, long term aspects and particularly the population dynamics of weeds becomes increasingly important. Rather than for their immediate effect on grain production, weeds in the cereals should be regarded for their seed producing-potential. Consequently, more attention should be given in crop-weed interaction research to the effect of the crop on growth and development of the weed (e.g. Mortensen et al., 2000).

An important role of crop-weed competition models in the future might thus be to support models of weed population dynamics, mainly through generating adequate quantitative information on weed seed production. Particular interest will be in weeds that grow under high levels of competitive stress; not being harmful for the current crop, but a potential threat for future crops through their reproductive output. Weeds growing under these circumstances generally demonstrate a high level of plasticity, mainly in morphological adaptations such as an increased allocation of dry matter to the leaves, an increased specific leaf area, and a more skewed vertical leaf area distribution (e.g. Bastiaans and Drenth, 1999; Cavero et al., 2000). In the current version of INTERCOM, most processes related to the morphological development of weeds are introduced in a dynamic, but descriptive way. Dry matter allocation patterns for instance are introduced as a function of the phenological development stage of the species, but are not related to the level of competitive stress experienced by the weeds.

Epilogue

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. 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.

Ecophysiological models for interplant competition were first developed in the early 1980s to obtain a better understanding of the harmful effect of weeds on crop productivity. Initially, the models were used for the construction of more robust damage relationships to support rational decision making on the use of herbicides. However, soon it was realised that such comprehensive models are inappropriate for prediction purposes due to their large input requirements. The strength of these models is their ability to analyse crop-weed subsystems, and therefore they have great potential to contribute to the identification and evaluation of tactical and strategic options for improving current weed management. Models are never complete and should continuously be updated and improved to meet the needs for newly defined applications. Some of the current needs are a better mechanistic understanding of early growth. This is particularly relevant since alteration of crop-weed competitive relations to the benefit of the crop holds huge potential as a major component of an integrated weed management strategy. Competitive relations are largely determined early in the growing season, and therefore an accurate simulation of early growth seems crucial for evaluation of the various options (e.g. competitive cultivars, increased sowing rate).

Also more attention should be given to the accuracy with which growth, morphological development and seed production of weed species are being simulated, as the long term development of weed populations is particularly important in systems with a reduced reliance on chemical control. In this way a functional link will be established between crop-weed competition research and research on weed population dynamics. Continuous interaction between modelling and experimental research will help determine the required level of detail in crop-weed competition models and will also provide leads for focusing future weed ecological research.

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