CHAPTER 21

EXPLOITING DIVERSITY TO MANAGE WEEDS IN AGRO-ECOSYSTEMS

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Abstract. Weed management systems that rely less on chemical control are needed globally. Next to curative chemical weed control, there are other ways of tackling weed problems, such as (a) reduction of the weed seed bank in the soil, (b) reduced recruitment of weed seeds from the soil seed bank, and (c) strengthening the relative competitive ability of the crop. A number of case studies are presented in which diversity is used as a basis for improved weed management. In the first case study, diversity refers to genetic variation within a crop species, which is utilized in breeding programmes aiming at the development of more competitive cultivars. In the other case studies, diversity refers to the reinforcement of weakly competitive crop species through the addition of a second species that contains a strong weed-suppressing function. Here a distinction is made between intercropping, where the species are grown simultaneously, and sequential or rotational cropping, where a cover crop is introduced in the cropping interval in between two main crops.

Weed-competitive cultivars, intercropping and rotational cover cropping all have potential to contribute significantly to the weed management of agro-ecosystems. Rather than making curative control completely redundant, they allow the regular curative control measures to be applied at a lower dose or in a less frequent manner. The weed-suppressive effect was largely determined by the combined effects of genotype (or species) and management. Obtaining a sufficient level of weed suppression while maintaining the yielding ability is a major issue in the development of weed-competitive cultivars and the design of intercropping systems. In both cases, competition models showed to be useful tools to analyse and optimize systems. Opportunities and potential obstacles for implementation of the proposed strategies are discussed.

INTRODUCTION

Weeds have always been a major disturbing factor in agricultural production systems. If left uncontrolled, weed plants compete with crop plants for resources

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essential for plant growth, thereby reducing crop yield and quality. To minimize the negative consequences of weeds on crop production, curative actions to remove or kill weed plants shortly after their establishment are often undertaken. In spite of intensive control activities in most agricultural systems, the loss in yield because of weed competition was still estimated to be 10% (Oerke et al. 1994). Weed management is largely herbicide-dominated. The widespread concern about environmental side-effects of herbicides combined with fear for public health has called for a reduced use of herbicides. These concerns have already led to the banning of several herbicides in various countries (Matteson 1995). At the same time, the release rate of new herbicides has decreased. Particularly for some minor crops this has caused situations where farmers are forced to rely on other weed control technologies. The development of herbicide-resistant biotypes is another mechanism through which the vulnerability of herbicide-dominated systems is increased. Despite the need for systems with a reduced use and reliance on herbicides, widely applicable alternative solutions are still lacking. This is most clearly illustrated in organic farming systems, where the application of herbicides is excluded and weed management often develops into a high-priority issue.

A number of directions have been suggested for minimizing the use of herbicides. A first strategy is to make a more efficient use of herbicides through technological solutions, such as an improved application technology, improved application timing, factor-adjusted dosages and spot spraying. A second strategy is to focus more on alternative curative weed control options such as mechanical weed control. A third strategy to minimize the use of herbicides is to develop methods other than direct weed control measures (Bastiaans et al. 2002). This is illustrated in Figure 1, where a hyperbolic curve is used to relate the yield loss of the crop to weed plant density. A second x-axis, representing the seed bank density, is added to illustrate that most weed plants evolve from seeds that are stored in the weed-seed soil bank. In Figure 1A curative weed control is represented. Weed seedlings are killed through, e.g., a herbicide treatment or a mechanical weed control intervention. Reducing the number of weed plants decreases the competitive pressure of the weed population on the crop and consequently the yield loss of the crop is diminished. Bearing in mind the life cycle of weeds, alternative weed management could be based on the following principles: (a) a reduced recruitment of seed or vegetative reproduction organs (Figure 1B); (b) alteration of crop—weed competitive relations to the benefit of the crop (Figure 1C); and (c) a gradual reduction of the weed infestation level in the soil (Figure 1D).

One way to achieve weed management based on alternative principles is through the exploitation of diversity, schematically represented in Figure 2B-D. A first option is to breed for weed-competitive genotypes. Then diversity refers to the heterogeneity within a plant species, and exploitation of diversity occurs through breeding rather than through crop management. Large variation within plant traits exists and breeding is directed towards accumulating favourable traits, such as weed-suppressive ability, in a single genotype. Another option for exploiting diversity is by combining two or more species with the purpose of strengthening the weed-suppressing function. A distinction can be made between intercropping, where the

species are simultaneously present for at least part of the growing season, and sequential cropping, where the cover crop is introduced to fill up a crop-free period in between two main crops.

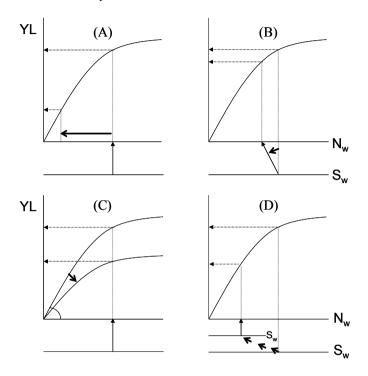


Figure 1. The hyperbolic yield loss (YL) – weed density relation used to illustrate various principles for reducing yield loss due to weeds. (A) Killing or removal of weed plants; (B) reduced recruitment of weeds from the seed bank; (C) alteration of crop—weed competitive relations; (D) gradual reduction or depletion of the weed seed bank. Thick arrows represent the major effect of a specific intervention. Weed density is expressed in two ways: as weed plant density (N_w) and as seed bank density (S_w) (after: Bastiaans et al. 2002)

A number of case studies will be presented. The case studies have in common that they were initiated to explore the potential of improving weed management through the utilization of diversity. The case studies either deal with the development of weed-competitive genotypes, intercropping or sequential cover cropping. All case studies were conducted at, or in connection with, the Crop and Weed Ecology Group of Wageningen University. Main findings and important aspects that were encountered during developing the conceptual frame works and the research process are presented. In a final section the various options and strategies are compared and attention is given to aspects such as effectiveness with regard to weed suppression, consequences for yielding ability, relevance of management, and opportunities for systems optimization and implementation.

	Weed suppressing function
Weed control strategy	Farmer's field: main crop ———
a. Herbicide-based	<u> </u>
b. Genetic improvement	
c. Intercropping	<u></u>
d. Rotational cover cropping	

Figure 2. Schematic representation of alternative weed management strategies based on the utilization of diversity. Solid line represents the growing season of the main crop. Dotted line represents the basis for the weed-suppressing function (a. herbicides; b. genes introgressed from weed-competitive germplasm; c. weed-competitive companion crop; d. weed-competitive cover crop grown in the cropping interval between two main crops)

WEED-COMPETITIVE GENOTYPES

Weeds: an increasing problem in rice production

In traditional irrigated rice systems, the weed problems are relatively small. Transplanting favours the crop in its competition against weeds, as it provides rice a 2- to 3-week head-start relative to the weeds. Also the presence of a water layer after transplanting is beneficial, as it effectively suppresses the emergence and growth of most of the weed flora. Therefore, irrigated lowland rice is a good system in terms of ease and cost of weed control (De Datta and Baltazar 1996). This system, however, is seriously under pressure. Firstly, the high labour cost coupled with the shortage of on-farm labour causes a rapid shift from transplanting to direct seeding (De Datta 1986; Erguiza et al. 1990). Secondly, the growing water scarcity is threatening this rice production system (Tuong and Bouman 2003). Water consumption per kg of rice ranges from 1000 to 3000 litres, which is about 2 to 3 times more than is needed to produce other cereals such as wheat or maize (Bouman and Tuong 2001; Cantrell and Hettel 2005). The increasing water scarcity for agriculture points to an urgent need to improve crop water productivity.

Aerobic rice is one of the water-saving systems proposed to replace the traditional lowland rice system that is now under threat (Cantrell and Hettel 2005). In aerobic rice, seed is sown directly into dry soil and irrigation is applied to keep the soil sufficiently moist for good plant growth, but the soil is never saturated. Though aerobic rice, just like 'upland rice', is grown under aerobic conditions, it is different in water management from traditional upland rice, which is completely dependent on rainfall. Changing the establishment system from transplanting to

direct seeding and soil hydrological conditions from flooded to aerobic conditions will definitely bring more severe weed problems. Successful aerobic rice production therefore requires effective weed management. For this reason the feasibility of breeding for weed competitiveness in rice was explored.

Comparing two contrasting cultivars

Differences in competitive ability between two contrasting rice cultivars (Mahsuri and IR8), grown in well-fertilized irrigated conditions, were analysed by means of a mechanistic simulation model for crop—weed interaction (Bastiaans et al. 1997). Mahsuri is a native cultivar that originates from Malaysia. It is a tall-growing, highly competitive cultivar, with fast growth during the early growth stages. It belongs to the more traditional leafy cultivars with a droopy plant type and a low harvest index. IR8 is the higher-yielding, but less competitive rice cultivar. This first IRRI-bred recommended cultivar has low stature relative to Mahsuri, a more vertical leaf orientation, and a harvest index of around 0.50. In the experiment, both cultivars were grown in pure stand and in the presence of purple rice, which was added as a model weed. In all situations, IR8 gave the highest grain yield, but obviously the yield of IR8 was more affected by the presence of the weed than was the yield of Mahsuri.

Based on regular periodic samplings and non-destructive observations in the pure stand plots, INTERCOM (Kropff and Van Laar 1993), a model for interspecific competition, was parameterized. Simulation of dry-matter production and grain yield of IR8 and Mahsuri in competition with purple rice resulted in a good agreement with observed data, implying that the differences in phenological, physiological and morphological attributes of IR8 and Mahsuri were able to explain the observed differences in their competitive ability. The validated competition model was then used for a sensitivity analysis to identify which traits were responsible for the differences in competitive ability. One by one, model input parameters were increased by 10% and the consequences for simulated weed shoot biomass determined.

The result was expressed as relative sensitivity: the ratio of percentage change in simulated weed shoot biomass and percentage change in the value of the specific input parameter. The model clearly pointed at the importance of early growth characteristics (Figure 3). Increased rates of early leaf area development (EGR-leaf area) and early height growth rate (EGR-height) both gave considerable reductions in simulated weed biomass, indicating their importance for weed-suppressive ability. Maximum plant height (Max-height), which determines the vertical position of leaf area in the mixed canopy, was also found important. Increases in crop growth rate (CGR), the light extinction coefficient (K-dif) and specific leaf area (SLA) only resulted in marginal reductions in simulated weed biomass, indicating that these factors are not major determinants of weed-suppressive ability. These results exemplify the role of mechanistic simulation models in guiding the plant-breeding process: the models enable a quantitative estimation of the potential contribution of various traits to an increased competitive ability.

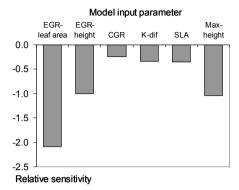


Figure 3. Relative sensitivity, calculated as the ratio of percentage change in simulated weed biomass and percentage change in model input parameter obtained for various model input parameters (EGR=early growth rate; CGR=crop growth rate; K-dif=light extinction coefficient; SLA=specific leaf area; Max height=maximum plant height)

Weed competitiveness and yielding ability of aerobic rice genotypes

In collaboration with the International Rice Research Institute (Los Baños, Philippines), the feasibility of breeding for weed-suppressive high-yielding aerobic rice was further investigated (Zhao 2006). In the experiments, conducted from 2001 to 2004, 40 aerobic/upland genotypes, including *indica*, *japonica*, *aus* and mixed types within *Oryza sativa* were used. Growing these genotypes in the presence of weeds revealed a large variability in weed-suppressive ability (WSA) among genotypes (Zhao et al. 2006a). Among the different germplasm groups, *indica* and *aus* germplasm appeared to be more weed-suppressive than tropical *japonica* germplasm (Figure 4). The *indica* group combined weed-suppressive ability with a strong yielding ability. Both under weed-free and weedy conditions the average grain yield was significantly higher than that of the other groups. The *aus* group showed the lowest yield reduction, which apart from its strong WSA might hint at a high level of weed tolerance. These findings indicate that *indica* and *aus* are likely to be the most suitable gene donors for improvement of WSA in aerobic rice in tropical regions.

Weedy yield and weed biomass, the two target traits in breeding for weed competitiveness, were both found to be moderately heritable, indicating that reasonable gains from selection can be expected. On top of that, early crop vigour and yield under weed-free conditions were found to have high estimated indirect selection efficiency for both weedy yield and weed biomass. This implies that selection for high-yielding, weed-competitive genotypes can be conducted in the absence of weeds. This has many practical advantages and saves breeding costs of seed, field and labour because of the smaller plot size and seed amount that are required, and the simplified selection process.

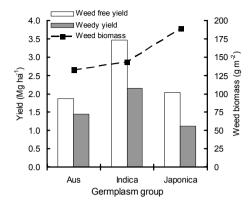


Figure 4. Weed-free yield, weedy yield and weed biomass for three germplasm groups evaluated over three wet seasons of 2001–2003 at IRRI, Los Baños, Philippines (after Zhao 2006)

Controversial conclusions have been drawn on the compatibility of yield potential and WSA. The current study showed that yielding ability and WSA were not only compatible, but also closely associated in aerobic/upland rice. One attribute of modern varieties is the vertical orientation of their leaves, creating a more even distribution of light over the canopy, resulting in a higher radiation use efficiency and a more productive crop. It is often assumed that vertical leaves are at the cost of the ability to suppress weeds. The results of the current study do not support this hypothesis, and even a negative association between droopy plant type and WSA was observed. One explanation for this is that WSA is determined by many different factors, such as growth rate, LAI, tillering, tiller angle, plant height and leaf erectness. Therefore, the contribution of droopy leaves to WSA might be very limited and cancelled out by the other factors. The association between plant type and WSA within the current germplasm population might also simply result from the fact that all the cultivars belonging to *indica* and aus germplasm groups were erect and had fast early growth. These kind of confounding factors hinder a clear analysis. What remains, however, is that nearly all studies addressed the importance of fast early growth in determining strong WSA (e.g., Johnson et al. 1998; Gibson and Fischer 2001; Zhao et al. 2006b).

One other objective of the study was to find out whether the use of more competitive cultivars can be combined with other cultural measures that strengthen the ability of the crop to suppress weeds. For this purpose three cultivars differing in competitive ability (APO, IR60080-46A and IRAT 216) were selected and sown at seeding rates of 100, 300 and 500 viable seeds m⁻². All weedy plots were handweeded once at either 3 weeks after sowing (WAS) (2003) or at 2 WAS (2004), and weeds were allowed to grow thereafter. In both years, and for all three cultivars, the weed biomass (WB; g m⁻²) in dependence of crop plant density (N_c ; plant m⁻²) could be accurately described by a rectangular hyperbola, according to Spitters (1983):

$$WB = \frac{N_w}{b_{w0} + b_{ww}N_w + b_{wc}N_c} \,. \tag{1}$$

In this function, $N_{\rm w}$ (plant m⁻²) represents the number of weed plants, $b_{\rm w0}$ (plant g⁻¹) represents the reciprocal of the average weight per weed plant in the absence of competition, $b_{\rm ww}$ (m² g⁻¹) is the intraspecific-competition coefficient for the weed plants. The effect of interspecific competition of a rice cultivar is expressed as the product of an interspecific-competition coefficient ($b_{\rm wc}$; m² g⁻¹) and crop plant density. In both years the competition coefficient of cultivar APO was about twice as high as that of the other two cultivars. This implies that the other two cultivars should be sown at a twice higher density to obtain the same weed-suppressive effect as APO. Time of weeding also had a clear effect. With weeding at 3 WAS (2003) crop plants were more competitive than with weeding at 2 WAS (2004). This illustrates that weed suppression is strongly determined by genotype × management interaction.

INTERCROPPING

Breeding for more competitive genotypes does not provide a solution for solving weed problems in all cropping systems. Particularly in production of vegetables there are some relatively slow-growing crops such as onion, carrot and leek that will never be able to suppress weeds sufficiently. In these situations, intercropping, in which two or more crops are simultaneously grown in the same field, is an alternative option for attaining improved weed management (Liebman and Dyck 1993; Teasdale 1998). Ideally, crops whose resource use characteristics are physiologically, temporally or morphologically complementary are combined. In this way, the crops are prevented from fully competing with one another (Vandermeer 1989). At the same time, these intercrops may use a greater share of available resources and, therefore, provide opportunities for suppressing weeds through niche pre-emption or resource competition. In the concept of Vandermeer (1989) component crops in an intercrop interfere with one another by affecting one another's growing environment. A distinction is made between *competition*, when one crop creates a less favourable environment for the other, and facilitation, when an improved growing environment is created. With regard to weed management, facilitation, or the creation of a weed-free environment, is created through competition. Perhaps the best known example of this type of weed suppression is the use of cover crops, which are solid-grown crops grown primarily to protect and cover the soil between crop rows. One of the main challenges of this approach is that the crop that is introduced for its weed-suppressing function should provide a sufficient level of weed control without putting too much competitive pressure on the main crop. Whether this is realized depends on the main crop, on the added crop, but particularly on the combination of both.

Suitability of the main crop

Options for utilization of intercropping systems for weed control first of all depend on the main crop. In perennial cropping systems, such as vineyards, annual cover crops are often successfully introduced. Here the main crop is well established and competition can be avoided by selecting a low-growing, shallow-rooting cover crop that is able to produce a closed cover. A quick cover-crop establishment than avoids the settlement of deeper-rooting, tall-growing weeds that compete with the grape plants or hinder the harvesting operations. With annual main crops it is far more difficult to avoid competition between main and cover crop. Suitability of the main crop is then largely determined by the ability of the main crop to tolerate a certain level of interspecific competition. In a joint experimental approach, intercropping of Brussels sprouts with barley was investigated. Entomologists observed that populations of several herbivore species (e.g., Brevicoryne brassicae, Myzus persicae) were reduced by intercropping Brussels sprouts with barley (Bukovinszky 2004). For weed management the results were disappointing. Introduction of barley in between the rows of Brussels sprout did not prevent the establishment of weeds such as Chenopodium album, whereas it precluded the use of mechanical weed control options such as hoeing. Most importantly, Brussels sprout suffered quite extensively from the competitive pressure that barley posed on this crop. Apart from a lower dry-matter production, the harvest index was dramatically reduced (Figure 5). De Wit et al. (1979) already pointed at differences in the response of crops to competition and distinguished between crops where, at higher levels of competition, individual plant size is affected but harvest index remains unaffected (e.g., small cereal grains) and crops where a reduction in plant size is complemented with a reduction in harvest index (e.g., maize, Brussels sprouts). The additional sensitivity of the last category to competition makes those species far less suitable for use in an intercrop.

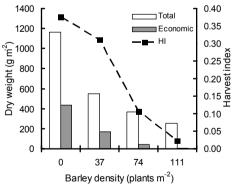


Figure 5. Total yield, economic yield and harvest index (HI) of Brussels sprouts grown in pure stand and in mixture with different plant densities of barley. Results represent averages obtained with Brussels sprouts grown at 4.4 and 6.7 plants m^{-2}

Determining the suitability of clover as a cover crop

Except for the main crop, the selection of a proper cover crop is important. It is obvious that cover-crop species that combine weed suppression with other functions are favoured. Clover species, e.g., as members of the Leguminosae, are, able to fix nitrogen. Furthermore, it is well established that clover species are able to reduce pest and disease pressure in a number of crops (Theunissen 1994). Both these characteristics are particularly favourable in organic agricultural systems. In addition, some clovers possess good potential as weed suppressor as they are able to produce a dense layer of biomass. The main constraint for using clover as an undersown cover crop is yield depression because of competition with the main crop. Attempts to reduce this competition include the screening for less competitive cover-crop species (Nicholson and Wien 1983). Recently, such a screening was carried out among a group of eight different clover species (Den Hollander and Bastiaans 2004).

In this comparison, Persian clover (Trifolium resupinatum) was among the fastest developing species. It produced a rapid soil cover and grew relatively tall. Subterranean clover (T. subterraneum) showed the slowest soil cover and remained relatively small. The differences between those two clover species were reflected in clear differences in the ability to suppress weeds. Persian clover gave a satisfactory suppression as, compared to the bare-soil control plot, the number of established weeds was reduced by 80% and those weeds that managed to survive remained relatively small. In plots with subterranean clover the number of weeds was reduced by only 25%. Regardless of clover species, the competition from clover led to unacceptable yield reductions of the main crop. When leek transplants were introduced in well-established clover canopies, individual leek plant dry weight was reduced by 75% in case of Persian clover, and still by 61% when introduced in subterranean clover. These findings indicate that species selection on its own is not sufficient to obtain an acceptable equilibrium between weed suppression and yield reduction of the crop when using clover as undersown cover crop. Obviously, additional control measures remain necessary to restrain the negative effects on the crop, a conclusion in line with findings of Lotz et al. (1997). Mechanical suppression of cover-crop growth through, e.g., mowing or root cutting (Brandsæter et al. 1998), and improved timing of establishment of the cover crop relative to that of the main crop (Müller-Schärer and Potter 1991), are examples of such management.

Competitive suppression of weeds in a leek-celery intercropping system

One alternative for minimizing the negative consequences of the competitive effect of the cover crop on the main crop is the introduction of a second cash crop. In collaboration with the Swiss Agricultural Research Station, Agroscope FAW Wädenswil a leek—celery intercropping system was studied and optimized with regard to crop yield, plant quality and weed-suppressive ability (Baumann 2001). In this case the leafy and competitive celery was introduced to improve the weed suppression of the vertically growing and weakly competitive leek (Baumann et al.

2000). Competition between leek and celery is to some extent acceptable, as long as leek is able to reach its minimum marketable plant size, simply because the resources captured by celery also result in a marketable product.

Field experiments were carried out to study the weed-suppressive ability and the intra- and interspecific competition of a leek-celery intercrop with and without additional weed competition (Baumann et al. 2001). Results showed that intercropping of leek and celery in a row-by-row replacement design provided a much better weed suppression than the leek pure stand, even though the intercrop was not able to suppress early-germinating weeds completely. Consequently, the critical period for weed control of intercropped leek lasted about two weeks shorter than that of leek pure stand. In an experiment in which *Senecio vulgaris* was planted, it was shown that the flower production and the offspring of mature weed plants was considerably reduced under intercropped leek compared with the pure stand of leek. This indicates that increasing the ability of the crop canopy to compete for light can reduce not only the biomass, but also the reproductive potential of weeds. The advantages of the intercrop relative to the pure stand with respect to weed management are schematically presented in Figure 6.

Next to weed management, crop productivity is an important element for justification of an intercrop. The experiment showed that the relative yield of the intercrop exceeded that of the pure stands by 10%, probably as a result of an optimized exploitation of resources. The percentage of marketable leek plants (pseudostem diameter \geq 20 mm) was, however, reduced by 20%. For this reason, the focus was put on optimization of the total plant density and the mixing ratio of the intercrop, using simulation modelling. An adapted version of the eco-physiological competition model INTERCOM was used to simulate interplant competition between leek, celery and *S. vulgaris* (Baumann et al. 2002a).

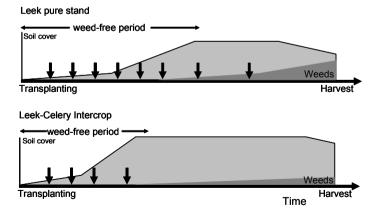


Figure 6. Schematic representation of the implications for weed management when leek is grown in a mixture with celery, rather than in pure stand. Arrows indicate weed control interventions. The weed-free period refers to the period during which weeds should be removed in order to avoid yield reduction. In the leek pure stand an additional weed control operation is conducted after the weed-free period to avoid weed seed production

After parameterization, based on the pure stands of the two crops and the weed. and validation, the model was used to simulate intercrop performance for various conditions and a wide range of crop densities, using different relative times of weed emergence (Baumann et al. 2002b). The results of these simulations were summarized using a descriptive hyperbolic yield density model (Spitters 1983). Based on the parameter estimates of this simple model it was found that the competitive ability of celery was about three times higher than the competitive ability of leek. Increasing the proportion of celery in the mixture will thus result in an improved weed-suppressive ability of the intercrop, but at the same time might cause severe reductions in the quality of leek. Optimization confirmed that the size of individual leek plants was the main limiting factor of this system. An intercropping system consisting of 19 leek and 9.4 celery plants m⁻² was found optimal. The revenues of this system were 7% higher than that of the highestyielding pure stand of leek and 9% higher than the revenues of the highest-yielding celery pure stand. Compared to leek pure stand, this mixed cropping system also gave a considerable reduction in reproductive potential of S. vulgaris. In conclusion, it was shown that intercropping of two main crops improved the sustainability of the system by reducing the need for labour and cost-intensive weed control measures. whereas the profitability of the system was maintained.

SEQUENTIAL COVER CROPPING

Use of cover crops in the crop-free period

Another strategy for using cover crops for weed management is to grow them during the period when the main crop is absent. Competition between the main and the cover crop is then no longer a pressing issue and problems with mechanization of the main crop are avoided. Inclusion of cover crops in crop rotations introduces two important mechanisms through which the development of weed populations might be hampered. In late summer and autumn the successful introduction of cover crops prevents growth, development and, most importantly, seed production of weeds that remain in the stubble. Cover crops fill gaps in cropping systems that would otherwise be occupied by weeds (Liebman and Staver 2001). As a result of this type of niche pre-emption, weed soil cover is substantially reduced.

In late winter and spring, cover-crop residues, used as surface mulches, suppress or retard weed emergence and growth due to both allelopathic and physical effects (e.g., Liebman and Davis 2000). Crop residues on the soil surface can also reduce weed densities by physically impeding weed seedling emergence and intercepting light that cues weed germination. Many plant species produce and release chemicals that are toxic to other plants, a phenomenon referred to as allelopathy. Allelochemicals may also be produced by microbes that transform plant products during residue decomposition. Living crops can have direct allelopathic effects on weeds, but the most important application involves the use of crop residue to suppress weed germination, establishment and growth. A number of classes of chemicals have been identified as allelopathic agents. Those found frequently

include alkaloids, coumarins, cyanogenic glucosides, flavonoids, phenolic acids, polyacetylenes, quinines and terpenoids (Einhellig and Leather 1988; Worsham 1989; Rice 1995).

In Dutch agriculture, cover crops have always played a modest role and the motives for using them have changed over time. Originally, these crops were mainly used as green manure or fodder crops, and this is how they still can be found in the Dutch List of Varieties of Field Crops (PRI 2005). On arable farms, cover crops were mainly used after the main crop, for increasing the organic-matter content of the soil. On mixed farms *Brassica* spp. were grown in the same period and used as additional feed for cattle. More strict regulations on emission of nutrients have given cover crops an additional role as catch crop, meant to avoid leaching in the crop-free winter period. Furthermore, Chinese radish (*Raphanus sativa*) is being used as hatch or trap crop for *Heterodera* spp., cyst nematodes that are pathogenic to sugar beet. For this purpose, the best results are obtained if the crops are sown in spring. In organic farming systems leguminous crops are used to supply nitrogen to the soil (e.g., Liebman and Davis 2000). The weed-suppressing function of these cover crops has so far received little attention.

Optimization of the weed-suppressing function

Recently, a research programme was started with the aim of exploring the potential of cover crops to contribute to the ecological management of weed populations in organic farming systems (Kruidhof and Bastiaans 2005). The aim of this project is to explore options for enhancing cover-crop performance by optimizing both the autumn (competition) and spring (allelopathic inhibition) weed-suppressing functions (Figure 7). From each of the families Brassicaceae, Poaceae and Fabaceae a frost-sensitive and a winter-hard species were selected. Weed suppression in autumn is studied and related to morpho-physiological characteristics of the cover crops. Particular attention is given to early growth, as a fast establishment and canopy closure of the cover crop is a prerequisite for sufficient weed suppression. Furthermore, it is investigated how the concentration of allelochemicals in the cover crop can be maximized. Plant density, nutrient level and mechanical damage are factors whose effects are investigated.

Incorporation of the cover-crop residues in the soil is another important aspect, as it mediates the effect of the residues on the target plants. Pre-treatment of residues before incorporation is one element. The crops can simply be mown, but cutting the residues in pieces of different sizes and crushing are other options. All of these treatments may affect the release pattern of the allelochemicals from the cover-crop residue material. Residue incorporation strategies will also be studied. Cover-crop residues might be left on the soil surface, mixed through the upper part of the soil (e.g., 5, 10 or 20 cm), or ploughed under at a specific depth. In field experiments different equipment is tested for pre-treatment and residue incorporation. Both distribution of residues in the soil and the undesired regrowth of the cover crops are evaluated.

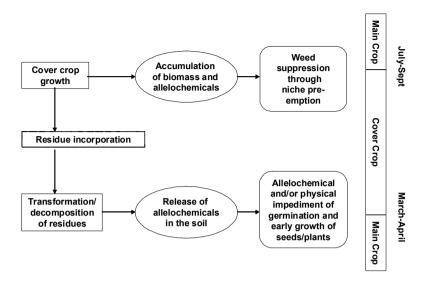


Figure 7. Framework showing the autumn and spring weed-suppressive mechanisms through which rotational cover cropping contributes to weed management in a crop rotation (after Kruidhof and Bastiaans 2005)

Often, allelopathic effects of plant extracts on germination of seeds in Petri dishes have been reported, whereas effects under field conditions are absent. For this reason, chemical analysis, laboratory bioassays, ring experiments and field experiments are conducted. In most experiments lettuce (*Lactuca sativa* L.) is used as test species, as seeds of this species are known to be sensitive to allelopathic compounds. In other experiments, seeds of a range of plant species are used to determine whether selective inhibition of seeds occurs. Seed size has often been reported an important mechanism of selectivity. Small-seeded species appear to be more susceptible to allelochemicals, whereas large-seeded species appear to be relatively insensitive (Putnam and Defrank 1983). As seeds of crop species are often larger than seeds of weed species this might be an important mechanism of selectivity for application of this strategy in practice.

CONCLUDING REMARKS

Especially after the introduction of herbicides, curative weed control has become the dominant strategy for dealing with weeds. Attention has shifted away from cultural control measures that largely try to avoid or reduce the potential negative consequences of weeds that are present in agro-ecosystems. The current problems related to the profuse use of herbicides have reinitiated an increased interest in alternative weed management options. A reduced recruitment of weeds from the soil seed bank, an increased competitive ability of the crop relative to that of the weed and a reduction of the weed soil seed bank all represent principles through which

weed problems in agro-ecosystems can be reduced. In a number of projects research was undertaken to investigate whether diversity could be employed for the utilization of these alternative principles. The use of weed-competitive cultivars, intercropping and rotational cover cropping all contribute significantly to the management of weed populations through at least two of the fore-mentioned principles. Apart from an improved competitiveness of the crop (weed-competitive cultivars; intercropping) or a reduced recruitment (rotational cover cropping) each method generates a positive contribution to the control of the size of the weed seed bank. It is also obvious that none of the proposed methods is able to replace curative control completely. Rather, the proposed measures allow curative control measures to be applied in a less intensive, and probably less frequent, manner.

For all methods the ultimate weed-suppressive effect is determined by a combination of genotype and management. For the competitive cultivars the weedsuppressive effect can be quantitatively characterized as the product of the seeding rate of the crop and an interspecific competition index. This interspecific competition index expresses the competitive ability of a single crop plant relative to that of a weed plant. Apart from the genetic component this competition index was shown to be influenced by the timing of weed control. Later removal of weeds gave the crop a clear competitive advantage, as mainly the weeds that emerge after the weeding operation put a long-lasting competitive pressure on the crop. Postponing the weeding control measure too much might, however, reduce the efficacy of the control operation. With intercropping, the selection of the main and the undersown cover crop is an important first step. Combined with relative planting time, overall planting density and the mixing ratio of the component crops they determine the weed-suppressive ability of the intercrop. If the cover crop becomes too dominant, additional management is required to restore the desired competitive balance between the component crops. In case of rotational cover cropping the choice of the cover crop should be based on the competitive ability in autumn and the allelopathic potential in spring. Important management aspects are mainly related to incorporation of the cover-crop residue material in spring. Not only does this residue handling determine the impediment of weed seed germination, it also determines the risk of undesired regrowth of the cover crop.

Both intercropping and the use of competitive cultivars are largely based on providing a more competitive environment for the weeds. In both situations an important aspect is whether the improved competitive ability of the crop is at the cost of yielding ability. In the current research, improved weed-suppressive ability of aerobic rice cultivars was closely related to early vigour, and this trait correlated well with yielding ability. Consequently, in this case, yielding ability and weed-suppressive ability can easily be combined. For intercropping systems a different situation was found. In this case the weed-suppressive ability is mainly determined by the cover crop, whereas the yield of the main crop is most important. Improved weed suppression is closely associated with a stronger competitive pressure on the main crop and consequently there is a clear tension between weed suppression and crop yield. Introduction of a competitive second cash crop is one option to minimize the financial consequences of yield reduction in the main crop. Another option is to use the cover crop in a rotational context and avoid the competition between main

and cover crop. Competition models showed to be useful tools for improved understanding and systems optimization. With breeding for more competitive cultivars they allow the quantitative assessment of the importance of various traits, whereas with intercropping they allowed the determination of the optimum mixture composition with regard to crop yield, plant quality and weed suppression.

Opportunities for implementation of the proposed strategies are quite different. Intercropping, despite its many advantages, is generally not considered a feasible system in high-input horticulture and agriculture in Western Europe. One of the obstacles is the risk of obtaining a lower yield compared to systems consisting of pure-stand crops. Furthermore, the difficulties with mechanization and hence the high labour requirement reduce the attractiveness of this system. Mechanization, however, does not necessarily have to be a major obstacle. In case of the leek-celery intercropping system, planting, tillage operations and harvesting could all be carried out using commercially available machinery. Growing cover crops in between two main crops is already common practice for many farmers. This practice is often used for many different reasons. The current research project focuses on optimization of the weed-suppressive effect of rotational cover cropping. Outcomes of this research might give directions for cover-crop selection and handling and incorporation of cover-crop residue material. For farmers that already use rotational cover cropping this might imply some simple adjustments to their current practices. For farmers who prefer to have their land fallow in between two main crops, implementation of this strategy is less likely. Competitive cultivars mainly require a serious breeding effort. For aerobic rice, indirect selection indices were developed, meaning that selection can be conducted in weed-free conditions and only requires few additional observations. Once the more competitive cultivars are available no major obstacles have to be overcome

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