SESSION 5A

CONSEQUENCES OF TOTAL HERBICIDE USE ON WEED POPULATION DYNAMICS

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Papers	5A-1 to 5A-4

Approaches used in the prediction of weed population dynamics

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ABSTRACT

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

INTRODUCTION

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

Three aspects of IWM systems can be distinguished: decision-making, prevention and weed control technology (Kropff *et al.*, 1997). If only the short-term perspective is considered, decision making mainly involves operational decisions on if, when, where and how weeds should be controlled. In order to answer this type of question quantitative insight into crop-weed interactions is highly relevant. If weed problems are examined on a longer-term

perspective, the first step in the decision making process deals with strategic decisions, which set the framework for tactical and operational decisions. Apart from the effect of the weeds in the present crop, the potential consequences for future crops are accounted for. For such considerations knowledge on the dynamics of weed populations in space and time becomes pertinent. Irrespective of the time dimension of the analysis, it is clear that attempts to reduce the present dependency on herbicides should focus on prevention. This can be based on cultural measures that favour the crop or through the use of more competitive varieties, on the development of better curative control techniques and on better long- and short-term decision making. This becomes even more important when precision farming techniques facilitate site and development stage specific weed control. Quantitative insight into both crop-weed interactions and the dynamics of weed populations in space and in time forms the basis for such explorations of opportunities to improve weed management.

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

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

PROCESSES DETERMINING THE LIFE CYCLE OF WEEDS

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

Seed bank dynamics

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

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

Weed establishment and growth in competition with the crop

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

situations (Kropff & Van Laar, 1993). Studies on the competitive relations of crop cultivars demonstrated the ability of the models to quantitatively explain varietal differences in competitive ability (Bastiaans *et al.*, 1997). The main gaps in knowledge are related to morphological development and especially the phenotypic plasticity of weeds with respect to these morphological features. Kropff & Van Laar (1993), for example, demonstrated the impressive plasticity of *C. album* with respect to height development in different competition situations.

Weed seed production

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

Seed dispersal

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

MODELLING POPULATION DYNAMICS

To obtain an integrated insight into life cycle processes mathematical models are indispensable. The state of the art in modelling life-cycle processes was described by Cousens & Mortimer (1995). Comprehensive models that are based on physiological principles are

only available for some parts of the life cycle including plant growth and competition (Kropff & Van Laar, 1993), germination and emergence (Vleeshouwers & Bouwmeester, 1993). In contrast, processes like seed shedding, seed dispersal and predation of seeds are poorly understood. The most detailed models that encompass the whole life cycle have been developed for *Avena fatua* L. (Cousens *et al.*, 1986), *Alopecurus myosuroides* Huds. (Doyle *et al.*, 1986) and *Galium aparine* L. (Van der Weide & Van Groenendael, 1990; Wallinga, 1998).

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

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

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

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

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

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

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

Most frequently the density of weeds is used as the key variable. From the density in a given year, the rate of change in density and the density in the next year are derived. An important

assumption underlying this approach is that each weed perceives a similar environment and that the system is homogeneous. Due to the conceptual clarity in modelling temporal changes in density this approach is widely used, ranging from exponential growth to bounded growth (Firbank & Watkinson, 1986).

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

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

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

EXPLORATION OF LONG-TERM WEED MANAGEMENT STRATEGIES

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

Prevention through increased crop competitive ability and weed populations.

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

Frequency of herbicide-application and thresholds

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

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

Critical kill rate

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

$$r_c = 1 - \frac{g + m}{ag} \tag{3}$$

where population dynamic characteristics are captured in the parameters a (the production of viable seeds per plant at low densities), b (the maximum production of viable seeds per unit area at high densities), m (the relative amount of seeds removed annually due to mortality), and g (the relative amount of seeds that germinate and emerge). In this equation, r_c denotes the critical kill rate, which is required to maintain the weed population at a low density. Any weed management strategy that does not aim for eradication and that avoids high yield losses

must have a kill rate that approximates to this critical kill rate. At very high kill rates, as $r >$ r_c, the weed population will die out eventually, unless there is a continuous import of weed seeds. When this import is virtually absent, it is also feasible to keep weeds stationary at a zero density, which must be the result of an eradication programme. This shows that an optimal control strategy leads in the long-term to the maintenance of a positive density (containment) or, as a particular case, to striving for a zero density (eradication).

Evaluation of systems based on herbicide resistant transgenic crops

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

Population dynamics in complex field situations

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

CONCLUSION

For the development of weed management systems which are effective at minimum cost, safe for the environment and adaptable to individual situations, an integrated weed management approach has to be developed analogous to the strategies developed for integrated pest management (IPM). Such systems should focus on the development of an environment that

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

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Weed seed bank dynamics under herbicide tolerant crops

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ABSTRACT

Successfully marketed herbicide tolerant crops (HTCs) are associated with herbicides that lack residual activity and the promotion of reduced tillage. As a consequence of these associations, consistently excellent weed control will be necessary to stabilize or reduce weed seed banks. For excellent weed control to occur in HTCs, application timing of associated herbicides will be the single most critical factor. The threshold for application timing will be simpler and more easily determined for weeds that emerge early and quickly. Weeds with protracted emergence periods, or those that simply emerge late, will be more difficult to control. Increases in seed bank densities may be expected for these latter species under HTC management.

INTRODUCTION

Recently synthesized HTCs will affect weed seed banks primarily through two inter-related factors. The first is application timing and the second is reduced tillage. Although many HTCs have been developed, those tolerant of herbicides that are broad-spectrum, non-residual, and applied postemergence have become successful examples of rapid adoption of agronomic technology. Widespread farmer acceptance of glyphosate-tolerant soybean and glufosinate-tolerant maize in the North America illustrates this fact well.

Application timing is a critical issue for seed banks because the herbicides used with successful HTCs have little or no residual activity. That is, these herbicides typically will kill only weeds with which contact was made at the time of application. If the herbicide was applied prior to full seedling or shoot emergence of the weeds, then weed seed production and seed bank augmentation may be expected. Similarly, seed banks also can be enriched if the herbicide is applied too late. In this latter case the crop canopy may protect small weed seedlings from contact with the herbicide.

Reduced tillage is another important element regarding seed banks. One of the "selling points" of HTC technology is that the associated postemergence herbicides are broad-spectrum and facilitate acceptance of low-impact forms of soil and residue management. The environmental benefits of reduced tillage systems are many and well known. For weed management, however, the costs and benefits of reduced tillage are not consistent. In terms of "costs," seedling or shoot emergence often is delayed when tillage intensity is reduced (Spandl *et al.*, 1999). In management systems that prolong the duration of weed emergence, the importance of application timing is magnified because the proportions of late-emerging weeds are increased. These late-emerging weeds may be more difficult to control than their early-emerging counterparts with a non-residual herbicide, and the seeds these plants produce can easily replenish or enhance seed banks. The two issues mentioned above will be the foci of this paper. These basic issues and their interactions will be used to explore potential effects on seed bank dynamics over time with the adoption of HTCs.

MATERIALS AND METHODS

Because the adoption of HTCs is too recent for definitive seed bank data to have been collected, this paper will employ literature-derived data and simple models to examine the expected fate of weed seed banks under HTC management. The model weed will be *Abutilon theophrasti* (velvetleaf), and the model crop will be glyphosate-tolerant *Glycine max* (soybean). Velvetleaf was chosen because of (a) the abundance of population dynamics information available in literature sources and (b) its importance in row crop production in North America and southern Europe. Glyphosate-tolerant soybean was chosen because of (a) its widespread sowing during the past two to three years and (b) velvetleaf being one of soybean's major recalcitrant pests.

The examination of the seed bank of velvetleaf, or any other species, must include several population and environmental variables. Complete understanding of the seed bank dynamics of any species is yet to be achieved, but we can synthesize available piecemeal information to arrive at some conclusions. This information includes the timing of seedling emergence for the entire population, proportional emergence from seed banks, seedling survival to reproduction, seed production as a function of emergence time, and seed longevity in soil. Integration of this information permits examination of the consequences of varying herbicide application times, herbicide efficacies, and tillage systems.

Cumulative seedling emergence information for velvetleaf was taken from field measurements weekly during 1993 in Minnesota, USA, as reported by Lindquist *et al.* (1995a). Weather data from this same site and time period also was used by the WeedCast software program (Forcella, 1998) to independently predict the daily pattern of emergence for the entire velvetleaf population. The predictions were compared to the observations. Daily predictions of emergence allowed calculations of sizes of daily emergence cohorts.

Proportional emergence from seed banks determines the magnitude of seedling densities. Values for this variable were derived from literature sources. From lowest to highest, these values were 0.05 (Pacala & Silander, 1990), 0.07 (Lindquist *et al.*, 1995a), and 0.09-0.54 (Forcella *et al.*, 1997). Reasons for the range in values are unknown at this time. However, as will be seen, these values are critical elements in determining the eventual size of seed banks, success of the weed, and necessary levels of control for containment.

Seed production of velvetleaf has been estimated frequently, probably because seeds are produced in capsules that are convenient for weed researchers to count and process. Values for seed production per plant, or fecundity, vary greatly. Lowest values, 45 seeds plant[-1], are for diseased plants in soybean (Lindquist *et al.*, 1995a). Highest values are 3000-4000 seeds plant[-1] for vigorous plants in maize (Zanin & Sattin, 1988). Most importantly, Lindquist *et al.* (1995a) reported seeds plant[-1] along with the timing of emergence of those plants within a soybean crop. This permitted calculation of a relationship between fecundity and thermal time (base temperature = 10 degrees C), which in turn allowed estimation of the contribution to total seed production of daily emergence cohorts.

Velvetleaf seed longevity was estimated by Lueschen & Andersen (1980) in natural seed banks over five years in Minnesota for several management practices. Production of new seeds was prevented in these experiments. Two of the management practices, (a) continuous cropping with annual tillage and (b) chemical fallow, were used here as analogues of conventional crop management and HTC plus zero-till management, respectively.

Relationships were developed between time (years) and decline of viable seeds in the seed bank for each management practice. These relationships permitted simulation of seed bank losses for each set of seeds produced annually over a period of ten years for both HTC management and conventional crop management.

RESULTS

Velvetleaf emerged fully during 1993 only after a thermal time of 400 growing degree days (GDD, base 10 degrees C) had elapsed since the soil was ploughed and the crop planted on 13 May (Lindquist *et al.*, 1995a). WeedCast predictions of velvetleaf emergence mimicked the observations satisfactorily (Figure 1). The predictions were based on estimated soil GDD and soil water potential. Relative sizes of daily emergence cohorts could be calculated from these predictions.
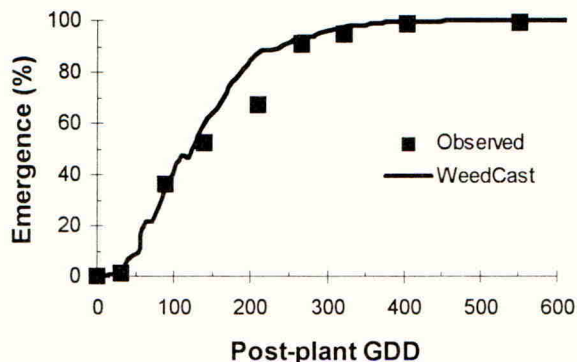
Figure 1. Observed and predicted cumulative velvetleaf emergence during 1993.

Maximum velvetleaf fecundity (F_{max}) during 1993 occurred for plants that emerged early (Lindquist *et al.*, 1995a). Fecundity decreased for plants whose emergence was delayed. Fecundity was related to post-planting thermal time at the time of seedling emergence, and it was estimated by the following equation: $F = F_{max} \times (-0.145 + 0.00021 \times GDD + 8920 / GDD^2)$. Caveats for use of this equation are that if GDD < 89 then $F = F_{max}$ and if GDD > 500, then $F = 0$. F_{max} was 45 seeds plant^{-1} in 1993 (Figure 2). Although maximum fecundity in 1993 was low, the overall relationship in Figure 2 may have general application and can be used to estimate total seed production.

Figure 2. Fecundity of velvetleaf is a function of post-plant thermal time at emergence.
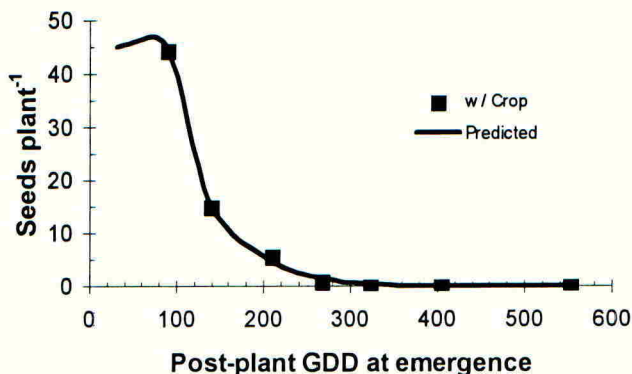
Total seed production is calculated by multiplying the fecundity of each daily emergence cohort by the number of plants emerging each day and then summing over the entire time span for emergence. This procedure is illustrated in Figure 3, wherein the total plant population was assumed to be 100 plants. Cohorts that emerged early (<50 GDD) or late (>150 GDD) produced few seeds because there were so few plants in those groups. Maximum seed production occurred in cohorts that emerged at about 100 GDD for two reasons. First, this is the time when most seedlings emerged (Figure 1); and second, competition by these seedlings with the crop was sufficiently intense to result in relatively high velvetleaf fecundity (Figure 2).
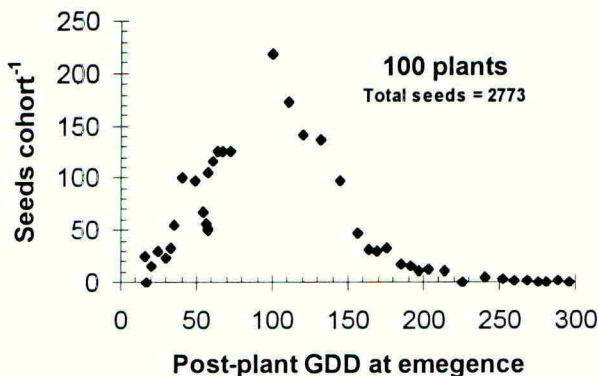
Figure 3. Seed production of cohorts varies with the time at which cohorts emerged.

The total number of seeds produced in the example, above, was 2773 for 100 velvetleaf plants (assuming $F_{max} = 45$). This example presumes an absence of weed control. If a non-residual, high-efficacy, postemergence herbicide (e.g., glyphosate) was applied at varying post-plant GDD, only velvetleaf plants that emerged after application could produce seeds.

This is illustrated in Figure 4, wherein any application time <200 GDD results in some seed production. Accordingly, to minimize velvetleaf seed production, glyphosate should be applied only after 200 GDD. Although some emergence still is occurring at this time (Figure 1), the late-recruited plants will produce insignificant numbers of seeds. Moreover, 200 post-plant GDD were accumulated as of 20 June during 1993. On that day, velvetleaf population structure was highly skewed (data not shown), with most individuals <20 mm tall, average height was 29 mm (WeedCast estimate), and maximum heights for the few earliest-emerging seedlings was about 90 mm. This range of seedling sizes coincides with standard rules-of-thumb for timing of glyphosate application to control velvetleaf.
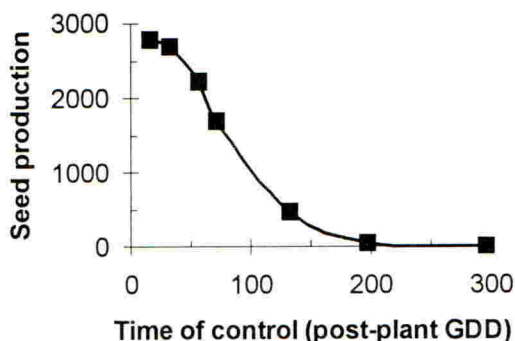

Figure 4. Total velvetleaf seed production according to time of control.

Although glyphosate application at 200 GDD after planting glyphosate-tolerant soybean may be ideal for minimizing velvetleaf seed production, ideals often are better suited to models than reality. What we really need to know is how little weed control we need to stabilize or reduce weed problems. To answer this question, we first need to estimate the fate of the seeds produced in the current year as well as those produced in past years.

Longevity of velvetleaf seeds in field soils varies according to management practices (Lueschen & Andersen 1980). Longevity is lowest and declines the fastest with annual ploughing, discing, and herbicide application, whereas it is highest and declines the slowest when only herbicides are used to kill weeds (Figure 5). This latter situation may best approximate zero-till management with HTCs, whereas the former situation is analogous to conventional crops (CC) and management. Survival percentages (SB) of velvetleaf seeds can be approximated mathematically in both situations. Equations representing both are $SB_{HTC} = 9.75 + 90^{(-Years)}$ and $SB_{CC} = 100 - 13.7 \times Years^2 + 2.38 \times Years^3$. Caveats for these equations are that SB can not increase once minima are reached after 5 or 6 years. For present modelling purposes, SB minima were reduced by a factor of 0.95 per year for years 6-10. Ecological reasons for seed bank decline are largely unknown at this time. Consequently, readers are reminded that the equations listed above are empirical and used solely for ease of calculations.
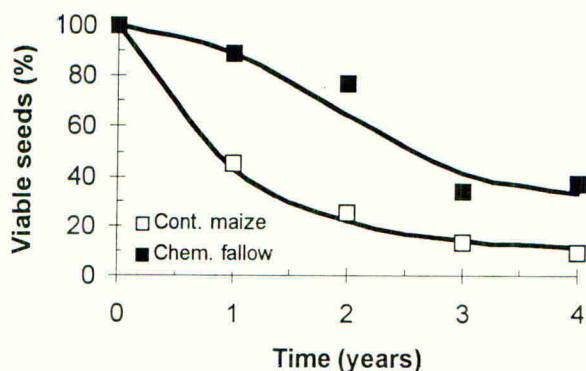
Figure 5. Survival of velvetleaf seeds in field soils under two forms of management.

Equations for seed bank survival can be integrated with variables for proportional emergence from seed banks (E), seedling survival (S), and seed production to determine seed bank densities through time under both HTC and CC systems. An example of this integration is shown in Figure 6 for a 10-year time sequence. In this case, E and S were set at 0.07 and 0.20, which are the values used by Lindquist *et al.* (1995b), and the pattern of velvetleaf seedling emergence for each year was assumed to be identical to that in 1993. Beginning with a population of 100 plants that produce a total of 2773 seeds in year 0, seed bank numbers in a simulated conventional crop decline to a near steady state (1000 seeds) by year 4. In contrast, seed bank numbers in a simulated HTC rise monotonically to about 8000 seeds. (Density dependence would cause oscillations over time. It was not included in the relationships for two reasons: [a] the relationships serve merely to illustrate potential differences between CC and HTC, and [b] few farmers ever would maintain a management system wherein weeds were dense enough to express density dependence.)

Figure 6. Projected velvetleaf seeds in seed banks over 10 years in simulated HTC and CC. Initial values in year 0 were 100 plants that produced 2773 seeds.

In Figure 6, E and S were set at specific values, and the resulting seed bank numbers are dependent entirely on these values. If these values are altered, then seed bank sizes can change dramatically. One illustration of this is Figure 7. In this case, the rationale was to maintain velvetleaf seed b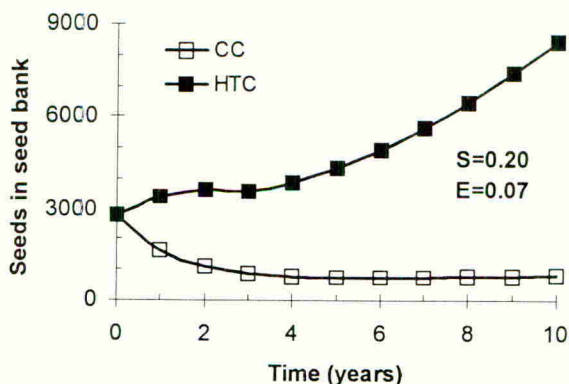anks at their initial levels (2773 seeds) despite varying E rates for both CC and HTC. The E values were varied according to values reported in the literature. These values ranged from 0.05 to 0.54. The y-axis in Figure 7 represents the inverse of S, that is mortality. In this example it can be conceived as the level of control from glyphosate plus natural causes for HTCs, and the control from glyphosate plus tillage plus natural causes for CCs necessary to maintain stable velvetleaf seed banks.
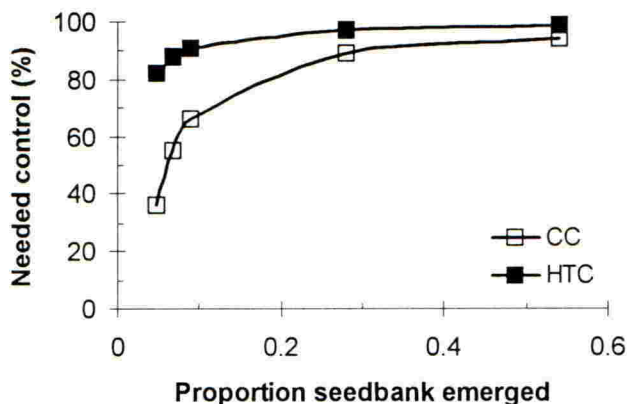
Figure 7. Velvetleaf control required to maintain a stable seed bank as proportional emergence from seed banks varies.

At least two important issues are apparent in Figure 7. First, as E rates rise, required levels of weed control increase accordingly for both HTCs and CCs. With high E rates weed control must be >90% consistently to maintain or reduce velvetleaf seed banks. In contrast, with very low values of E (Lindquist *et al.*, 1995a,b; Pacala & Silander, 1990), stable velvetleaf seed banks may occur even when control levels drop below 90%. The second issue is that HTCs always require a higher level of velvetleaf control than CCs to maintain a stable or declining seed banks.

The requirement for unwavering excellence in weed control in HTCs will place great demands on this crop management system. The requirement is due, in large part, not to HTC agronomy needs, but to its marketing strategy, which involves zero-tillage. At least in the USA, promotional efforts for HTCs, which have been aimed towards both farmers and policy makers, have emphasized the environmental benefits of HTCs as critical components of reduced tillage systems. Under more conventional tillage practices, the requirement for excellent weed control may be relaxed somewhat. Additionally, applications of the typically non-residual herbicides associated with HTCs must be accomplished in a timely manner. The timeliness has less to do with preventing crop yield losses than with stopping weed seed production and seed bank augmentation. Applications that are too early will be a weak link in the management chain for HTCs. Unlike more conventional systems where soil-applied herbicides may exert their effects over the course of several weeks, the residual effectiveness

of herbicides such as glyphosate is infinitely small. Applications of these chemicals must be made only after critical thresholds have passed. For velvetleaf, this threshold appears to be about 200 GDD after planting.

Velvetleaf is a relatively early-emerging species, and its control in HTCs probably will be adequate if timeliness thresholds are recognized and accepted. On the other hand, weeds that emergence late (*Amaranthus rudis*, *Ipomoea purpurea*) or that have an extended duration of shoot emergence (*Cirsium arvense*, *Elytrigia repens*) may prove to be the bane of HTCs. Identifying thermal time thresholds for non-residual herbicide applications for these species will not be as simple as that for species like velvetleaf, which emerge early and quickly. Consequently, seed banks of these late-emerging species, and attendant problems with weed control, may be expected to increase with adoption of HTCs.

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Herbicide tolerant crops and weed population dynamics in western Canada

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ABSTRACT

Both genetically modified and conventionally derived herbicide-tolerant canola varieties have been available on a commercial basis in western Canada for five years. Approximately 80% of the 5.6 million ha of canola grown in 1999 were herbicide tolerant. These new technologies have offered producers a means of controlling previously unmanageable weeds, controlling herbicide resistant weeds and diversifying cropping systems. Weed populations have been changed by these new modes of action within canola crops, but long-term changes in weed dynamics have not occurred. Controlling volunteer canola has become more complex. The potential for adverse changes in weed community composition exists if this technology becomes the dominant selection pressure acting on weeds due to the increased frequency of canola within rotations or the introduction of herbicide tolerant cereal crops. Changes are more likely to occur in reduced-tillage systems where there is a greater reliance on glyphosate and could compromise the sustainability of conservation tillage in the semi-arid regions.

INTRODUCTION

Weed community changes due to technological developments, such as herbicide tolerant crops, are not new. For example, the introduction of the combine harvester, 2,4-D, and reduced-tillage systems have all had an impact on weed community composition (Froud-Williams, 1988; Derksen *et al.*, 1993). The basis for technologically driven changes in weed community dynamics is selection pressure. If applied excessively, a weed management strategy will select for weeds not controlled by that strategy or for the development of resistance or avoidance. This is a problem if control measures for the resultant weed community are costly or do not exist. For example, many weeds in western Canada have developed resistance to herbicides when a single mode of action is applied on a regular basis (Morrison & Devine 1994), and multiple resistance has led to situations where few herbicide options exist for controlling common weeds.

Crops modified to be herbicide tolerant to non-selective herbicides have been tested in Canada for ten years and have been in farm usage for five. In Eastern Canada, herbicide-tolerant corn and soybeans are used in 10 to 20% of production. In western Canada canola is the only crop with herbicide tolerance. Cultivars are commercially available with resistance to glyphosate, glufosinate, and imidazolinone (imazethapyr +/- imazamox) herbicides. The former two were derived using genetic engineering and the latter from conventional means. Commercially they are marketed as Roundup Ready, Liberty Link and Pursuit Smart, respectively. Given the new

Table 1. Relative selectivity of herbicide tolerant* and conventional canola varieties (Manitoba Guide to Weed Control 1999).

	glufosinate*	glyphosate*	imazethapyr imazamox*	imazethapyr*	ethylfluralin
Setaria viridis	G	G	NR	G	E
Avena fatua	G	G	NR	F	G
Polygonum convolulus	G	F	NR	G	G
Seline noctiflora		G			
Stellaria media	G	G	NR	G	G
Galium aparine	G	G	NR	G	P
Taraxacum officinale		S			
Galeopsis tetrahit	G	G	NR		P
Kochia scoparia	G	G	NR		G
Chenopodium album	G	G	NR	P	E
Brassica kaber	G	G	NR	E	
Amaranthus retroflexus	G	G	NR	G	E
Agropyron repens	F	S			
Salsola pestifera	G	G	NR		P
Capsella bursa-pastoris	G	G	NR		
Polygonum persicaria	G	G	NR	G	
Thalaspi arvensis	G	G	NR	E	
Sonchus arvensis	G	S			
Cirsium arvense	F	S			
Triticum aestivum	F	G	NR	P	P
Hordeum vulgare	F	G	NR	P	F

E=excellent control under wide ranging conditions (depending on specific graminicde chosen), G=good control under mos. conditions, F=fair: control depends on conditions, P=poor control, S=suppression of perennial weeds, NR = registered but no ratings, empty cell=not registered. Based on rates of: 593 g ai/ha for glufosinate, 440 g ai/ha for glyphosate, 50 g ai/ha for imazethapyr, and 30 g ai/ha for imazethapyr plus imazamox (50:50)

weed management options provided by this technology, approximately 80% of the 5.6 million ha of canola grown in 1999 were herbicide tolerant (Harker 1999). The broad application of this technology has implications for weed community dynamics.

To understand the implications of herbicide tolerant crops in western Canada, it is important to be aware of canola production and agronomy. Canola has developed from a relatively minor crop on the Canadian prairies to become a dominant part of crop rotations. In many areas, canola comprises 30% of annually cropped land. The increase in production is primarily due to better economic returns for producers compared to cereals. Herbicide tolerant canola may be grown every 2-4 years on a field with extensive selection pressure placed on weed communities if the same herbicide/cultivar system is used repeatedly.

WEED MANAGEMENT IN CANOLA

Weed management in canola has always been key to producing economic yields (Blackshaw & Harker, 1992; Harker *et al.*, 1995). With few herbicides available in the early days of canola production, it was generally grown only on clean fields that had often been fallowed the previous year. Developments in weed control have included the dinitroanaline herbicides for grassy and broadleaved weeds, selective post-emergent graminicides for grassy weeds and volunteer cereals, clopyralid for thistle control, and ethametsulfuron for Cruciferae weeds. Combinations of these herbicides have provided options for broad spectrum weed control and improved yields (Blackshaw, 1989a & 1989b; Blackshaw & Harker, 1992). Although triazine tolerant canola was developed as a means of controlling Cruciferae species, the yield penalty associated with these cultivars has relegated them to a minor usage. The recent introduction of herbicide tolerant crops, particularly glyphosate and glufosinate resistant varieties, has provided growers with the ability to control or suppress previously unmanageable weeds in canola (Table 1) and new modes of action to control herbicide resistant weeds. Canola has become the "clean up" crop of choice for weedy fields, thereby intensifying the selection pressure imposed by glyphosate, glufosinate, and imazethapyr.

The development and adoption of reduced-tillage systems (Table 2) has led to canola production in dry areas of the prairies and greatly increased the area seeded to canola in western Canada. The benefits of soil moisture storage and reduced crop stress has resulted in the diversification of the semi-arid prairie region (Lafond & Derksen, 1996). Given the reliance of reduced-tillage systems on glyphosate, the introduction of glyphosate tolerant canola has increased the potential for changes in weed dynamics. If used to eliminate the pre-seeding application of a non-selective herbicide by seeding early and obtaining weed control from one in-crop application of glyphosate or glufosinate then selection pressure and herbicide usage is decreased. If used excessively, adverse changes in weed dynamics will occur.

Herbicide tolerant canola varieties provide a broader spectrum of weed control options than previously available herbicides, particularly for Cruciferae species (Table 1). Although glyphosate and glufosinate were initially developed as "non-selective" herbicides, they do not control all weeds or all weeds equally well, particularly at the lower rates used for weed control in herbicide tolerant crops. Common rates used in canola are about one quarter to one half of rates used in non-crop situations. In general, glufosinate does not control grasses as well as glyphosate and provides only "top-growth" control of perennials compared to control or suppression with glyphosate. Experience in reduced tillage systems has shown that glyphosate

Table 2.   Relative abundance and density of the twenty most common weeds in
            Saskatchewan cereal oilseed and pulse crops in 1995 (Thomas *et al.*, 1997).

Species	Relative Abundance (provincial basis)	Ave. Density /m^2 (provincial basis)	Ave. Density /m^2 (Field of occurrence basis)
Setaria viridis	50.4	9	16.8
Avena fatua	39.1	5.2	7.6
Polygonum convolvulus	31.3	2.5	3.9
Thlaspi arvense	21.8	2.7	6.8
Cirsium arvense	17.4	1.2	2.7
Chenopodium album	12.4	0.9	2.8
Sonchus arvensis	11.8	0.8	2.5
Salsola pestifera	9	0.8	3.4
Brassica kaber	8	0.6	2.7
Amaranthus retroflexus	7	0.4	1.9
Capsella bursa-pastoris	6.6	0.7	4.3
Brassica napus	6.6	0.7	5.1
Kochia scoparia	5.2	0.3	2.3
Taraxacum officinale	5.1	0.2	1
Agropyron repens	4.6	0.6	5.6
Galium aparine	4.4	0.4	4.1
Equisetum arvense	3.9	0.5	5.1
Euphorbia seryllifolia	3.6	0.3	4.7
Sapronaria vaccaria	3	0.2	3.1
Triticum aestivum	2.9	0.2	2.4

Relative Abundance=relative frequency + relative field uniformity (all fields) + relative mean
field density.

provides inadequate control of *Polygonum convolvulus*, misses weeds such as *Malva pusilla* and has difficulty controlling overwintered *Erigeron canadensis*, *Crepis tectorum*, *Matricaria maritima*, *Hordeum jubatum*, and *Taraxacum officinale*. Therefore, continued usage of one of these products for weed control in canola will change weed communities. Different weed management strategies will be needed in subsequent crops to ensure that problem weeds do not become dominant. Combinations with conventional herbicides can be used to increase the number of weeds controlled in herbicide tolerant canola.

When the spectrum of weeds controlled by the herbicide/cultivar systems is compared to the list of common weeds (Table 2), changes in weed composition and dynamics can be anticipated. Prior to the introduction of ethametsulfuron and herbicide tolerance, crop rotations with canola had high levels of Cruciferae weeds (Brandt, 1989). Given the increased level of Cruciferae weed control with all three herbicide tolerant canola types, there is potential for *Thlaspi arvense*, *Capsella bursa-pastoris*, and *Brassica kaber* to become less abundant. Furthermore, imidazolinone-canola provides options to control *Galium aparine* and *Erodium cicutarium* which may also decrease relative to other species. The abundance of perennial weeds is not likely to change given the suppression/top-growth control nature of glufosinate and glyphosate at rates used in canola. Grass weeds and volunteer cereals have been easily controlled in canola and other crops, but are still relatively abundant compared to other weeds, therefore, it is unlikely that they will become less abundant.

Weed management implications arise from agronomic differences among the three herbicides/cultivar systems. Given the soil persistent nature of some of the imidazolinone herbicides, post-emergence application provides early removal of weeds and controls late germinating Cruciferae species thereby maximizing yield potential (Harker *et al.*, 1999) and reducing seedbank contributions of late emerging weeds. Glyphosate, a less expensive herbicide, is registered for two applications in canola. Consequently, producers get early removal of weeds to maximize yield and can control late emerging weeds, especially perennial broadleaf species which tend to emerge after annual weeds in early spring sown canola. Glufosinate resistant hybrid varieties are available and appear to compete more vigorously with weeds. When coupled with the relative selectivity of the herbicides, these agronomic factors can contribute to integrated weed management and the management of difficult to control species, thereby reducing adverse weed community changes.

HERBICIDE RESISTANT WEEDS AND VOLUNTEERS

Herbicide resistance has become a large problem in western Canada with resistance occurring in *Avena fatua*, *Setaria viridis*, *Brassica kaber*, *Sonchus asper*, *Stellaria media* and other common weeds. Since glufosinate and glyphosate represent new modes of action, they are frequently used to manage existing resistence problems, reducing the densities of these species. However, over usage of herbicide tolerant canola has the potential to select for resistant and multiple resistant weeds. Species with high densities, such as of *A. fatua* and *S. viridis*, and those susceptible to imidazolinone herbicides, such as *S. media*, *Kochia scoparia*, and *Salsola pestifera* are likely candidates. Selection pressure is particularly acute with glyphosate in conservation-tillage systems where it is often used as a pre-seeding treatment for general weed control, a pre-harvest treatment for perennial weed control, and as a post-harvest treatment to control winter annual and perennial weeds. These concerns are also expressed in Australia where a similar production system exists (Felton *et al.*, 1999). Furthermore, selection pressure for resistance will

Table 3. Percentage change in land management practices (million ha) in western Canada from 1991 to 1996 (Census of Agriculture)

	Manitoba	Saskatchewan	Alberta
area incorporating crop residues ("conventional tillage")	-10.4% (2.5)	-27.0% (6.1)	-25.4% (4.3)
area retaining crop residues on soil surface ("minium tillage")	-9.9% (1.1)	31.9% (4.4)	29.0% (2.5)
no-tillage	70.4% (0.4)	116.9% (3.0)	215.3% (0.8)

increase with the imminent release of glyphosate resistant wheat making it possible to continuously apply glyphosate in a rotation of cereals and canola. Although genetic drift of herbicide tolerance from canola to weedy relatives is thought to be a remote possibility, should it occur it will further complicate weed management for producers, particularly those with reduced tillage systems.

In the short-term, volunteer herbicide tolerant canola may be a bigger problem than the development of weed resistance. Canola has been shown to have dormancy (Pekrun *et al.*,1998) and can be a weed problem for several years after canola production. This has been a particular problem with glyphosate tolerant canola in reduced-tillage systems. Controlling volunteer herbicide tolerant canola has not been a great expense for producers; however, controlling volunteer glyphosate tolerant cereals will likely be expensive. Apart from immediate agronomic problems due to volunteers within a field, genetic drift of the herbicide tolerant trait into the field margins of neighbouring conventional canola fields has created unexpected weed problems. Problems may arise for producers unaware that they need to change their herbicide selection for controlling volunteer canola on field margins, for organic crops where transgenes are prohibited, and for producers of Identity Preserved (IP) canola varieties, especially if the crop is destined for GMO (genetically modified organism) free countries.

Changes in weed dynamics may come from a production system change facilitated by herbicide tolerant canola. Due to harsh winter conditions in western Canada, winter canola cannot be produced and winter wheat can only survive when seeded into standing stubble to catch a layer of insulating snow. Therefore, the production systems are dominated by spring crops and high densities of annual spring weeds. To reduce the densities of these weeds, a more varied cropping system, including winter crops, is required. Fall-seeded dormant canola has been pioneered by Kirkland & Johnson (1999). Spring canola is seeded very late in the fall, remains dormant over winter and germinates in the spring. Initial efforts failed due to difficulties controlling winter annual weeds. The use of herbicide tolerant canola varieties have solved this problem. This system has increased canola yields particularly in dry seasons/areas and canola can be harvested in time for winter wheat seeding. The potential for two years of winter crops rotating with traditional spring crops would vary selection pressure on weed communities and reduce the dominance of the many common weeds (Table 3). While the same herbicides would be applied in the dormant seeded canola, the weed community present would be different, thereby reducing the likelihood of resistance development and adverse weed community shifts.

CONCLUSION

Is the potential impact of herbicide tolerant crops on weed dynamics different than past introductions of highly selective technologies, such as combine harvesters or triazine herbicides? It will depend on the intensity and frequency of the selection pressures exerted on weed communities. If the different herbicide/cultivar systems are rotated within a field over time and problem weeds are managed in intervening years, adverse changes in weed communities should not occur. To date, no dramatic shift in weed species has happened in western Canada, but the control of volunteer canola has become more complex and its persistence within fields can create problems for producers. Short-term differences within a crop occur due to differences in selectivity among the herbicides. Positive and negative long-term changes could develop. Using herbicide tolerant canola to manage current resistance problems and to diversify cropping systems will reduce the dominance of certain problem species. Producers have seen these

benefits already. Overuse of the technology, particularly if herbicide tolerant wheat is introduced, will increase selection pressure and lead to weed populations resistant to these new modes of action, and/or to weed community changes towards species not controlled or poorly controlled. The issue is particularly real for glyphosate dependent reduced-tillage producers and may jeopardize the sustainability of annual-cropping systems in semi-arid regions.

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Weed species shifts in response to broad spectrum herbicides in sub-tropical and tropical crops

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ABSTRACT

Weed species shifts in response to broad spectrum herbicide use in cotton, maize, rice, citrus and rubber and oil palm plantations are reviewed using data from long term studies available from the literature. Broad spectrum herbicide use has changed the composition of the weed flora in all of these crops. In maize and cotton, zero tillage regimes have resulted in successional changes towards ephemeral broadleaf weed species. Shorter term shifts and cyclical changes in abundance of weeds have been documented in citrus and in oil palm and rubber plantations; in the latter the response of perennial grasses to non-selective herbicides is strongly influenced by mulching. In irrigated rice, weed species shifts (species composition and abundance) are rapid and responsive to both method of crop establishment and herbicide use, competitive release being one mechanism by which relative abundance is altered. The absence of sufficient knowledge of life histories of tropical and sub-tropical weeds means that it is difficult to speculate on the impact of long-term use of non-selective herbicides in resistant crops on the weed flora and emphasises the need for experimental assessment.

INTRODUCTION

By their very nature, broad spectrum herbicides and mixtures of herbicides have found favour with farmers for crop protection from the damaging effects of weeds. Well known responses of a weed flora to chemical and cultural control measures include changes in composition towards weed species naturally tolerant to the means of control (inter-specific selection on ecological time-scales) and the evolution of herbicide resistance (inter-genotypic selection on evolutionary time-scales). Commonly, the lack of complete selective control of weeds within a crop has resulted in increases of intransigent or noxious weeds, often highly competitive and possessing fitness traits which confer persistence. Crops resistant to non-selective herbicides such as glyphosate and glufosinate therefore offer considerable inherent advantages in future weed control programmes. The advent of such crops (transgenic or non-transgenic) resistant to broad spectrum herbicides comes with the implicit corollary that these herbicides may be used serially, either within or over cropping seasons in monoculture cropping and in crop rotations. Farmers may use the same herbicide in seed-bed preparation, as well as during crop establishment and later crop growth. In consequence, the processes of inter-specific and inter-genotypic selection in weed communities and weed species respectively may be intensified.

High cropping intensity is a feature of sub-tropical and tropical crops and cropping systems are as complex as they are diverse, particularly where cereal crops have a predominant role (Beets, 1990; Castillo, 1995). On an area basis, irrigated monoculture rice exemplifies one of the most intensively cropped cultivation systems, in global terms (Greenland, 1997). In the tropics, a typical farm in the Mekong Delta is 1.1 ha in size, approximately 80% of the area being devoted to rice where three crops may be grown annually giving average yields of 5.8, 4.1 and 4.4 ton ha^{-1} in the dry, wet and spring–summer seasons, respectively (Xuan & Matsui, 1998). At the other end of the continuum, oil palm and rubber plantations in Malaysia and Indonesia may yield continuously over a period of 20 to 25 years (Tjitrosemito, 1996). Contrastingly, in the sub-tropics where both temperature and radiation imparts seasonality, near continuous cropping, with short fallow periods, is often achieved by crop diversification as for example in the extensive rice-wheat systems of the Indo-Gangetic plains (Paroda *et al.*, 1994).

Omnipresence of weeds is therefore a feature of these agroecosystems (Akobundo, 1987) and not surprisingly, the weed flora in the tropics and sub-tropics is voluminous given the diversity of cropping practices. Moody (1989) noted for instance that over 1800 plant species have been reported as weeds of rice in Asia and representatives of all of Raunkier's (1934) life forms are evident as weeds, although not in every ecosystem. Herbicide use is rapidly increasing as an inevitable consequence of labour shortages (Labrada, 1996; Naylor, 1996) but the rate of adoption in developing countries is governed by a variety of external factors and not solely the marginal benefit–cost ratio in any given crop (Terry, 1996). Chemical weed control is extensively used in particular countries in a wide range of crops including irrigated rice, maize, wheat and cotton and permanent plantation crops.

Herbicide use for weed management typically results in weed species shifts (changes in weed community composition) over cropping seasons. These changes may either be cyclical and reflect resilience in the weed community to management or reflect succession, the non-seasonal, directional continuous patterns of colonisation and extinction on a site by species populations. Many authors have emphasised the importance of temporal and spatial scales in considering community stability and succession and the importance of long term studies. This is equally true for weed communities in tropical and sub-tropical crops in which the responses of the weed flora may be expected to be rapid, given multiple crops per year and short generation times in weed species. In this respect they provide valuable opportunities to assess successional events in relation to weed management.

In this paper we briefly review evidence from the literature that attests to the nature and pattern of weed species shifts in response to the use of non-selective and broad spectrum herbicides. In conclusion, we speculate on the possible ecological implications for the long-term use of crops resistant to broad spectrum herbicides.

SEASONAL CROPS

Cotton, maize and rice provide three crops in which the weed flora has been observed to exhibit marked changes in community composition over seasons in response to weed management.

Pu *et al.* (1995) examined changes in weed community composition in a cotton-chinese milk vetch rotation in southern China under two contrasting management regimes. Conventional inversion tillage practices, wide row cotton spacing (24 x 70 cm), crop residue removal and mechanical weeding (regime 1) was compared with a second regime of zero tillage (glyphosate), narrow spacing (15 x 33 cm), crop residue retention and use of post-emergence herbicides (fluometuron, alachlor). These regimes were applied to six sites for three years and then for a further four years with the omission of chemical weed control in regime 2. Yields over the six years were consistently higher under regime 2 (mean 1.15 ton ha^{-1} ginned cotton) than under regime 1 (mean 0.94 ton ha^{-1}). In the first cropping season, the weed flora was dominated by grasses (*Digitaria ischaemum* (Schreb.) Schreb, *Eleusine indica* (L.) Gaertn., *Setaria glauca* (L.) Beauv. and *Paspalum distichum* L.) and *Cyperus rotundus* L. with similar overall mean weed densities (470 plants m^{-2}, census taken mid-season) in regimes 1 and 2 respectively. After six cropping seasons in regime 1, weed abundance was again similar and the weed community composition had not altered from that in the first season. In the zero tillage regime, three relatively short-lived, annual broadleaf species predominated (*Phyllanthus urinaria* L., *Portulaca oleracea* L. and *Mollugo pentaphylla* L.) ; other species were rare. Despite these differences in weed flora the proportional yield difference between regime 1 and regime 2 in years 1 and 6 was unaltered.

An even longer cropping trial was conducted in maize by Utomo & Susanto (1997) who followed the effects of conservation tillage practices on weed dynamics in Sumatra over 21 cropping seasons. A no tillage (NT) practice, (4.8 kg a.i. ha^{-1} glyphosate, in the first year and one third of this rate in subsequent years) was compared with minimum tillage (MT) (involving initial manual and chemical removal of *Imperata cylindrica* L., followed in subsequent years by surface cultivation and manual weeding, residues being left on the surface) and with intensive tillage (IT) (seasonal, weed and crop residue removal after ploughing). After 21 maize crops, yield differences were not detected amongst these practices, and weed communities differed marginally in overall composition, but marked differences occurred in relative abundance of species. In all treatments, *Euphorbia geniculata* L. had the highest or second highest dominance ranking, and broadleaf species predominated under NT. Contrastingly under IT the grasses *Echinochloa colona* (L.) Link, *Setaria plicata* (L.) P. Beauv. and *Digitaria sanguinalis* (L.) Scop were ranked in the upper third of the hierarchy and under MT, *I. cylindrica* was the second dominant species. In IT and NT, either one or two species (*E. geniculata* and/or *Richardia brasiliensis* (Moq.) Gomez) each achieved a relative abundance of more than 25% in the community, whereas *E. geniculata*, *I. cylindrica* and *Bidens pilosa* L. together contributed to more than 50% of relative abundance in MT.

It is well known that water constitutes a powerful, selective herbicide in irrigated rice. Figure 1 indicates the composition of the weed community of irrigated transplanted rice fields in Kemubu, Malaysia in 1989 and the corresponding community after wide scale adoption of direct seeding by 1993. Field surveys were conducted in each year, the same farmers' fields being revisited each time at which samples from a minimum of six randomly chosen 1 metre quadrats were taken 60 days after seeding/transplanting (DAS/DAT) (Azmi and Mashor, 1995). A total of 46 species was recorded in 1989 in transplanted rice, semi-aquatic and aquatic species predominating in a community, logarithmically distributed in terms of species abundance. The practice of direct seeding of rice onto saturated puddled soil with subsequent flooding 10 – 12 DAS resulted in the inclusion of 21 new species to the community and the
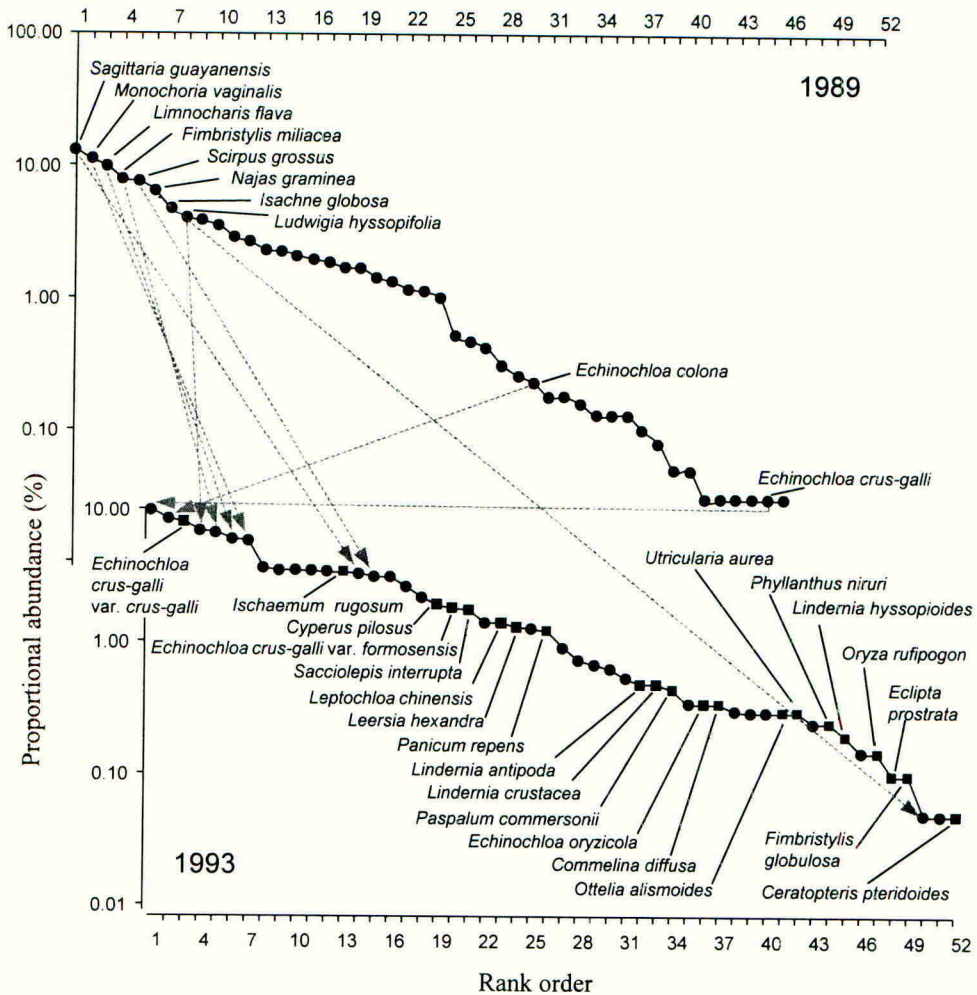
Figure 1. The change in weed species composition in farmers' rice fields in Kemubu, Malaysia as a result of the change from transplanting (1989) to direct seeding (1993) of rice. Species are ranked in order of proportional abundance based on area coverage in 1m² quadrats, sample sizes of 56 (1989) and 103 (1993). Species not present in 1989 are indicated by squares in the 1993 abundance curve. Data from Azmi and Mashor (1995).
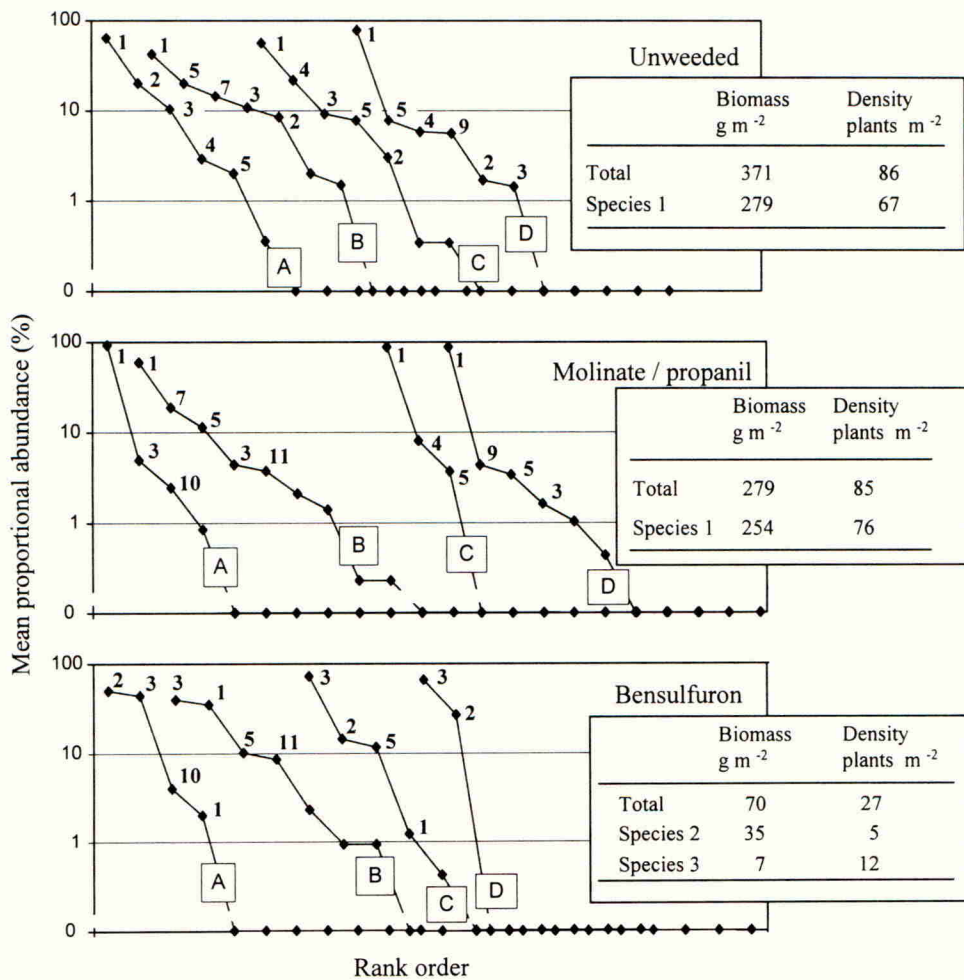
Figure 2. Rank abundance curves of weed communities in wet seeded rice in relation to herbicide treatment over four cropping seasons, A : 1996 / 97; B : 1997; C : 1997 / 98; D : 1998. Ranks are based upon counts of weed density taken 60 days after seeding in 8 random 1 m ^{2} quadrats. Molinate / propanil (5 l product) and bensulfuron (0.05 kg a.i. ha $^{-1}$) were applied 10 days after seeding. Rice was sown at 80 kg / ha. Tabulated data for biomass and density refer to the 1998 cropping season.

Species recorded and codes :

1 *Monochoria vaginalis*; 2 *Echinochloa crus-galli*; 3 *Scirpus grossus*; 4 *Scirpus juncoides*; 5 *Paspalum vaginatum*; 6 *Ludwigia hyssopifolia*; 7 *Fimbristylis miliacea*; 8 *Leptochloa chinensis*; 9 *Sagittaria guayanensis*; 10 *Limnocharis flava*; 11 *Cyperus iria*. Not all species indicated. (Unpublished data, Azmi and Mortimer).

exclusion of 15 others. A dramatic change in dominance of species was evident, however, with *Echinochloa* species displacing the three dominant species *Sagittaria guayanensis*, H B K, *Monochoria vaginalis* (Burm f) Presl and *Limnocharis flava* (L.) Buchenau in transplanted rice. One of the rarest species, *E. crus-galli* under transplanting became the commonest under direct seeding whilst *Najus graminea* (non Del) Ridl became exceedingly rare. It should be noted that not all farmers were practising direct seeding in 1993, so that some species present solely under transplanting may be represented in 1993 and, conversely, some may be absent because of low sample size. Differences in weed management practices were unrecorded.

Figure 2 illustrates the changes in abundance of weeds under two herbicide applications in replicated trials in wet directed seeded rice over four seasons (data selected from an ongoing experiment, Azmi & Mortimer, unpublished). Communities were depauperate (11 species in total) in comparison to those described above as a result of previous on-station land use, but homogeneous over the area studied prior to the start. Unweeded plots developed a weed flora in which *M. vaginalis* predominated and there was a progressive decline in abundance of *E. crus-galli* and *Scirpus grossus* L. f. over four cropping seasons, some species recorded prior to the experiment being absent. The use of bensulfuron (broad spectrum, sedge and broadleaf herbicide) rapidly reversed this dominance and resulted in a significant exclusion of weed species. Four seasons of continuous use of molinate and propanil retained the dominance of *M. vaginalis* and relegated most other species to low abundance and excluded *E. crus-galli*. By the fourth season, total weed (dry) biomass (60 DAS) was reduced by both herbicide applications and greater than 5 fold with bensulfuron, a three fold reduction in weed density being observed under this treatment. Rice yields ranked by treatment were ordered bensulfuron > molinate+propanil > unweeded.

PERENNIAL CROPS

Major perennial cropping systems in the tropics and sub-tropics include rubber, coconut and oil palm in addition to citrus. Large scale plantation of tree crops, often involves the utilisation of cover crops in strips between crop rows with bare or mulched soil surfaces between them. In both cases habitat heterogeneity exists in terms of areas of open ground and of disturbance frequency and the potential diversity of the weed flora is therefore very large. Tjitrosemito (1994) noted that the list of common weeds in rubber plantations includes 96 species and sub-tropical perennial citrus orchards may have an equally long species inventory (Ito & Ueki, 1979).

Weed management is essential in citrus crops in Japan since perennial weeds may invade from uncultivated banks on the typical steep slopes of orchards and result in yield loss (Ito *et al.*, 1975). In a three year trial Ito and Ueki (1979) examined the impact of systematic spraying of three different herbicide combinations on the changes in weed community in comparison with a regular mowing sequence (Table 1). Predictably weed cover was lowered with herbicide use, the greatest reduction occurring with the use of residual herbicide. Total weed cover showed a cyclical change, increasing during summer and decreasing over winter. The amplitude of this fluctuation was greatest in the mown treatment and least under bromacil and dichlobenil. The reduction in weed cover was associated in all herbicide treatments with a decrease in percentage cover by annual species at the start of each season (April). At the end of each year (October), however, an increase in the % cover by annual species was commonly

Table 1. The response of the weed flora to herbicide combinations and to mowing over a three year period in a satsuma citrus orchard. Spray applications were made in mid April, mid July and early October from 1976 - 1978. Mowings were made at the same time and additionally in early June. Data presented for April and October (1976-1978) are prior to herbicide application and taken from 0.75 m^{-2} plots. (Data from Ito & Ueki, 1979).

Treatment	Attribute	Years of treatment application (3 application yr^{-1})							
		1975	1976 April	Oct.	1977 April	Oct.	1978 April	Oct.	1979 April
Mown									
	% weed cover	22	24	93	48	89	50	91	61
	% cover by annual species		25	18	10	13	19	4	13
	Number of species		42	51	25	43	34	22	33
Paraquat and propanil+carbaryl (0.75 and 5.0+1.0 kg ha^{-1} ; contact)									
	% weed cover	16	30	43	11	60	24	45	30
	% cover by annual species		32	61	36	54	16	39	18
	Number of species		44	53	50	65	44	50	47
Asulam and ametryn (3.0 and 3.0 kg ha^{-1} ; systemic and residual)									
	% weed cover	18	15	50	11	45	32	45	31
	% cover by annual species		45	71	36	34	16	29	38
	Number of species		56	21	41	44	19	38	35
Bromacil and dichlobenil (2.0 and 5.36 kg ha^{-1} ; residual)									
	% weed cover	16	7	21	7	35	15	37	28
	% cover by annual species		20	32	13	2	4	4	14
	Number of species		42	41	15	23	6	35	40

recorded except under continual mowing and residual herbicide treatment. On average, the total number of weed species was consistently higher under contact herbicide application. After termination of herbicide treatments in the third year, the number of species present in the following April (1979) was similar to that observed in the previous October on all herbicide treated plots but significantly elevated in plots previously treated with systemic / residual herbicides. During the course of this experiment the dominant perennial weeds were *Pueraria lobata* Ohwi, *Miscanthus sinensis* Anderss and *Solidago altissima* L., being most abundant under bromacil and dichlobenil. The principal summer annuals were *Erigeron* species and *Digitaria adscendens* L. .

Weed management in rubber and oil palm plantations is primarily an issue of vegetation management. A system of planned and responsive activities is followed to promote rapid establishment of the crop and subsequent canopy dominance and a low under-storey of vegetation. Ideally this functions to halt soil erosion, biologically fix nitrogen and prohibit invasions of weeds species that compete strongly for water and nutrients in young

plantations (Madkar and Kuntohartono, 1986). Chee (1990) has estimated that 24% of the total replanting cost of a rubber plantation is expenditure on weed control prior to production starting. Within Asian countries, there is often similarity in the weed flora in these two plantations and nurseries and immature plantations are particularly vulnerable to weed invasion by perennial grasses (*I. cylindrica* L. and *Ischaemum* species) and shrubs (e.g. *Chromolaena odorata* L.).

The potential for biomass production by *I. cylindrica* is well known. In unshaded mature stands, populations can exhibit shoot densities of 600 m^{-2} with an above ground biomass of 11 tons ha $^{-1}$ and an underground rhizome biomass which can reach 7 tons ha $^{-1}$ (Soerjani, 1970). In field experiments, Eussen (1980) measured an intrinsic rate of shoot production of approximately one shoot and at least two rhizome buds per week. These statistics emphasise the propensity for population increase which arises through clonal growth, rhizome fragmentation as well as through prolific seed production. Imazapyr, glyphosate and glufosinate ammonium offer chemical control options of which imazapyr is the most effective (Brook, 1989). Typically, regular applications of these herbicides are required to exhaust the bud bank of perennial grasses to prohibit re-growth of shoots.

Immediate responses of the other weed components in the flora to single applications of each of these three herbicides to *I. cylindrica* have been recorded in open grassland and in an oil palm plantation. In open grassland, removal of *I. cylindrica* with glyphosate (1.65 kg a.i. ha^{-1}) and with glufosinate ammonium (3 kg a.i. ha^{-1}) resulted in a significant increase

Table 2. Changes in weed coverage and composition in an oil palm plantation over a three month period. Data from Wiroatmodjo & Utomo (1990).
Treatments: 1, Untreated check; 2, Manual removal of above ground biomass; 3, Paraquat (2 l ha^{-1}), dead biomass retained as a mulch; 4, Manual removal of above ground biomass followed by ametryne 80 WP (2.2 l ha^{-1}); 5, Ametryne (2.0 l ha^{-1}) and paraquat (1.0 l ha^{-1}).

		Treatment				
		1	2	3	4	5
Rate of change in weed coverage after application of treatment (% month $^{-1}$)		0	26	1	14	12
Rate of change in weed dry weight after application of treatment (g month $^{-1}$)	*Ottochloa nodosa*	-3	0	8	0	0
	Ischaemum timorense	10	15	6	2	2
	Mikania micrantha	4	0	0	0.5	2
	Paspalum conjugatum	-	5	1	1	2

Relative dominance (%) of weeds at the start of the experiment	*Ageratum conyzoides*	6.8	*Ischaemum timorense*	17.4
	Axonopus compressus	7.6	*Mikania micrantha*	6.2
	Borreria latifolia	3.9	*Ottochloa nodosa*	18.5
	Chromolaena odorata	3.7	*Panicum repens*	3.7
	Imperata cylindrica	4.3	*Paspalum conjugatum*	8.1

(mean 77 plants m^{-2}) in plants of broadleaf species and a much lesser increase (mean 10 plants m^{-2}) in the number of grass plants, when examined sixteen weeks after treatment (Mohamad & Hock 1990). A similarly low increase in broadleaf species was recorded with imazapyr (0.75 kg a.i. ha^{-1}) together with a small decline in grasses.

Studies in oil palm plantations by Wiroatmodjo & Utomo (1990), indicate the importance of biomass residues in determining weed species response after herbicide treatment (Table 2). Manual removal of above ground biomass substantially encouraged *Ischaemum timorense* Kunth. regrowth from below ground rhizomes and halted increase in *Ottochloa nodosa* (Kunth.) Dandy; however paraquat and mulching encouraged both species, the rate of overall weed coverage being significantly delayed. The use of the triazine, ametryne, with or without prior manual removal of weed biomass, promoted rapid weed coverage selecting for *I. timorense*, *Mikania micrantha* Kunth. and *Paspalum conjugatum* Berg. In rubber plantations, Yeoh & Pushparajah (1976) found that manual removal of *I. cyclindrica* led to rapid invasion of *M. micrantha*, *Mikania malabathricum* and *C. odorata*. Contrastingly repeated use of glyphosate resulted in a dominance of broadleaf weeds including *Borreria latifolia* (Aubl.) Schum, *Ageratum conyzoides* (L.), *Cleome ciliata* DC., *Asystasia intrusa* (L.) and *Mimosa pudica* L.

DISCUSSION

Cousens & Mortimer (1995) remarked on the lack of detailed long-term studies of the dynamics of weed communities and emphasised the importance of manipulative experimental studies to expose mechanisms underlying weed species shifts. This paper reaffirms this view for the tropics and sub-tropics. Understanding the processes underlying weed species shifts is particularly important in determining both the long term sustainability of a given weed management practice and for designing integrated weed management practices that optimise herbicide use and prevent evolution of resistance to a particular herbicide (Mortimer, 1998).

Succession is a scale dependent phenomenon and changes to weed communities as a result of weed management may simply be anthropogenic constructs which retain community resilience. In Asia, seasonal switching between a diverse terrestrial vegetation in dry season crops and a much altered aquatic and semi-aquatic flora in the wet season rice crop on the same area of land over time is a common occurrence (Moody, 1983). This supports the view that rice weed communities in farmers' fields are seasonally arrested primary autotrophic successions from a common seed bank. Figure 1 illustrates that a change in crop establishment method can result in a rapid change in weed community composition with weed species replacement and additions. This shift may be perceived as within field succession. However a number of factors support the argument that weed communities at the farm level are primarily a consequence of habitat manipulation in a heterogeneous landscape within dispersal distance of most weed species. These include a) the persistence of substantial, floristically diverse, seed banks in irrigated rice fields (Sahid *et al.*, 1995), b) the fragmented landscape of rice agriculture simultaneously offering terrestrial (bunds), aquatic (irrigation channels) and semi-aquatic (drainage channels) habitats for weed growth (Schoenly, 1998), and c) the occurrence of multiple vectors for dispersal of weed propagules (both biotic and abiotic - irrigation water). Pre or early post-emergence herbicides may dramatically alter relative abundance of individual species (Figure 2) by selective prohibition of seedling

recruitment and by subsequent alteration of competitive inter-relationships within the flora. *E. crus-galli* occupied a low dominance position in unweeded plots but assumed dominance together with *S. grossus* when *M. vaginalis* and other broadleaf species were removed with bensulfuron. The role of *Monochoria* in competitively displacing *S. grossus* is strongly suggested from its lowered dominance when *Echinochloa* was selectively removed with molinate/propanil.

Results from the study of Ito & Ueki (1979) in citrus orchards support the earlier findings of Mahn and Helmecke (1979) that overall species composition may remain unaltered by herbicide use, although short term species dominance relationships may be changed. Indeed, the use of contact herbicide (paraquat) increased the diversity of annual weed species. Conversely the observations in maize (Utomo & Susanto, 1997) and in cotton rotation (Pu *et al.*, 1995) suggest that weed succession may indeed occur given unaltered cropping practices over time. In both cases, zero tillage resulted in dominance of short-lived broadleaf weed species, associated in the case of the cotton rotation with a recorded (Pu *et al.*, 1995) substantive decline in the size of buried soil seed banks. Some of these broadleaf species (e.g. *Portulaca oleracea*) are reported to have little or no seed dormancy and freely germinate on the soil surface, whilst decaying *in situ* when buried by tillage. Directional change in weed composition may arise through this means but contingent upon the exclusion of competitive grasses. Equally important is the role of weed and crop residues acting as a mulch which in turn selectively alters the habitat for seed germination and weed growth (Table 2).

Consideration of the ecological responses by weed species to herbicide use is important in evaluating the role and use of herbicide resistant crops especially in the tropics. However it is only possible to speculate on the long-term consequences of the impact of non-selective herbicides on the weed flora, since appropriate knowledge of the life histories of perennating and seed producing species is largely absent. Non-selective herbicide use during early establishment and growth of a resistant crop may result, through competitive release, in the occurrence of ephemeral, weed species which can complete their life cycle during later crop growth and maturation. The broadleaf species, *Phyllanthus urinaria*, *Portulaca oleracea* and *Mollugo pentaphylla* mentioned earlier in conjunction with zero tillage in cotton possess such life histories. Whilst such species may have no deleterious effects on yield, their prolific seeding will predicate the continued requirement for herbicide use at crop establishment in subsequent cropping, even though the seed bank of other species may be expected to decline. Similarly, increase in rapidly growing rhizomatous grass species which express tolerance to non selective herbicides because of regrowth from bud banks may necessitate routine herbicide applications. It is interesting to note that *Paspalum vaginatum* retained an intermediate dominance in both unweeded and herbicide treated plots in direct seeded rice (Figure 2) although absent in some seasons. Shade tolerance and regrowth from vegetative parts are potential traits which may allow this stoloniferous species to persist in a rice crop and become competitive at later stages if not otherwise controlled.

Summarisation of these studies lead us to an oft-quoted conclusion, namely that the assessment of new weed control technologies requires a strategic dimension beyond the immediate impact of economics and efficacy. This is equally true for 'total' weed control options with non-selective herbicides in resistant crops. Whilst weed species shifts may not be as rapid as seen to date with selective herbicides, in the tropics and sub-tropics it is likely that the flora will respond through interspecific selection of short-lived annual species and for

perennating species. Whether or not these assume damaging levels with a crop will depend in part on the frequency of herbicide use during the cropping season. Whilst perhaps not as a pressing concern as the issues relating to gene flow in the deployment of transgenic crops, assessment of the nature and likelihood of weed species shifts is an important component of environmental impact analysis and stewardship of this technology.

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