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An emerging system management approach for biological weed control in crops: *Senecio vulgaris* as a research model

H. MÜLLER-SCHÄRER AND J. FRANTZEN
Institute of Plant Biology, University of Fribourg, Pérolles, CH-1700 Fribourg, Switzerland

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Summary

A 'system management' approach of biological weed control in crops is proposed and compared with other methods of biological weed control. It is based on the management of a weed pathosystem in order to maximize the natural spread and disease severity of a native or naturalized pathogen. This approach may be well-suited to situations where it is necessary to control single weed species in crops, and where no immediate and complete control is required, the production of large amounts of the agent is rather limiting (e.g. when using biotrophic fungi), and/or the importation of an exotic agent is not possible. This strategy provides fundamental knowledge of underlying mechanisms of crop production systems and is aligned with the view of modern agro-ecology, in which complete eradication of weeds is not desirable. The fundamental research required for a successful application of the 'system management' approach will be illustrated with the biological control project of *Senecio vulgaris* L. using the naturalized rust fungus *Puccinia lagenophorae* Cooke. A five-step procedure, together with selected results, will be presented. Main emphasis is given to the infection window, the study of the genetic structure of the plant and pathogen population, and the management of the infection conditions (a) to maximize the spread of the disease and the impact on the plants, and (b) to minimize the development of resistant plant populations. Joint application of herbicides at low doses, additional necrotrophic pathogens, and of biochemicals interfering with the weed's defence also will be envisaged, as well as their integration into general pest control practices. In this regard, biological weed control agents have to be seen as stress factors, not as weedkillers, and biological weed control as an integral part of a well-designed pest management strategy, not as a sole cure.

Changing weed control requirements in crops imply changing the biological control approach

The advent and early success of chemical herbicides has stimulated the idea of crop production in a weed-free environment, and up until recently, the clean-crop option has been the ultimate aim of weed control. Resulting environmental contamination, difficulties in controlling specific weed species and increasing consumer pressure against all pesticide use have contributed to a re-examination of weed control strategies. Situations where it is necessary to control single weed species in crops are manifold (Gressel *et al.* 1996), and the use of biological control as a direct replacement for or supplement to existing chemical control has become attractive. To satisfy the demands for rapid and complete weed control, the inundative method of biological control (see below) has been developed. This has resulted in the commercial production of some fungal pathogens as mycoherbicides. Used like conventional herbicides, they can be applied when and where a specific weed problem occurs, with the aim of directly killing the target weeds (Hasan & Ayres, 1990).

Today, the protection of biodiversity is becoming a key component in developing sustainable agro-ecosystems. Various studies have shown the ecological importance of increased species diversity, for example of companion plants interfering with pests and pathogens of the crop (Müller-Schärer & Potter, 1991; Theunissen, 1994). Thus, complete eradication of non-crop plants is clearly not compatible with modern views of agro-ecology. Changes in the attitudes of consumers towards an environmentally friendly agriculture that question yield maximization as the only objective have greatly supported this other view on 'weeds' (Müller-Schärer, 1995). In this respect, the 'clean crop' option is slowly being replaced by an approach that understands weed control as the management of the crop's environment (Watson, 1992). Non-crop plants will only need to be controlled down to the level where they are no longer the cause of an economically defined negative impact. With regard to target weeds, this may be achieved by infection with a pathogen causing a sub-lethal effect on the host, and by exploiting subsequent reduction of competitiveness.

In this paper, a 'system management' approach to biological weed control in crops is proposed that takes the described changes in weed control requirements into account. The approach is based on the management of a weed pathosystem, in order to maximize the natural spread and disease severity of a native or naturalized pathogen.

The system management approach as compared with other methods of biological weed control

In the inoculative or 'classical' approach of biological weed control, an introduced (exotic) control agent is merely released over a small area of the total weed infestation area (Fig. 1). The control is achieved slowly and depends on favourable conditions promoting an epidemic and gradual increase in disease of plants. Manipulations to increase the efficacy of control are not planned and may be difficult or impossible. There is increasing concern over the potential risk of introducing exotic organisms.

The inundative or bioherbicide method consists of the application of massive doses of inoculum of an indigenous pathogen over the entire weed population to be controlled. According to Charudattan (1988) the term 'inundative control agents' should be 'reserved for pathogens that can be mass-produced *in vitro* and applied as

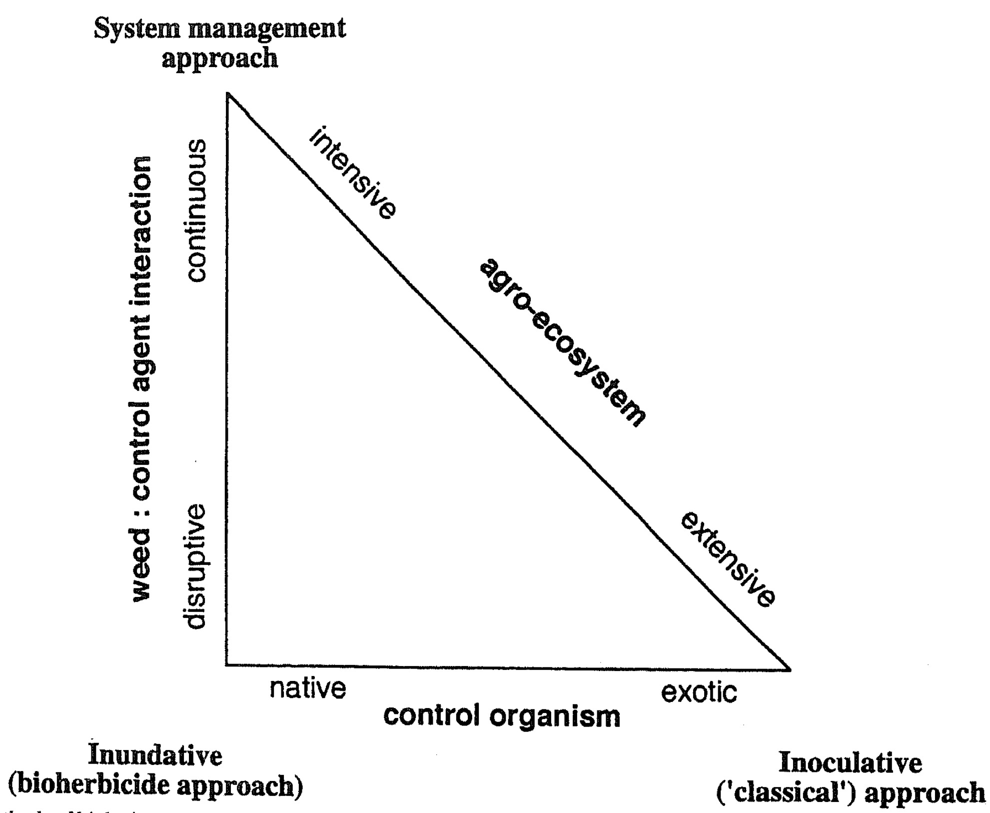

Fig. 1. Methods of biological weed control in agro-ecosystems.

herbicidal preparations'. Such biological agents generally are manufactured, formulated, standardized, packaged and registered like chemical herbicides. The inoculative and inundative approaches have been used to control weeds of contrasting habitat types, the choice of these being mainly due to differences in the costs involved and the time period allowed to achieve a potential control success (Fig. 1). Weeds of rangeland, waterways and semi-natural areas (extensive agriculture) have traditionally been controlled through the inoculative approach (mainly using insects) whereas bioherbicides (fungi) have been used to control weeds in crops (intensive agriculture).

The 'system management approach' is related to the conservation and augmentative approach distinguished by some authors. These terms, however, are differently used and only vaguely defined, the augmentative approach being viewed predominantly as intermediate between the inoculative and the inundative method, and described as 'periodic re-establishment of a classical biocontrol agent' (Charudattan, 1988), or 'manipulative inoculation tactic' (Hasan & Ayres, 1990). We therefore propose the new term 'system management approach' to emphasize its qualitative aspects related to the cautious manipulation of a weed pathosystem (Fig. 1). The aim of this system is to shift the balance between host and pathogen in favour of the pathogen, mainly by stimulating the build-up of a disease epidemic (epiphytotics) on the target weed population. It excludes disruptive events, such as the introduction of exotic control organisms (classical approach) or the mass release of inoculum (inundative approach) (Fig. 1).

On facilitating epiphytotics

Plant disease epidemics relate both to the spread of the disease, i.e. the number of host plants infected, and to the increase in disease severity on a given host plant. Constraints on disease development involve lack of adequate inoculum, including spatial and temporal disjunction between the host and pathogen, host resistance, and environmental deficiencies (Shrum, 1982). The main objective of the system approach is to develop management strategies that remove these constraints, which generally limit native pathogens at endemic levels. This can be achieved by (a) the introduction of (more) inoculum in a weed population, especially elaboration of the time of introduction with regard to the infection window, (b) the careful selection and manipulation of the genetic composition of the pathogen population, and (c) the specific management of the infection conditions. In the following, we will briefly discuss how these three aspects may influence disease development, and how they could be managed to increase the impact of a pathogen on the host population, and thus the efficacy of biological weed control.

Once a pathogen has been selected, host damage can be increased by extending the epidemic: the presence of inoculum one infection cycle earlier in the growing season may well create an epidemic equivalent to that of several hundredfold increases in inoculum provided at a later date (Charudattan, 1988). In natural ecosystems, inoculum is often limiting early in the season, especially for obligate foliar pathogens, owing to severe reductions in inoculum over-winter. Therefore, introduction of inoculum in spring may be an efficient and practical intervention for weed management. Spring application is facilitated by environmental conditions that are often more suitable for host infection and survival of a pathogen than during summer (Burdon, 1987). The time of application, however, needs to coincide with the time window for host susceptibility, as related to the developmental stage of the host plant. Together with the length of time that the host is susceptible and the degree of susceptibility of the host, they greatly determine disease development.

Innate resistance of the weed host is arguably a major factor influencing disease development (Burdon, 1987). Examples from crop pathology, however, show that epidemics are often prevented or retarded by inoculum deficiency rather than resistance or environmental constraints. Shrum (1982) therefore argues that the significance of host resistance and the role of genetic diversity in preventing epidemics by native pathogens has been overestimated. Epidemics could be successfully created above the natural level of disease by a well-timed application of inoculum. However, both avoidance (host characteristics that reduce the contact between susceptible tissue and infectious dispersal units of the fungus) and resistance (mechanisms that operate after the establishment of the parasitic contact, reducing the growth and or the development of the pathogen) have a genetic basis (Burdon, 1987). Therefore, selection following biocontrol may become important on a longer time scale by building up resistant weed populations, which will decrease control efficacy and reduce sustainability of biological control. Little is yet known on the levels and components of disease resistance in natural plant populations (but see Alexander, 1992).

Furthermore, there are a number of environmental constraints on the successful build-up of a disease epidemic and the effect of disease on the host plant. Of these, perhaps the most important is water, which, in the form of rain or dew, is essential for the development of many fungi both for spore dispersal and for host infection (Burdon, 1987). On the other hand, once plants are infected, damage caused by some diseases is greatly increased by mild drought. In irrigated crops, the watering regime could be altered to provide a brief dry period and so maximize host damage. In contrast to drought, nutrient deficiency, especially nitrogen, may reduce host injury caused by fungal infection through changes in both frequency and intensity of infection, and severity of physiological disruption damage (Paul *et al.,* 1993). Application of fertilizer could be adjusted to coincide with the introduction of the initial inoculum.

Based on the aspects discussed so far, a new research protocol is slowly emerging for biological control of weeds in crops. In the following, this is discussed using studies on the weed:pathogen system *Senecio vulgaris* L.:*Puccinia lagenophorae* Cooke, which have recently been initiated. Most of the results are only preliminary, and they are mainly intended to illustrate the research procedure.

The weed:pathogen system *Senecio vulgaris*: *Puccinia lagenophorae*

The organisms

Senecio vulgaris L., common groundsel (Asteraceae), is one of the five target weed species selected for detailed investigations in the framework of the COST project 816 *Biological Control of Weeds in Crops* (Müller-Schärer, 1993; Müller-Schärer, 1996a). *Senecio vulgaris* is a short-lived, predominantly inbreeding annual, originating most probably from southern Europe (Kadereit, 1984), but now common throughout the world. In temperate climates it is capable of up to three generations within one year. This short generation time, coupled with the capacity for large-scale seed production and rapid germination throughout the year, are all characteristics of successful weed invaders, making *S. vulgaris* a troublesome weed, especially in horticulture where frequent cultivation occurs. The weed problem caused by *S. vulgaris* declined rapidly with the advent of chemical herbicides but has reemerged owing to the evolution of s-triazine herbicide-resistant genotypes. Herbicide resistant populations are now common and widely distributed, especially in Europe and North America (Holt & LeBaron, 1990).

The rust fungus *Puccinia lagenophorae* Cooke (Basidomycetes: Uredinales), native to Australia where it infects some native Asteraceae, was first found in Europe in the early 1960s (Wilson & Walshaw, 1963). Although teliospores are produced, infection of plants by these spores or basidiospores has not yet been observed and plants seem to be infected only by way of aeciospores. Extensive and detailed studies on how the physiological effects of infection by *P. lagenophorae* may be modified by interactions with environmental factors have been carried out at Lancaster University, Lancaster, UK, by Peter Ayres, Nigel Paul and co-workers during the past 15 years. Damage caused by *P. lagenophorae* is enhanced under mild drought conditions, during periods of frost in winter and by competition between *S. vulgaris* and neighbouring plants, but is reduced by nutrient deficiency (Paul *et al.,* 1993). Host damage was also greatly increased by secondary infection of *P. lagenophorae* pustules by a range of necrotrophic fungi. In some associations, this led to selective kill of *S. vulgaris*, and the effective inoculum dose of both fungi could be significantly reduced (Hallett *et al.,* 1990)

Based on the rapid spread of this rust fungus in Europe, and the observed host impact, especially in combination with secondary necrotrophic fungi, *P. lagenophorae* has been selected for detailed studies to evaluate the potential of this biotroph as a biological control agent for *S. vulgaris*.

Target habitats

Today, *S. vulgaris* is predominately a weed problem in annual crops like ornamental and treeseedling nurseries, strawberries and some vegetable crops, but also in perennial cropping systems such as vineyards, orchards and perennial container crops (Cross & Skroch, 1992; Paul *et al.*, 1993). In United States nursery agro-ecosystems, *S. vulgaris* is the third most important weed species (Cross & Skroch, 1992). As the target crops include both annuals and perennials, and cropping systems with different weed damage thresholds, the speed of the epidemic necessary for acceptable level of weed control will differ and thus require crop-specific manipulations of the weed pathosystem.

The research procedure

The basic aim of this project is to gain a better understanding of the mechanisms underlying this weed: pathogen system, both at the individual and at the population level (Table 1). Such knowledge is vital for the successful implementation of the system management approach.

We will initially investigate the potential impact of *P. lagenophorae* alone. Epiphytotics, developing from a carefully selected inoculum applied at an appropriate time, might sufficiently lower the competitive ability of *S. vulgaris* where it is established as a permanent weed (e.g. orchards, plant nurseries or vegetable cropping systems). Under such conditions, total weed kill may not be necessary. The ability to reduce the competitive vigour of *S. vulgaris* by infection with *P. lagenophorae* has been shown in a study by Paul & Ayres (1987), where infection of *S. vulgaris* improved yield of lettuce (*Lactuca sativa* cv. 'Avon Defiance') without pronounced weed mortality.

In some vegetable crops, where damage thresholds are low and suppression of competition is not sufficient, rapid and short-term knock-down of *S. vulgaris* is demanded. This is also the case in cropping systems where qualitative aspects of damage predominate, such as in some ornamental crops. In such systems, the effect of *P. lagenophorae* may be enhanced by joint applications with synthetic herbicides, necrotrophic fungi, or biochemicals interfering with the weed's defence to the rust fungus. The last of these three possibilities has recently been proposed by Gressel *et al.* (1996) to reduce the effective inoculum density for mycoherbicides, but could also be exploited in the system management approach, especially when it can rely on herbicides that are applied against other weeds.

In order to introduce biological control into integrated production systems, its compatibility with commonly applied pest-control measures needs to be examined. A series of small-scale field experiments conformable to integrated production systems are planned towards the end of this project (Table 1). In parallel, the elaboration of simulation models to describe, analyse and

Table 1. Synopsis of the project on the biological control of *Senecio vulgaris*, using the rust fungus *Puccinia lagenophorae*

Basic studies
- Analysis of the problem situation: identify target habitats and their management (including pesticides used)
- Isolation and culture of plant and pathogen lines
- Biology and genetics of plant and pathogen lines
- Study of monocyclic infection process

Plant–pathogen interactions
- Plant resistance to pathogen
- Pathogenic impact on plants

Dynamics and genetics of populations
- Genetic structure of plant and pathogen populations
- Epidemiology
- Pathogenic impact on plant population dynamics

Additional stress on plants
- Other pathogens or insects
- Low dosage of herbicides
- Biochemicals interfering with the weed's defence to the fungus (anti-metabolites of phytoalexins)

Integration into crop-specific pest control strategies
- Compatibility of the fungus with other phytosanitary measures (including pesticides) taken
- Optimal crop specific application technology
- Practical control attempts under various conditions

optimize interactions between the various stress factors is planned. In order to increase the stress on the target weeds, special attention will be given to manipulations of crop-weed resource competition via choice of crop variety, crop spatial arrangement, crop population density, irrigation placement and timing, and fertility sources and placement (see for example Theunissen, 1994; Müller-Schärer, 1996b; and references therein), in order to elaborate crop- and site-specific solutions.

Results (preliminary)

In the field, infections of *P. lagenophorae* were most severe in late summer and autumn, but in spring, some young seedlings have also been found with infection. This may indicate that absence of rust inoculum, and not unfavourable environmental conditions, is limiting in spring. Early infection with *P. lagenophorae* therefore seems a promising approach.

The infection process by aeciospores has been studied in considerable detail using a component- or life-table-analysis. The infection process followed between adhesion of the spores on the leaf to the formation of primary hyphae was divided into six components detectable with fluorescence microscopy. This allows comparison of plant and rust fungus lines to be assessed for resistance/virulence, provides a tool for carrying out host-specificity tests and enables evaluation of combined effects with other pathogens or synthetic herbicides (Wyss & Müller-Schärer, 1995). The monocyclic infection process, however, is

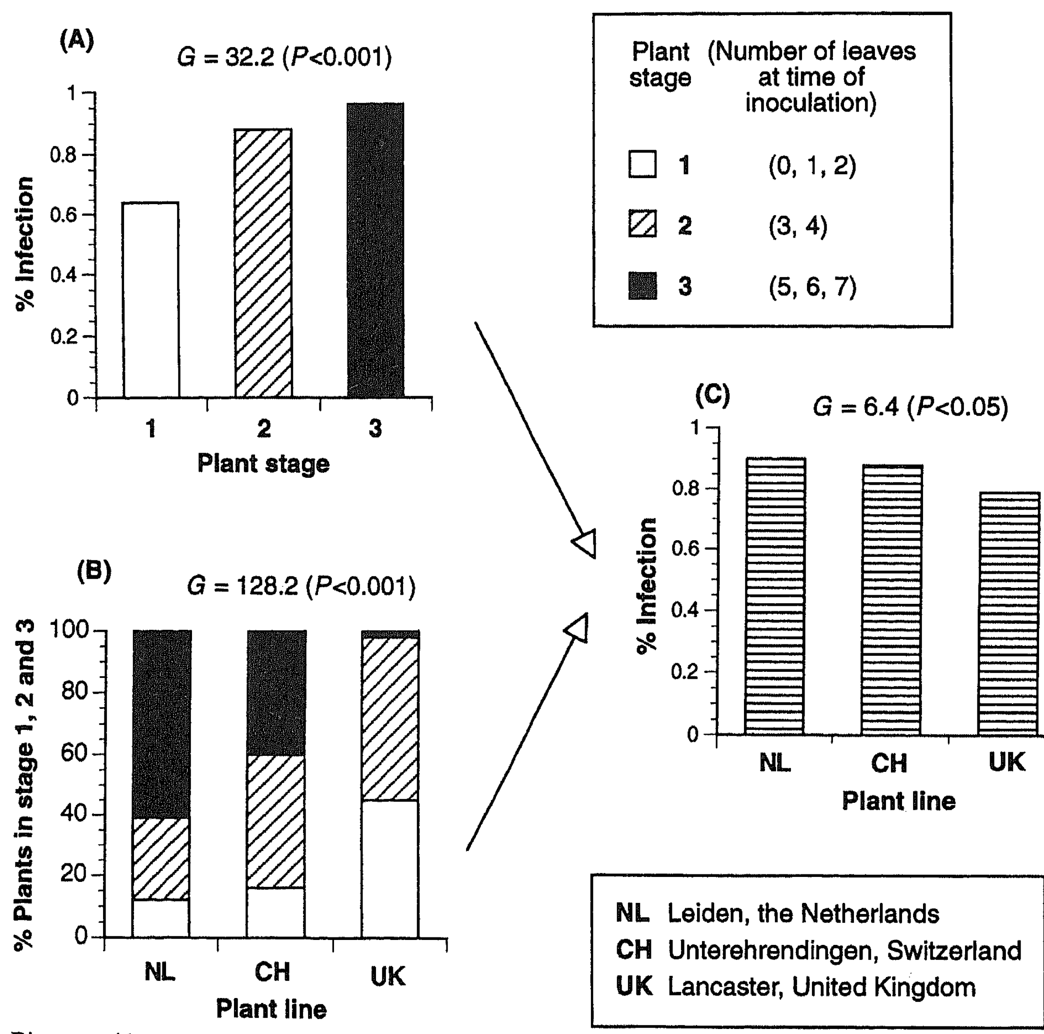

Fig. 2. Disease avoidance mechanisms in the *Senecio vulgaris: Puccinia lagenophorae* weed pathosystem (adapted from Frantzen *et al.*, in preparation). (A) effect of plant stage on infection; (B) effect of plant line on growth development; (C) effect of plant line on infection. Differences between plant stages in fraction of plants infected (A), differences between lines in the distribution of plants over the stages (B), and differences between lines in fraction of plants infected were tested on significance by the log-likelihood ratio test (G-test; Sokal & Rohlf, 1981).

not yet understood, and winter survival of teliospores, aeciospores and mycelium in the plant is presently under investigation.

Several experiments have been initiated to study factors that limit the impact of the fungus on individuals and populations of *S. vulgaris* (Table 1). To date, we have concentrated on avoidance and resistance mechanisms, and especially on phenotypic differences between *S. vulgaris* lines, and their reaction to infection. In contained environment studies of the reaction of three plant lines to infection by a single *P. lagenophorae* line, susceptibility varied between plant developmental stages, independent of plant line. Susceptibility to the fungus increased in later developmental stages (Fig. 2A). Plant lines differed also in developmental rate (Fig. 2B), and the combined effect of plant stage on infection, and of plant line on developmental rate resulted in differences in susceptibility to the fungus between plant lines (Fig. 2C) (Frantzen *et al.*, in preparation). Similar results were found using two nearly isonuclear triazine herbicide-resistant and -susceptible *S. vulgaris* lines. Plant lines that grew faster showed increased disease severity and suffered more damage from the fungal infection. Both effects of the nuclear and chloroplast genome on these plant variates were significant (Müller-Schärer *et al.*, unpubl. obs.). In order to quantitatively follow the infection process of the *P. lagenophorae* spores, we used component analysis, a form of a life-table analysis (Wyss & Müller-Schärer, 1995; cf. above). Penetration and development of the mycelium within the leaf tissue was studied for a single *P. lagenophorae* line and three *S. vulgaris* lines. Both effects of plant line and of plant developmental stage were found mainly on components early in the infection process, indicating that discrimination might occur primarily at or near the leaf surface. With regard to a biological control attempt, this indicates that a weed population that is heterogeneous with respect to the rate of development may be more difficult to control, as the disease epidemic will be slowed down and host impact reduced. If the importance of avoidance of *P. lagenophorae* is confirmed, a survey to find lines that are pathogenic to early plant stages might be most rewarding.

With regard to the plant–pathogen interactions at the population level, a few experiments have been conducted to monitor the disease spread from an inoculated *S. vulgaris* plant in plots with randomly assigned seedlings of different lines of the weed species. Growth rates of *S. vulgaris* lines, the impact of the fungus on plant biomass as well as interactions between effects of plant line and infection have been analysed (Frantzen & Müller-Schärer, unpubl. obs.). The main objective of a recently started study is to compare the amount and distribution of phenotypic and genetic variation in life history traits, including sensitivity to *P. lagenophorae*, between *S. vulgaris* populations in agrestal (crops) and ruderal (road verges, disturbed sites) habitats. It has been postulated that genetic change and phenotypic plasticity may be alternative strategies to contend with a wide range of environments, and that these two types of variability should be inversely related (Bradshaw, 1965; Barrett, 1982; Barrett, 1988). Because agrestal habitats are assumed to be environmentally more homogeneous than ruderal habitats, we predict that genetic variability within agrestal populations of *S. vulgaris* will be less than in natural (ruderal) populations, possibly leading to genetically differentiated nutrient specific genotypes. Alternatively, the greater environmental variation in ruderal habitats is assumed to favour greater levels of plasticity. Initially, variation in quantitative traits associated with growth and reproductive success to nutrient levels and fungal infection will be studied. Later detailed genetic analyses using molecular markers will be conducted. Present knowledge suggests that successful biological control is favoured when there are low levels of genetic variation in the target populations. The agrestal habitat would therefore be a promising habitat for a biological control attempt using *P. lagenophorae*, if agrestal populations prove to be genetically more uniform.

In contrast with the general view derived from crop pathology, that resistance *per se* is the major determinant of the impact of pathogens on plant populations, we hypothesize, based on the results discussed above (Fig. 2), that in the short term disease escape (non-genetic) and avoidance (genetic) will be more important in the *S. vulgaris*:*P lagenophorae* system than resistance (genetic). The amount and nature of this variation will greatly determine the genetic composition of the initial fungal inoculum that would optimize the effectiveness and sustainability of biological control (cf. previous section). Genetic variation of the rust populations will be the subject of a parallel study.

The study of factors that influence infection has been started only recently. These studies presently involve effects of storage, temperature, water and *P. lagenophorae* lines on the germination of aeciospores. Three selected fungal lines will then be tested on pathogenicity under climate room conditions, using the component analysis, and later in the field. An experiment on the influence of *P. lagenophorae* on the competitive effect of *S. vulgaris* in celery (*Apium graveolens* L. var. *rapaceum* (Mill.) Gaud.) has been performed in 1996. Effect of introduction of initial inoculum on the competitiveness of *S. vulgaris* will be studied in plots with and without herbicides applied. The incorporation of additional stress factors and the integration of biological control into general pest control measures (Table 1) will be studied in the near future, and will be elaborated in collaboration with other research groups involved in the COST action.

Conclusion

Biological control has traditionally been practised by entomologists against weeds in extensively managed agro–ecosystems or semi-natural habitats, adopting the inoculative approach. The recent interest of plant population biologists in biological weed control has been to the mutual benefit of both disciplines. On the one hand, it resulted in a better understanding of the role of insect pests in regulating plant populations, and on the other hand, it helped to render biocontrol more predictable.

Stimulated by problems caused by intensive use of herbicides, methods for biological control of weeds in crops have been developed. During the short history of biological control using fungi, efforts have been mainly directed towards the development of analogues of chemical herbicides, capable of a rapid knock-down effect. Relatively little attention had been paid to aspects of weed and pathogen biology. Until recently, epidemics on weeds have been of peripheral concern to epidemiologists and plant pathology has been limited to disease prevention on crops (Burdon, 1987). However, principles developed for crop pathology are also useful in applying biological weed control. In this regard, weeds can be viewed as plant populations with characteristics of 'wild' populations, growing in an agricultural environment (Frantzen, 1994).

The system management approach both depends on and provides fundamental knowledge of mechanisms underlying pathogen–plant interactions at the individual and population level. It combines knowledge from epidemiology and more general plant pathology with that from weed ecology, population biology and physiology. Its objective is to provide a tool that is basic for successfully managing weed populations. This will be greatly needed in developing sustainable agro–ecosystems, where weed control no longer aims at crop production in a weed-free environment, but simply at a reduction of weed-induced yield losses. Consideration might be given to the use of pathogens not only as therapeutic agents to reduce weed interference against a current crop, but also as preventive agents to limit future weed populations by reducing seed output.

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References

ALEXANDER HM (1992) Evolution of disease resistance in natural plant populations. In: *Plant resistance to herbivores and pathogens* (eds RS Fritz and EL Simms), pp. 326–44. University of Chicago Press, Chicago.

BARRETT SCH (1982) Genetic variation in weeds. In: *Biological Control of Weeds with Plant Pathogens* (eds R Charudattan & H L Walker), pp. 73–98. John Wiley & Sons. Inc., New York.

BARRETT SCH (1988) Genetics and evolution of agricultural weeds. In: *Weed management in agro-ecosystems: ecological approaches* (eds MA Altieri and M Liebman), pp. 55–76. CRC Press, Boca Raton.

BRADSHAW AD (1965) Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**, 115–155.

BURDON JJ (1987) *Diseases and plant population biology*. Cambridge University Press, Cambridge.

CHARUDATTAN R (1988) *Inundative control of weeds with indigenous fungal pathogens*. Manchester University Press, Manchester.

CROSS GB & SKROCH WA (1992) Quantification of weed seed contamination and weed development in container nurseries. *Journal of Environmental Horticulture* **10**, 159–61.

FRANTZEN J (1994) *Studies on the weed pathosystem* Cirsium arvense-Puccinia punctiformis. PhD thesis, University of Wageningen, the Netherlands. CIP-DATA Koninklijke Bibliotheek, den Haag.

GRESSEL J, AMSELLEM Z, WARSHAWSKY A, KAMPEL V, MICHAELI

D (1996) Biocontrol of weeds: overcoming evolution for efficacy. *Journal of Environmental Sciences B*. **31,** 399–405.

Hallett SG, Paul ND & Ayres PG (1990) *Botrytis cinerea* kills groundsel *Senecio vulgaris* infected by rust *Puccinia lagenophorae*. *New Phytologist* **114,** 105–10.

Hasan S & Ayres PG (1990) The control of weeds through fungi: principles and prospects. *New Phytologist* **115,** 201–22.

Holt JS & LeBaron HM (1990) Significance and distribution of herbicide resistance. *Weed Technology* **4,** 141–9.

Kadereit JW (1984) The origin of *Senecio vulgaris* (Asteraceae). *Plant Systematics and Evolution* **145,** 135–53.

Müller-Schärer H (1993) Biological control of weeds in crops: a proposal of a new COST action. In: *Proceedings 4th International Conference on 'Non chemical weed control'*, Dijon, France, 181–5.

Müller-Schärer H (1995) Weeding with insects and pathogens – prospects for European crops. In: *Proceedings 9th EWRS Symposium – Challenges for Weed Science in a Changing Europe*, Budapest, 21–7.

Müller-Schärer H (1996a) A European programme for the biological control of weeds in crops: objectives and present status. In: *Proceedings of the IX International Symposium on Biological Control of Weeds*, Stellenbosch, South Africa, 336.

Müller-Schärer H (1996b) Interplanting ryegrass in winter leek: effect on weed control, crop yield and allocation of N-fertiliser. *Crop Protection* **15,** 641–8.

Müller-Schärer H & Potter CA (1991) Cover plants in field grown vegetables: prospects and limitations. In: *Proceedings 1991 Brighton Crop Protection Conference – Weeds 1991*, 599–604.

Paul ND & Ayres PG (1987) Effects of rust infection of *Senecio vulgaris* on competition with lettuce. *Weed Research* **27,** 431–41.

Paul ND, Ayres PG & Hallett SG (1993) Mycoherbicides and other biocontrol agents for *Senecio* spp. *Pesticide Science* **37,** 323–9.

Shrum RD (1982) Creating Epiphytotics. In: *Biological Control Of Weeds With Plant Pathogens* (eds R Charudattan & HL Walker), pp. 113–35. John Wiley & Sons, Inc., New York.

Sokal RR & Rholf FJ (1981) *Biometry*. Freeman, San Francisco.

Theunissen J (1994) Intercropping in field vegetable crops: pest management by agrosystem diversification: an overview. *Pesticide Science* **42,** 65–8.

Watson AK (1992) Biological and other alternative control measures. In: *Proceedings 1st International Weed Control Congress*, Monash University, Melbourne, 64–73.

Wilson IM & Walshaw D (1963) A new rust disease on groundsel. *Nature* **200,** 382.

Wyss GS & Müller-Schärer H (1995) Aecidial infection process of *Puccinia lagenophorae* Cooke on *Senecio vulgaris* L.: relevance for biological control of weeds. In: *Proceedings 9th International Symposium on Challenges for Weed Science in a Changing Europe*, Budapest, 686.