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CARFAX

Epidemic Spread of the Rust Fungus *Puccinia lagenophorae* and its Impact on the Competitive Ability of *Senecio vulgaris* in Celeriac During Early Development

HEINZ MÜLLER-SCHÄRER[1] AND STEPHANIE RIEGER[1,2]

[1] *Institute of Plant Biology/Ecology, University of Fribourg, Pérolles, CH-1700 Fribourg, Switzerland;* [2] *Institute of Plant Sciences/Phytomedicine, Swiss Federal Institute of Technology, CH-8092 Zürich, Switzerland*

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The 'system management approach' of biological weed control was applied in a small-scale field experiment with celeriac (root celery), intersown with an inbred line of the annual weed Senecio vulgaris *L. The naturalized rust fungus* Puccinia lagenophorae *Cooke (Basidiomycetes: Uredinales), a common and widespread pathogen of* S. vulgaris *in Europe, was introduced into parts of the plots, and its impact on the competitive balance between the crop and weed in the presence and absence of an additional herbicide treatment was studied. Competition by* S. vulgaris *(at a realized density of only 50 plants/m^2) during the first 10 weeks of growth was substantial, reducing the fresh weight of the celeriac bulbs by 28%. The epidemic spread of the rust fungus was relatively fast, and the time to infection was similar to that in full-area applications. Inoculation with the rust fungus strongly reduced crop losses due to competition with* S. vulgaris. *The fresh weight of the celeriac bulbs in plots with both* S. vulgaris *and the fungus was not statistically different from the celeriac yield in plots without* S. vulgaris. *This effect was mainly the result of the reduced biomass of* S. vulgaris, *and not reduced survival. Infected plants may, therefore, still contribute to soil cover and may help to suppress later germinating weed species. Older plant stages were found to be infected earlier than younger stages. No significant interactions were observed between the effects of the fungal infection and a low-dose application of the herbicide chlorbromuron on weed performance. Basic studies necessary to develop the system management approach further are discussed.*

Keywords: *biological weed control, system management approach,* Senecio vulgaris, *rust fungus, weed–crop competition, celeriac*

INTRODUCTION

Concepts of weed control in agriculture have changed greatly during the past decades, shifting from maximum weed suppression (the clean-crop option) to economic crop

Correspondence to: H. Müller-Schärer. Tel: 41 26 300 88 35; Fax: 41 26 300 97 40; E-mail: heinz.mueller@unifr.ch.

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production based on various thresholds for weed control (Hurle, 1997). This has been mainly due to the availability of specific herbicides that are applied only if the treatment results in a net gain of benefits. More recently, the augmentation and use of biodiversity has become a key component in developing sustainable agro-ecosystems (United Nations Conference on Environment and Development, 1992). In this respect, optimal crop production may be achieved by a cautious manipulation of the crop's environment, based on carefully balancing the negative and positive effects of non-crop plants. The ecological importance of increased species diversity, for example of companion plants interfering with pests and pathogens of the crop, has been demonstrated in various studies (e.g. Müller-Schärer *et al.*, 1992; Theunissen, 1994 and references therein).

For dominant weed species that are difficult to control by traditional means, the development of new, selective weed control methods that can be implemented in integrated pest management (IPM) strategies is essential. Such situations have recently been discussed by Müller-Schärer (1995) and Gressel *et al.* (1996). In these cases, biological weed control is an appropriate means of control due to its high degree of selectivity and level of environmental safety (Müller-Schärer & Scheepens, 1997). The aim of this 'new' form of weed control is not to eradicate plant species, but to shift the competitive balance in favour of the crop. This is one of the explicit underlying ideas of the recently described 'system management approach' of biological weed control (Müller-Schärer & Frantzen, 1996). Reduction of the competitive ability of the target weed is attempted by stimulating the build-up of a disease epidemic or insect outbreak on the target weed population, using naturally occurring or naturalized antagonists.

To develop this approach further, the control of the annual weed *Senecio vulgaris* L. (Asteraceae) using the widely distributed naturalized rust fungus *Puccinia lagenophorae* Cooke (Basidiomycetes: Uredinales) has been chosen as a research model (Müller-Schärer & Frantzen, 1996; Frantzen & Hatcher, 1997). *S. vulgaris* has become a problem weed in horticultural crops due to its short generation time, high seed production and rapid germination throughout the year. Moreover, s-triazine-resistant populations and partial insensitivity to phenylurea herbicides have been widely documented (Müller-Schärer & Wyss, 1994). Celeriac (root celery), *Apium graveolens* L. var. *rapaceum* (Mill.) Gaud. (Apiaceae), is often heavily infested by *S. vulgaris* in Switzerland (D. T. Baumann, personal communication, 1997). Registered herbicides are known to have only a partial effect on *S. vulgaris* (Baumann, 1996). A reduction of yield due to competition by *S. vulgaris* has been demonstrated for lettuce (Paul & Ayres, 1987), tomatoes (Quasem & Hill, 1994) and carrots (Wyss, 1995). The potential of *P. lagenophorae* infection to reduce the competitiveness of *S. vulgaris*, and thus to lower yield reduction without pronounced weed mortality, has been shown by Paul and Ayres (1987) for lettuce. Complete killing of *S. vulgaris* infestations in vegetable crops by natural infection with *P. lagenophorae* has occasionally been reported (G. S. Wyss, personal communication, 1997). Present knowledge on interactions between *S. vulgaris* and the rust fungus *P. lagenophorae* has recently been reviewed by Frantzen and Hatcher (1997). *S. vulgaris* is one of the five weed species selected for detailed studies in the framework of COST-816 (European cooperation in the field of scientific and technical research) on 'Biological Control of Weeds in Crops' (Müller-Schärer & Scheepens, 1997).

The aim of this study was to apply the system management approach in a small-scale field experiment in celeriac, intersown with *S. vulgaris*, in order to monitor the epidemic spread of the rust fungus *P. lagenophorae* from initial inoculum sources. A further aim was to quantify the impact of the fungus, in the presence and absence of an additional herbicide treatment, on the early development of celeriac, as mediated by its effect on the competitive ability of *S. vulgaris*. The following specific questions were addressed.

(1) What is the effect of competition by *S. vulgaris* at a sown density of ca. 100 plants/m^2 on celeriac during the first 2 months after planting?
(2) Do single and joint applications of the rust fungus with the herbicide treatment alleviate crop losses due to competition with *S. vulgaris*?

(3) Can the effects of these treatments on celeriac adequately be explained by their effects on the biomass of *S. vulgaris*?
(4) How fast does the rust fungus spread, and does the time to infection depend on plant stage?
(5) Are there interactions of the herbicide treatment with plant stage and fungal rust infection?

MATERIALS AND METHODS

Species

Celeriac (root celery), *A. graveolens* var. *rapaceum* cv. Kojak, was sown on 26 March 1996 in small pots in a greenhouse. Immediately before planting in the field, the celeriac was treated with Ortho-Difolatan (0.15%; Maag Agro AG, Dielsdorf, Switzerland) for protection against infection by the pathogens *Alternaria radicina* and *Septoria apiicola*.

Seeds of an inbred line of *S. vulgaris* L. (Asteraceae), most probably *S. vulgaris* subsp. *vulgaris* var. *vulgaris*, were used, originally collected on old dunes near Leiden, the Netherlands. This plant line is known to develop relatively fast and to be readily susceptible to the rust line used (Müller-Schärer & Frantzen, 1996).

Aeciospores of the rust fungus *P. lagenophorae* were used for the experiment. The selected fungal rust line originated from an isolate collected on *S. vulgaris* in a vegetable field at Unterehrendingen, Switzerland. The isolate was sprayed on *S. vulgaris* plants and the specific rust line was selected from a single aecium. Both *S. vulgaris* and *P. lagenophorae* lines were maintained in a climate chamber with 16 h of light (150 μmol m^{-2} s^{-1} at 23°C and 60% relative humidity (RH)) and 8 h of dark (at 15°C and 80% RH).

Field Site and Experimental Design

The field experiment was carried out in 1996 at the experimental farm of the Agricultural Institute Grangeneuve, at Posieux (10 km from Fribourg), Switzerland. A vegetable plot was ploughed in autumn 1995 and left uncovered during the winter. In spring, after preparation of the beds for planting, the experimental field was harrowed twice to reduce subsequent weed pressure (i.e. after 2 weeks and the day before planting the celeriac). Subsequently, four treatments were set up, each with five replications, and the resulting 20 plots were arranged in a completely randomized design in two adjacent celeriac crop beds (Figure 1). There were four treatments: a control without *S. vulgaris* (C plots); intersown *S. vulgaris* (S plots); intersown *S. vulgaris* and a rust-infected *S. vulgaris* plant transferred into the centre of each plot (R plots); and R plots with an additional herbicide treatment (R + H plots). Each plot was 1.2 m wide and 3 m long. The two celeriac crop beds (each 1.2 m wide) were separated by a 30-cm walkway, and plots were horizontally displaced to reduce the chance of cross-infection between plots of the two rows (Figure 1). A buffer zone of 2 m was planted with celeriac around the experimental plots.

Establishment of Field Plots and Application of Treatments

Crop. Celeriac was planted on 29 May 1996 in four rows/bed (30 cm apart) and at a distance of 30 cm within the rows. Base-fertilization was carried out according to soil analyses prior to planting with P_2O_2, K_2O and Mg to reach 170 kg of N/ha (over the total vegetation period), 70 kg of P/ha, 20 kg of K/ha and 20 kg of Mg/ha. Nitrogen (as ammonium nitrate) was applied as a top dressing on three occasions (13 June, and 3 and 25 July), each with 40 kg of N/ha. No insecticides or fungicides were applied to the experimental plots.

Senecio. On 29 May, 5400 *S. vulgaris* seeds were placed on agar (2%) in Petri dishes (15 cm in diameter, each containing 12 × 12 seeds). On the next day (i.e. 1 day after planting the

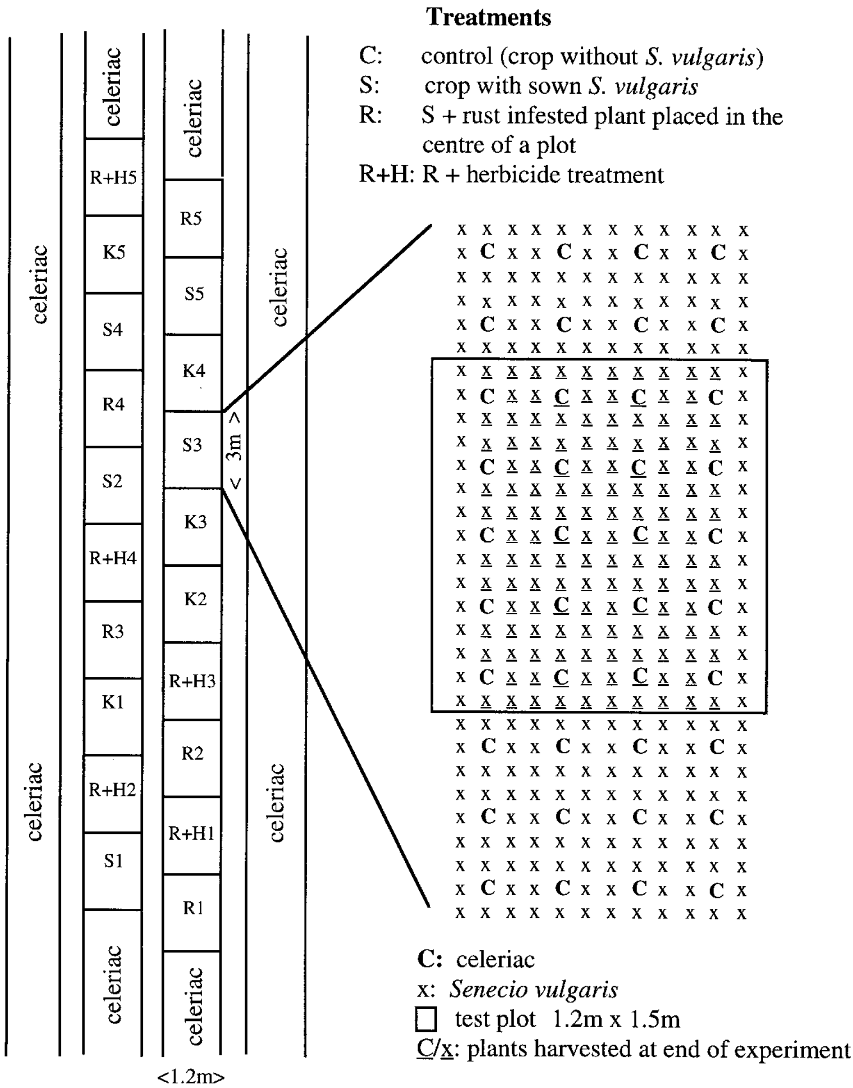

FIGURE 1. Experimental design and position of plants in the plots.

crop), imbibed seeds were placed into the experimental plots with a piece of agar (S, R and R + H) using a spoon. This method was suggested by Kempenaar and Schnieders (1995) to obtain fast and uniform emergence of weeds for field experiments. Seeds were placed in a grid of 10×10 cm into 12 rows of each plot (Figure 1), resulting in ca. 100 *S. vulgaris* plants/m^2 (320 seeds/plot). The germination rates had been assessed 2 weeks before the start of the experiment and were found to be 80% (on agar plates after 5 days at 12 h of daylight at 21°C and a light intensity of 150 μmol s^{-1} m^{-2}, and 16°C in the dark). The central half of each plot (1.2×1.5 m) was used as a test plot only, thus containing 4×5 crop plants and ca. 60 *S. vulgaris* plants. This allowed for a 3-m buffer zone between the test plots in the beds and alternating placement in the two beds due to the horizontal displacement (Figure 1).

Apart from *S. vulgaris*, the experimental plots were kept weed-free by hand weeding, and the surrounding buffer zone was weeded using an inter-row cultivation implement. On 26 June and 16 July all experimental plots were lightly hoed between the crop and the *S. vulgaris* plants to avoid encrusting the soil. Hot, dry weather immediately after sowing severely limited establishment of *S. vulgaris* (Figure 2). To fill in the gaps, seedlings sown in parallel in the greenhouse were transferred from seed trays. On 22 June, the position of each *S. vulgaris* and celeriac plant established in the test plots was recorded.

Inoculation. On 21 June, a single rust-infected *S. vulgaris* plant was placed in the centre of each R and R+ H test plot. These plants had been sprayed at the five-leaf stage on 31 May with an aecidiospore suspension of *P. lagenophorae* (0.5 mg ml^{-1}). The germination rates were assessed in parallel on agar plates (2%): 51% germination was achieved after 4 h.

Herbicide application. Chlorbromuron is a commonly used post-emergence herbicide in celery (including celeriac) crops in Switzerland. When using the suggested does of 1.0–1.25 kg of a.i./ha its effect on *S. vulgaris* is described as only partial (Baumann, 1996). A series of pre-trials was conducted to determine the dosage to be applied in the experiment (Rieger, 1996). In order to study the interaction between the herbicide and the rust fungus, *S. vulgaris* plants need to show only moderate symptoms of phytotoxicity, not be killed directly. On 9 July, 18 days after the transfer of inoculum plants to the plots, 0.75 kg of a.i./ha of commonly available chlorbromuron (Maloran, 50% a.i.; Ciba Agro, Dielsdorf, Switzerland) was applied in a spray volume of 500 l ha^{-1} to the five R+ H plots using a hand sprayer with standard nozzles and a spray pressure of 200 kPa.

Evaluation

The initial size of the celeriac plants was assessed on 28 June by estimating total leaf area. This was done by projecting the leaf area on to a grid frame placed beneath each crop plant. The total leaf area was estimated for all 10 crop plants of the two middle rows of each test plot. On 26 June, the numbers of leaves of all *S. vulgaris* plants in the test plots were recorded, together with their positions in the plot. In the R+ H plots, the numbers of leaves were counted a second time on 9 July. The numbers of leaves were taken as an indication of the phenological stage of the plants and used to relate fungal rust infection and herbicide effects respectively to plant stage.

Epidemics. *S. vulgaris* plants in the R and R+ H plots were checked daily for rust infection from 1 to 19 July (i.e. starting 10 days after the transfer of the inoculum plants to the field plots). The date of the onset of sporulation was recorded. These test plots were later subdivided into 12 × 12 cells each 10 × 10 cm in size, and one *S. vulgaris* plant was randomly assigned per cell if more than one plant was present per cell. Spatial autocorrelation was performed using the Moran statistic (Sokal & Oden, 1978) and subsequent geostatistics (Anon, 1995).

The effects of the herbicide were assessed on four occasions (3, 6, 10 and 16 days after application). Phytotoxic symptoms of all *S. vulgaris* plants in the R+ H plots were individually ranked according to the European Weed Research Society (EWRS) classification scheme for plant tolerance (1–9; with 1 indicating no symptoms/healthy plant and 7–9 indicating heavy damage to total kill) (Anon, 1992).

On 5 August, 68 days after planting the crop, the numbers of *S. vulgaris* plants in the test plots were counted and the numbers of plants with sporulating *P. lagenophorae* were recorded. Plants were then cut at ground level and the total biomass/plot was determined (dry mass at 70°C after 36 h). The two borderlines of each test plot were not included because the plants there predominately escaped herbicide application. The 10 celeriac plants of the two centre rows of each test plot were dug out, and the bulb diameters and fresh weights of the bulbs and the leaves were determined.

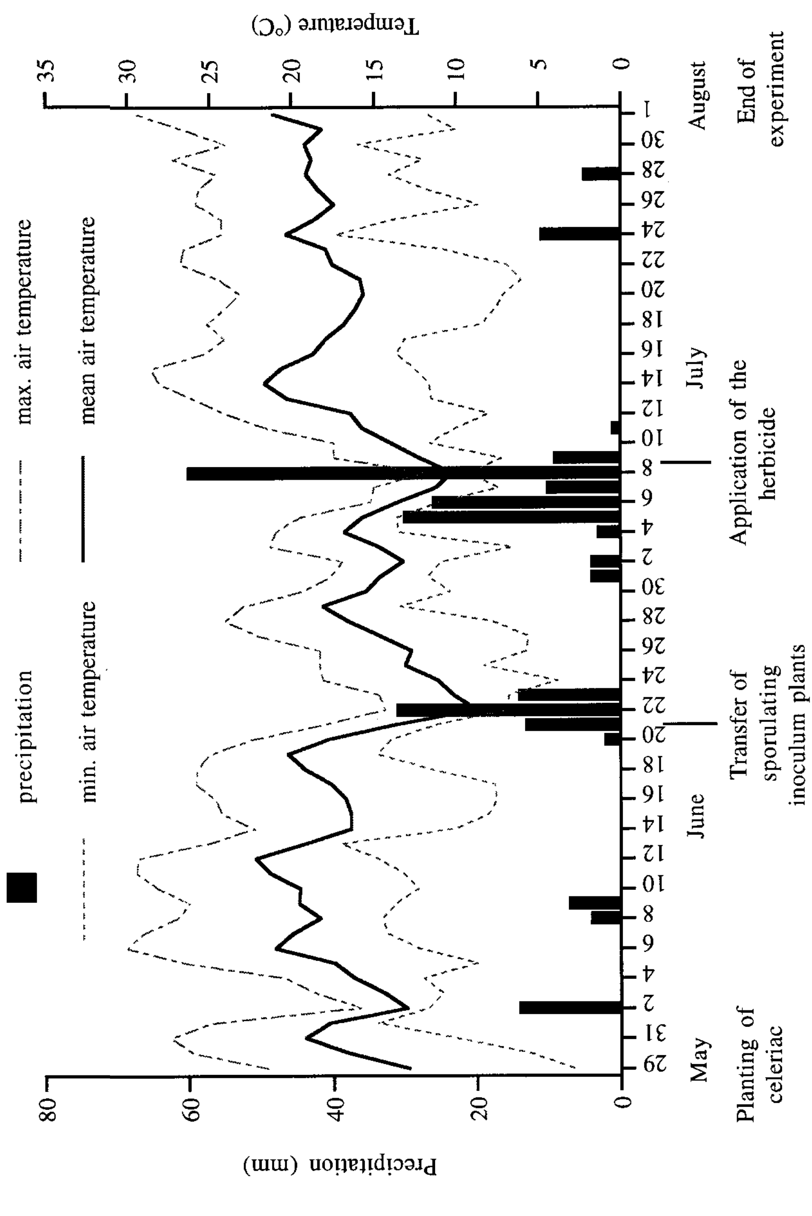

FIGURE 2. Temperature and precipitation at the experimental site during the course of the experiment.

Weather data. Temperature, precipitation, wind speed and wind direction were recorded during the experiment using data from the Federal Weather Station located 200 m from the field site.

Statistical Analyses

The effect of the four treatments was analyzed as a completely randomized design using analysis of variance (ANOVA) and analysis of covariance (ANCOVA). ANOVAs for yield parameters were based on plot means to avoid pseudoreplications. The developmental stage of the plant was used as a covariate to study whether the herbicidal effect was influenced by the presence of rust in the R + H plots. Although the dependent variate (i.e. the score of phytotoxicity symptoms) represented classes from 1 to 9, ANOVAs were conducted as these values are based on a continuous variate with linearly increasing steps (classes). Moreover, a logit log-linear analysis based on three phytotoxicity classes showed similar results. Mean separations in the ANCOVA models were performed using simple contrasts (each treatment was compared with the respective control treatment) and joint Bonferroni intervals to reduce multiple comparisons and to avoid bias (Norusis, 1990). SPSS (Norusis, 1990) and SuperANOVA (Gagnon *et al.*, 1989) were used for regression analyses and ANOVAs, and GS+ Geostatistics (Anon, 1995) for analyses of the epidemiological data.

RESULTS

Establishment

Due to hot, dry weather following the sowing of *S. vulgaris* (Figure 2) and the limited number of greenhouse seedlings available for transfer to the field, only half the plant density envisaged could be realized (i.e. ca. 50 *S. vulgaris* plants/m^2). In addition, the density varied greatly between the 15 plots, ranging from 37 to 70 plants/plot. This was mainly because additional transfer of *S. vulgaris* seedlings to replace non-established plants in the field plots could be achieved only for three randomly selected plots of each treatment. On 26 June (i.e. before possible effects of the rust treatment and before the application of the herbicide), initial *S. vulgaris* density and individual plant stage were assessed. These parameters did not vary among the *Senecio* treatments, and the treatment means ranged from 42.4 to 49.8 plant/m^2 with 3.8–4.2 leaves/plant respectively. All 20 crop plants of each of the test plots became established, and the average size of these celeriac plants did not vary between the treatments (range, 130–150 cm^2 of total leaf area/plant).

Treatment Effects on Early Biomass of Celeriac

The individual biomass of celeriac at the end of the experiment (i.e. 68 days after planting) was highly correlated with the initial plant size. As the slopes of the regression lines were the same for all four treatments (treatment $\times$ covariate interactions not significant), an ANCOVA model with a common slope was fitted and the treatment effects on celeriac variates were adjusted for initial crop size by using initial size as a covariate. The treatments significantly influenced bulb diameter, bulb fresh weight and the foliage:bulb ratio, but not the fresh weight of the foliage (Table 1). The effect of competition with *S. vulgaris* was most severe for the fresh weight of the bulbs (the target yield variate), significantly reducing it by 28% compared with *S. vulgaris*-free control plots (Figure 3). The presence of the rust greatly diminished this effect to only 15.9% weight reduction, and the yield parameter in these plots was not significantly different from the control plots. The additional herbicide application showed no further effect on this crop variate (Figure 3). A similar trend was found for all other crop variates.

Treatment Effects as Mediated by *S. vulgaris*

Rust infection reduced the plot dry weight of *S. vulgaris* by 48% but plant numbers only by 16% when compared with the S plots (Table 1 and Figure 3). Hence, during the course of

TABLE 1. ANCOVA table of treatment effect on early yield variates of celeriac and on *S. vulgaris*. Sums of squares and significance levels of *F*-ratios are given

Source of variation	df[a]	Celeriac (mean/crop plant) Bulb diameter (mm)	Bulb FW[b] (g)	Shoot FW[b] (g)	Total FW[b] (g)	Foliage : bulb ratio	*S. vulgaris* (mean/test plot) Total DW[c] (g)	No. of plants	Mean plant DW[c] (g)
Covariate (initial crop size)	1/–	329***	1 404***	4 821***	11 431***	0.17*	–	–	–
Treatment	3/2	54*	240*	291	1 038(*)	0.44*	41 437***	16 828***	2.40**
Residual	15/16	71	241	754	1 748	0.47	17 794	2 416	1.65
Adjusted means									
Control		44.24	37.35	77.26	114.61	2.05	–	–	–
S		39.39	27.05	65.9	92.94	2.49	134.07	84.4	1.55
R		41.98	31.4	70.38	101.78	2.30	70.17	71.0	0.95
R + H		42.26	30.27	71.86	102.13	2.37	5.33	7.6	0.58

[a]Degrees of freedom for effects on celeriac and *S. vulgaris* variates respectively.
[b]FW, fresh weight.
[c]DW, dry weight.
(*)$P < 0.07$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

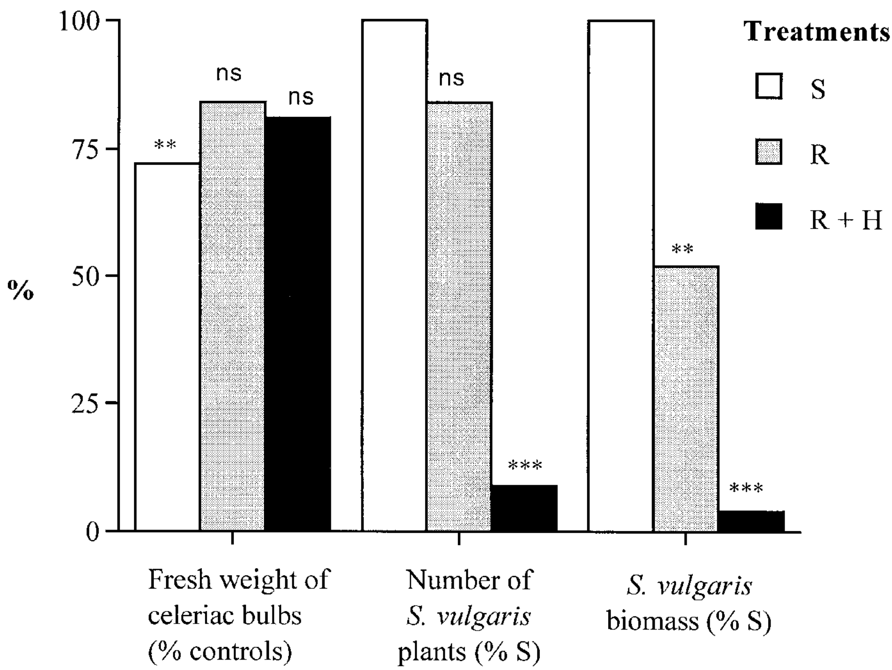

FIGURE 3. Treatment effects on early crop yield and *S. vulgaris* variates. Relative plant means are given (S, crop+ *S. vulgaris*; R, S+ rust fungus; R+ H, R+ herbicide). Differences from the respective controls were tested using simple contrasts and joint Bonferroni intervals. ns, not significant; **$P < 0.01$; ***$P < 0.001$.

TABLE 2. ANOVA table of treatment effects (fungal rust treatment with (R + H) and without (R) additional herbicide application) and plant stage on infection period of *P. lagenophorae* (treatment effects were tested at the plot level). Sums of squares and significance levels of *F*-ratios are given

Source of variation	df	Infection period
Treatment	1	2.8
Plot	8	64.6***
Plant stage	11	197.8***
Treatment × plant stage	11	12.9
Residual	611	759.9

***$P < 0.001$.

the experiment, the rust fungus *P. lagenophorae* mainly influenced plant biomass and had only a small effect on plant survival. The herbicide killed most *S. vulgaris* plants, but this was too late to influence crop yield (Table 1 and Figure 3).

S. vulgaris biomass was used as a further covariate to investigate whether treatment effects on the crop could be explained adequately through their effect on weed biomass. When analyzed at the plot level, *S. vulgaris* biomass, as assessed at the end of the experiment, significantly explained the variation in all crop variates ($P < 0.01$). For bulb diameter and bulb fresh weight no independent treatment effects were found ($P > 0.5$). Treatments, however, still had an effect on the fresh weight of the shoot, independently of their effect on weed biomass. This was mainly because crop values in the R + H plots were lower than expected based on observed weed biomass (data not presented).

Epidemic of Rust Fungus and Effects of Plant Stage on Infection Period

The inoculum plants transferred were relatively old, surviving in the field for only 1 week, and sporulation may have been limited to a few days. The infection period—in this case the time interval between transfer of the inoculum plants and the onset of sporulation—was 17 days on average. The variation in infection period within plots was relatively low, but it varied significantly among plots (Table 2), ranging from 15.9–17.9 days.

The additional herbicide application had no influence on the infection period (Table 2). It did, however, have a highly significant effect on the developmental stage of *S. vulgaris* plants at the time inoculum plants were transferred to the plots (Table 2). A significant negative linear correlation was found between plant stage and infection period (Figure 4). Sporulation of *P. lagenophorae* occurred on younger plants (one to two leaf stage) ca. 2 days later than on older plants (nine to 11 leaf stage). For this analysis, only plants with sporulating *P. lagenophorae* up to 3 weeks after transfer of the inoculum plants were considered. At that time, less than 1% of the *S. vulgaris* plants in the S plots showed signs of infection (i.e. were sporulating). Observations indicated that a second cycle of aeciospore production may have started around 4 weeks after the transfer, and by the end of the experiment (6 weeks after the transfer) almost all plants of the entire experiment showed symptoms of fungal rust infection.

Effect of the Herbicide and Interactions with Plant Stage and Fungal Rust Infection

The effect of the herbicide was severe, and most plants were dead 2 weeks after it was applied. The evaluation of herbicidal action by classifying phytotoxicity symptoms showed a significant effect of the plant developmental stage at the time of application (Table 3). Damage symptoms were found earlier in younger plants, which died before older, flowering plants (Figure 5). If results were adjusted for the effect of plant stage, the presence of the rust infection at the time of herbicide application had no significant effect on damage caused by the herbicide (Table 3).

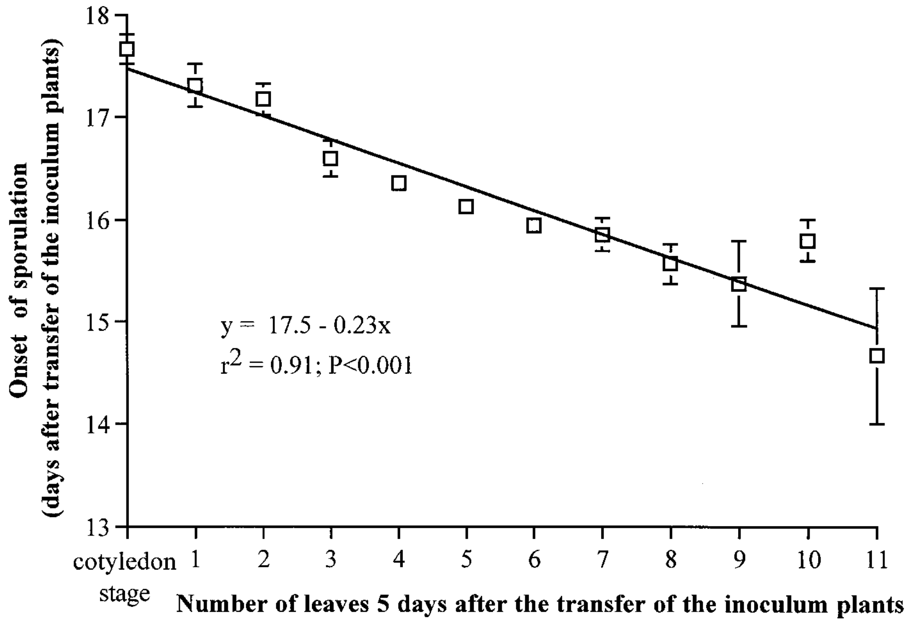

FIGURE 4. Effect of plant stage on infection period of the rust fungus *P. lagenophorae* (mean and standard error).

TABLE 3. ANCOVA table of effects of plant stage (covariate) and presence of fungal rust infection on phytotoxicity symptoms of *S. vulgaris* caused by the herbicide (chlorbromuron). Herbicidal effects were assessed 3 days after application. Sums of squares and significance levels of F-ratios are given

Source of variation	df	Score of phytotoxicity symptoms caused by the herbicide
Plot	4	182.2***
Plant stage (covariate)	1	419.2***
Fungal rust infection (yes/no)	1	4.8
Plant stage × fungal rust	2	13.7
Residual	413	1811.5

***$P < 0.001$.

DISCUSSION

Effects of Competition

The experiment demonstrated substantial competition of *S. vulgaris* on celeriac during the first 10 weeks after sowing of the weed, resulting in 28% reduction in bulb fresh weight (Table 1 and Figure 3). This was especially impressive, as the realized density of *S. vulgaris* on average was only ca. 50 plants/m^2. A field survey in Switzerland showed this density to be quite realistic, although densities of well over 100 and even 200 plants/m^2 have been observed in field vegetables and newly established orchards (Müller-Schärer & Wyss, 1994). In a field experiment, Paul and Ayres (1987) found over 50% reduction of lettuce fresh weight 10 weeks after sowing the crop at a *S. vulgaris* density of 256 plants/m^2. Similarly, Wyss (1995) observed a 50% reduction in commercially grown carrots when *S. vulgaris* was sown at a density of 1000 plants/m^2. *S. vulgaris* is typically an early competitor, based on

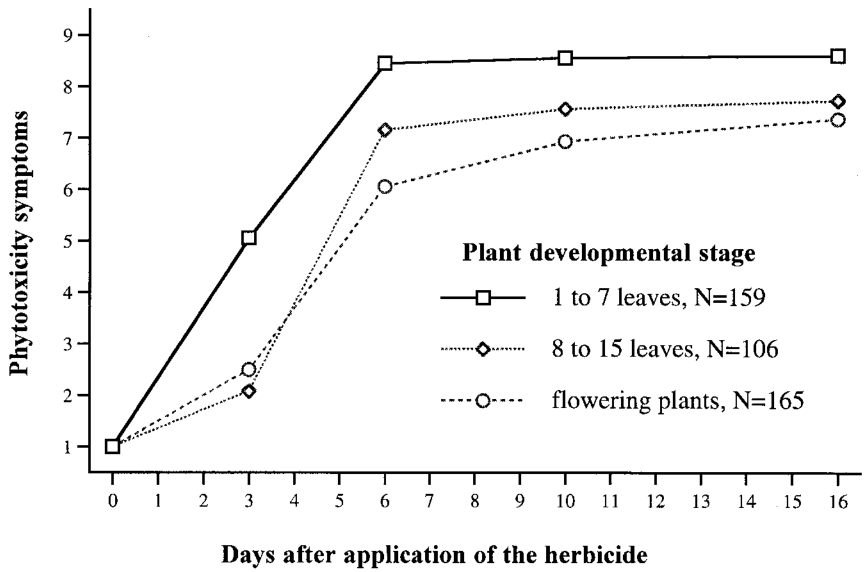

FIGURE 5. Plant stage-specific effects of the herbicide treatment; phytotoxicity symptoms are based on the EWRS classification scheme. Plant developmental stage was assessed at the time of herbicide application.

its short generation time of 3 months during the summer and its rapid establishment after soil disturbance. Hence, its impact can be assumed to be higher in sown crops compared with drilled drops. The observed results are well in agreement with those of studies on the critical time period for weed competition in vegetable crops, showing that yield reductions are mainly caused by competition during the first half of the vegetation period (Roberts, 1976; Müller-Schärer & Baumann, 1993). For celery and celeriac, Schwarz *et al.* (1990) recommend a weed-free period between the third and seventh week after planting.

Effects of the Rust Fungus

Due to adverse weather conditions, the inoculum plants were transferred relatively late (i.e. 23 days after sowing and when *S. vulgaris* plants had an average of 4.3 leaves already developed). The effect of the fungal rust treatment was still substantial, reducing crop losses due to competition with *S. vulgaris* by nearly 50%. The fact that this effect was mainly mediated by reducing *S. vulgaris* biomass and not survival is most positive, as infected plants still contribute to soil cover and may thus help to suppress later germinating weed species. A significant reduction in yield loss through infection of *S. vulgaris* by *P. lagenophorae* was also found by Paul and Ayres (1987) for lettuce, with a threshold of around 4000 rusted plants/m^2, below which lettuce yield were not significantly reduced compared with uninoculated plants. Similarly, in 1:1 mixtures of lettuce and *S. vulgaris* grown in tubs, lettuce yield was reduced by about one third at densities equivalent to 560 and 1120 plants/m^2 when plants were uninfected compared with infected ones (Paul & Ayres, 1987).

The spread of the rust fungus from the inoculum plant was relatively fast, but was non-uniform, depending on wind directions. A more in-depth study on the development of such primary foci is in preparation (Frantzen & Müller-Schärer, unpublished). The time between transfer of the sporulating inoculum plant to the onset of sporulation on the test plants in the field averaged only 17 days. This speed is comparable to results obtained from garden plot experiments, where infection periods of 12–18 days were observed for distances of up to 1.2 m from the inoculum plant. These values differed only slightly from those of plots with full-area application of aeciospores, showing infection periods of 10–14 days (Frantzen & Müller-Schärer, unpublished). The fact that nearly all plants in all experiments were infected at the end of the experiment (i.e. 6 weeks after transfer of the inoculum plants) clearly shows the potential of rapid natural spread of this rust fungus. Further, a clear plant stage-specific effect of the infection process already found in previous studies (Müller-Schärer & Frantzen, 1996; Wyss, 1997) could be confirmed. Infected plants that died often had infected shoots, especially at the shoot base. Such hypocotyl infection leading to plant kill has also been reported by Paul and Ayres (1986), and may be caused by secondary infections of necrotrophic fungi.

Effects of the Herbicide

The herbicide killed most *S. vulgaris* plants within 2 weeks of application (Figure 5), even though only 75% of the minimal recommended dose was applied and most plants were already flowering at the time of application. This treatment, however, was too late to reduce the effect of competition by the weed on celeriac yield (Table 1 and Figure 3). As the rust–herbicide interaction was to be studied, the present authors intended to apply the herbicide 1 week after the transfer of the inoculum plants. However, unfavourable weather conditions (see Figure 2) resulted in a further delay of 2 weeks. Application of this herbicide is generally recommended at the two to four leaf stage of the weeds (Baumann, 1996). The observed mortality of flowering plants was not expected on the basis of preliminary experiments (Rieger, 1996) or application guidelines (Baumann, 1996), and may reflect the increased susceptibility of rusted plants to the herbicide. As the herbicide was not applied as a sole treatment this hypothesis could not be tested. The fact that crop values in the R + H plots were lower than expected based on the observed final weed biomass (ANCOVA) could be due to both the limited time available to mediate reduced biomass to crop yield and to direct phytotoxic effects of the herbicide (J.-P. Mayor, personal communication, 1997). The observed plant stage-specific effect of the herbicide has also been found in preliminary greenhouse experiments (Rieger, 1996), and is a common phenomenon of foliar-applied herbicides. The greater than expected effects of the herbicide limited the scope for detailed, differential assessment of the impact of the herbicide and the rust. Analysis of such interactions between chemical and biological control is most important, as joint applications may be necessary to control other components in the weed complex. Both positive (synergistic) and negative effects of herbicides on the performance and efficiency of fungal pathogens have been described, the outcome sometimes also varying between simultaneous and sequential application of the pathogen and the herbicide (Phatak *et al.*, 1983; Callaway *et al.*, 1987; Scheepens, 1987; Wymore *et al.*, 1987; Hasan & Ayres, 1990). In this context, rust fungi are of special interest; as they erupt through the epidermis and cuticle of the host in order to liberate their spores, they destroy the high cuticular resistance to diffusion of water vapour away from the leaf and the movement of foliar-applied herbicides into the leaf (Hasan & Ayres, 1990).

CONCLUSIONS

The change in weed control requirements in crops has resulted in changes to the biological control approach (Müller-Schärer & Scheepens, 1997). The system management approach does not involve weed kill, but relies on both the competitive interaction between the target weed and non-host plants (i.e. the crop and other weed species) and the natural spread of the control agent. Unfortunately, little is known of the dynamics of the interaction between the control organism and plant competition. However, several studies, mainly from biological weed control literature, have clearly shown that disease reduces host competitive fitness in inter- and intra-specific mixtures with non-hosts (Burdon *et al.*, 1984; Massion & Lindow, 1986; Paul & Ayres, 1987; DiTomaso *et al.*, 1996; Sheppard, 1996). Ayres and Paul (1990) reviewed studies of the impact of *P. lagenophorae* on competition of *S. vulgaris* with various non-host plants. The main effect of the rust fungus was to promote growth of the non-host, but the proportions of host : non-host, particularly plant density, were found to influence competition greatly. As already mentioned, disease increased the threshold density at which weeds reduced crop yield (Paul & Ayres, 1987). In all these experiments, the rust fungus was applied repeatedly on all plants to be treated. The present study showed that similar effects could be achieved by using the intrinsic potential for natural spread of the rust fungus, thus confirming the potential of the system management approach in biological weed control in crops.

Further data are needed to identify the critical period of weed–crop competition for the target crops envisaged (Müller-Schärer & Baumann, 1993) in order to determine the time available in which adequate pressure on the *S. vulgaris* population can be achieved. Secondly, the consequences of a successful suppression of the target weed population for biomass and abundance of other species in the weed complex need to be studied, particularly in combination with commonly used herbicides. Thirdly, *S. vulgaris* populations may be composed of several genotypes, and recent studies have shown genotype-specific reactions to a given *P. lagenophorae* line (Müller-Schärer & Frantzen, 1996). Hence, strategies to avoid the build-up of resistant/tolerant populations may have to be developed. Finally, more detailed knowledge on the type and speed of the epidemic on a larger spatial scale will be necessary to identify the 'density' of initial inocula needed to achieve adequate control. Various greenhouse and field studies on these four topics are underway or will soon be started.

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