

Biological control of *Senecio vulgaris* in carrots (*Daucus carota*) with the rust fungus *Puccinia lagenophorae*

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Abstract

Senecio vulgaris is a troublesome weed in horticulture that is tolerant or resistant to a range of herbicides, and is therefore a candidate for biological control. The rust fungus *Puccinia lagenophorae* is a potential control agent, but being biotrophic, it is not suitable for use as a mycoherbicide. We tested the effects of induced rust epidemics on *S. vulgaris*, and investigated the resulting shading dynamics within this system. We sowed carrots at 267 seeds m⁻² on five farms in western Switzerland in plots either with or without *S. vulgaris* seeds (also at 267 seeds m⁻², within crop rows), and with or without strong sources of rust spore (four inoculum sources placed every 2 m along crop beds). Plots with *S. vulgaris* and no inoculum source produced low total carrot yields (18% of yield from *S. vulgaris*-free plots), whereas plots with *S. vulgaris* plus rust inoculum sources produced 48% of the yield from *S. vulgaris*-free plots. There were, however, no significant differences in several commercially important yield parameters such as the number of first grade carrots between *S. vulgaris*-free plots and those with *S. vulgaris* plus inoculum sources. Carrots grown with *S. vulgaris* were smaller and had skewed size distributions compared with the weed-free controls, but adding rust inoculum reduced this effect. This reduced size variability and reduced weed competition have important economic benefits to farmers. Carrots had longer leaves when grown with *S. vulgaris*, suggesting that carrots and *S. vulgaris* competed for light. Percent ground cover and height of *S. vulgaris* relative to carrots was reduced by the presence of rust, and these effects were most obvious one month after placing inoculum sources in the field. Our results are encouraging, even with artificially high weed competition, but further research is needed before this paradigm can be proposed for practical applications.

Senecio vulgaris, ein hartnäckiges Unkraut im Gartenbau, ist tolerant oder resistent gegenüber mehreren Herbizidgruppen und daher zur biologischen Bekämpfung geeignet. Der Rostpilz *Puccinia lagenophorae* gilt als potentieller Kontrollorganismus, ist aber als biotropher Pilz nicht als Mycoherbizid einsetzbar. Wir untersuchten die Wirkung dieses Rostpilzes auf *S. vulgaris* durch Induktion und Stimulation einer Epidemie, und analysierten die resultierende Beschattungsdynamik dieses Systems. Wir säten Karotten (*Daucus carota*) in einer Dichte von 267 m⁻² (100 m⁻¹) auf fünf Betrieben in der Westschweiz in Parzellen mit und ohne zusätzliche *S. vulgaris* Samen (ebenfalls 267 m⁻² in den Karottenreihen), und mit oder ohne Rostpilzinokulum (je vier Inokulumpflanzen alle 2 m über die gesamte Parzellenlänge). Parzellen mit *S. vulgaris* und ohne Rostpilzinokulum ergaben einen geringen Karottenertrag (18% des Ertrages der Unkraut-freien Parzellen), während Parzellen

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mit *S. vulgaris* und Rostinokulum 48% des Unkraut-freien Ertrages erzielten. In einigen wirtschaftlich wichtigen Ertragsparametern wie Anzahl Karotten erster Qualität bestanden jedoch keine signifikanten Unterschiede zwischen den Unkraut-freien und denjenigen mit *S. vulgaris* und Inokulum. Karotten, die mit Unkraut wuchsen, waren kleiner und hatten eine schiefe Größenverteilung im Vergleich zu den Unkraut-freien Kontrollen, und die Zugabe des Pilzes reduzierte diesen Effekt. Diese reduzierte Heterogenität und geringere Unkrautkonkurrenz bedeuten einen wichtigen wirtschaftlichen Nutzen für den Produzenten. Karotten, die in Konkurrenz mit dem Unkraut wuchsen, hatten längere Blätter, was auf Lichtkonkurrenz zwischen Karotten und *S. vulgaris* hindeutet. Die Anwesenheit des Rostpilzes reduzierte die relative Bodendeckung und Höhe von *S. vulgaris* im Vergleich zu Karotten, und dieser Unterschied war einen Monat nach dem Transfer der Inokulumspflanzen ins Feld am größten. Unsere Resultate sind trotz des applizierten, künstlich hohen Unkrautdruckes ermutigend, weitere Forschung ist jedoch notwendig, bevor dieses Konzept zur Einführung in die Praxis vorgeschlagen werden kann.

Key words: *Puccinia lagenophorae* – groundsel – rust pathogen – weed biocontrol – weed competition – allometry – shading – system management approach – size inequality

Introduction

Senecio vulgaris L. (Asteraceae) is a troublesome weed in organic horticulture (Peacock 1991) and in conventional farms in many parts of the world (Holm et al. 1973), which requires new weed control methods. Herbicides registered for use in umbelliferous (Apiaceae) crops such as carrot (*Daucus carota* L.) often have little effect on *S. vulgaris* (Baumann 2000). Given the community pressure to reduce chemical use in agriculture (Sindel 2000) and the ability of *S. vulgaris* to rapidly develop resistance to herbicides (Ryan 1970, Müller-Schärer & Wyss 1994), *S. vulgaris* is a candidate for biological control.

The rust fungus *Puccinia lagenophorae* Cook (Basidiomycetes: Uredinales) is a potential biological control agent against *S. vulgaris* (Frantzen & Hatcher 1997). Naturally occurring *P. lagenophorae* epidemics in Europe are commonly limited by availability of spore early in the growing season (Paul & Ayres 1986, Frantzen & Müller-Schärer 1999, Leiss & Müller-Schärer 2001), unfortunately crops often appear to be most sensitive to competition from *S. vulgaris* early in the season (Peacock 1991, Müller-Schärer & Rieger 1998). Increasing the amount of *P. lagenophorae* spore present early in the growing season would probably reduce yield losses resulting from *S. vulgaris* competition. *Puccinia lagenophorae* is an obligate parasite, and therefore difficult to produce in sufficient quantities for use in inundative mycoherbicides.

Rust epidemics can be initiated by placing infected *S. vulgaris* plants into weed-infested crops. This approach is part of the System Management Approach (SMA) to weed biocontrol (Müller-Schärer & Frantzen 1996, Müller-Schärer & Rieger 1998), where

the weed-pathogen system is manipulated to make the weed less competitive. The SMA has reduced crop yield losses due to *S. vulgaris* (Frantzen 2000, Müller-Schärer & Rieger 1998). There is, however, a need for further large scale experiments to verify these results. Previous investigations used planted crops, had no replication (Frantzen 2000) or did not entirely prevent infection between plots on the one farm (Müller-Schärer & Rieger 1998). Furthermore, crops were harvested before they reached marketable size, so it is unknown how much crops can compensate for early setbacks from competition, as *S. vulgaris* can begin senescing naturally c. 2 months after emergence.

A modelling framework, which combines rust epidemiology with crop-weed interactions, has been elaborated for the SMA (Frantzen et al. 2001). The epidemiology of rust spread through *S. vulgaris* populations has been well studied (Frantzen & Müller-Schärer 1998, Frantzen & van den Bosch 2000), however the effects of *S. vulgaris* with and without rust on crop yield as a function of time needs to be further explored under field conditions (Frantzen et al. 2001). In a small scale field study, Frantzen (2000) observed a relationship between time, severity of *S. vulgaris* infection, and celeriac (*Apium graveolens*) yield within 2.7 m of inoculum sources, when celeriac was harvested prematurely (8 weeks after planting). Together with predictions from the abovementioned theoretical studies, this indicates that inoculum sources placed every 2 m throughout a crop may be adequate for the SMA. The mechanisms involved in *P. lagenophorae* – *S. vulgaris* – crop interactions have been poorly investigated to date, but a better understanding of these mechanisms would help develop a more realistic modelling framework, and in understanding size distribution of individual carrots.

As there are minimum and maximum size thresholds for marketable carrots (eg Anon 1994), size distributions are commercially important. Plant populations commonly comprise a few large individuals with many smaller plants, and such size inequality may increase with increasing competition (Weiner 1985). Carrot size variability decreased with the logarithm of size when carrot growth was affected by intraspecific competition (Li et al. 1996). Burdon et al. (1984) investigated how rust infection affected size distributions of resistant and susceptible *Chondrilla juncea* populations growing in competition, but little is known about size distributions when interspecific competition is altered by a pathogen. The marketable portion of carrot plants is also influenced by patterns of biomass allocation within individual plants, which can be affected by both intra and interspecific competition (Currah & Barnes 1979, Li & Watkinson 2000). Little is known about how these patterns change when interspecific competitors are affected by a pathogen.

Celeriac plants were more variable in size when grown in the presence of *S. vulgaris* than in weed-free plots, and even more variable when a *P. lagenophorae* epidemic was induced (Frantzen 2000). The effect of the rust can be explained by the uneven spread of the pathogen from one end of the plot, resulting in heterogeneous levels of weed competition within the plot. Regularly spaced inoculum sources within a *S. vulgaris* population may result in homogeneous levels of infection and therefore weed competition, and reduce crop plant variation from that of weedy plots without inoculum sources. Such reduced variability, combined with higher total yield should result in increased marketable yields in plots with *S. vulgaris*.

This paper aims to investigate the effects of *S. vulgaris* on carrot yields, and how this is affected by *P. lagenophorae* applied using the SMA. We test this using large field plots, with multiple sources of infection, and make comparisons with plots with natural levels of rust infection. We also investigate shading dynamic as a mechanism involved in crop-weed interactions and size distributions.

Materials and methods

Site Descriptions and Experimental Design

Field trials were conducted on five vegetable farms near Fribourg, Switzerland (Table 1). Three main treatments were applied at each site; plots had either no *S. vulgaris*, *S. vulgaris* without inoculum plants, or *S. vulgaris* plus four inoculum plants placed every 2 m along each bed. The *S. vulgaris* treatments with and without inoculum plants were placed near opposite ends of each farm in order to reduce the probability of

cross infection. Each farm had two replicates of the *S. vulgaris*-free plots to include effects of spatial heterogeneity. Treatments were allocated at random on each farm within this general pattern.

Plots were 10 m long along freshly prepared 1.3 m wide vegetable beds. Four rows of carrot seeds (cv. Napoli 1.4–1.6 mm; Bejo Zaden, Holland) were sown in all plots at 100 seeds m⁻¹. Rows were 30 cm apart along freshly prepared beds. *S. vulgaris* seeds, when sown, were at 100 seeds m⁻¹, together with the carrot seeds. *S. vulgaris* seeds were of the Swiss line described by Wyss & Müller-Schärer (1999), from plants grown in the University of Fribourg glasshouse. Plots were sown on 4 May at Sedeilles, Rosé and Cousiberlé, and 9 May 2001 at Courlevon and Posieux.

Plots without inoculum sources may be contaminated by plots with inoculum plants, so we included additional fungicide treatments to compare carrot yields from plots with low levels of rust to those from plots that were essentially rust-free. Two treatments were applied on the three non-organic farms; we sprayed Difenoconazol (Belrose Spray, Maag, Dielsdorf Switzerland) weekly to runoff (c. 150 g a.i. ha⁻¹) onto plots with carrots and *S. vulgaris*, and onto plots with only carrots. There were two replicate plots of these fungicide treatments per farm, each 2 m long, located at random near the plots with rust inoculum.

Two glasshouse trials were established to determine the effects of Difenoconazol on carrot, *S. vulgaris* and the rust. *S. vulgaris* plants were assigned to four treatments 14 days after germination; plants were sprayed with Difenoconazol solution until runoff, sprayed with *P. lagenophorae* (4 mg plant⁻¹ ELS isolate (Wyss & Müller-Schärer 1999), in distilled water), sprayed with fungicide plus rust, or unsprayed (control). Plants were then enclosed in plastic for 24 hours to ensure high humidity. There were eight replicates per treatment. The percentage of the third true leaf that was infested by rust was estimated using image analysis for each plant (NIH Scion Image 1.57, see Leiss & Müller-Schärer (2001)) two weeks after the rust was applied. Plants were dried and weighed after 3 weeks. In a second experiment, carrot plants were subjected to three treatments; plants were either sprayed weekly to runoff, sprayed every two weeks, or unsprayed (control). Treatments were applied for 7 weeks, then carrot roots and shoots were dried then weighed.

Inoculum plants were grown in the University of Fribourg glasshouse, and were sprayed with rust as above at 4–5 leaf stage, and again 1 week later. These plants were then enclosed in plastic for 24 hours after spraying, then kept in the glasshouse until placed in the field. Inoculum plants were placed in field when sporulating, beginning on 18 May, when *S. vulgaris* seedlings first emerged. Any dead plants were replaced.

Plots were kept free of weeds other than *S. vulgaris* growing in rows throughout the experiment, by spraying with Pendimethalin (160 g a.i. ha⁻¹, Stomp SC, Maag, Dielsdorf Switzerland), which does not affect carrots (Baumann 2000), *S. vulgaris* or the rust (J. Frantzen pers. comm.) on 30 May on the non-organic farms. All plots were hand weeded when necessary.

Rust spread

Ten *S. vulgaris* plants chosen at random from each plot every week were checked for the presence of rust pustules. To investigate the timing of natural rust dynamics, an additional site was established as above, but without any inoculum sources. Sampling and weeding always proceeded from the uninoculated plot towards the inoculated plot on each farm, and hands and implements were washed and sprayed with alcohol between farms.

Carrot Yield and Allometry

Carrots were sampled twice; on 11 July, 9 weeks after sowing when most *S. vulgaris* had died in the plots with inoculum sources, and again on 8 and 9 August, 13 weeks after sowing when they were marketable in the *S. vulgaris*-free plots. Five subplots of 50 cm along one row were harvested from each experimental plot. These subplots were placed at random in one of the centre two rows of each plot, but not within 1 m of the plot ends. In an effort to reduce variation from patchy carrot emergence, subplots with more than 10 cm between any neighbouring carrots were replaced by another randomly chosen subplot. One subplot was taken from each fungicide plot. In the second harvest, subplots were placed as above, but any subplots within 30 cm of the area sampled in the first harvest were replaced with another randomly chosen subplot.

For both harvests, the maximum root diameter, root length and fresh weight, maximum leaf length and shoot fresh weight were measured for each of ten randomly selected carrots per subplot. The number of carrots in each subplot was also counted. In the second harvest, carrots were graded as either marketable (1st or 2nd grade), or not marketable. First grade carrots weigh 40–200 g, are <20 cm long and <30 mm in diameter, and second grade carrots have crown diameters >30 mm (Schweizerische Gemüseunion 1994). Data was pooled across all subplots in each plot. The root and shoot dry weights of 73 randomly selected carrots from Rosé were also measured. In this paper “carrot root” refers to orange portions of storage root >2 mm diameter, and “carrot yield” refers to fresh weight of these carrot roots per unit area.

Shading

The height of 10 randomly chosen carrot plants in each plot, and of neighbouring *S. vulgaris* plants, were recorded once a week most weeks. The percentage of ground covered by carrot and living *S. vulgaris* foliage in each plot were estimated each week to the nearest 5%. These measurements all commenced on 23 May, when carrot and *S. vulgaris* emergence was first noted.

Data Analyses

The time when 50% of plants in each plot were infected was estimated using a log-logistic equation similarly to Frantzen & Müller-Schärer (1998). Equations were fitted using nonlinear least squares algorithms (MathSoft 1999). Effects of fungicide on carrots and *S. vulgaris* dry weights were assessed by ANOVA, and appropriate orthogonal contrasts were used to compare individual treatments. The proportion of *S. vulgaris* leaf area infected was analysed by ANOVA after appropriate transformation, and the proportion of plants sprayed with rust that showed signs of rust infection was compared between fungicide treatments by logistic regression.

Total carrot yield per unit area was estimated for each plot by multiplying the total number of carrots by the mean root fresh weight for each subplot, and then averaging this yield over all subplots in each plot. Yield parameters were analysed with ANOVA, after appropriate transformation and removing site effects as random intercept terms using restricted maximum likelihood algorithms (REML) (MathSoft 1999). Differences between the two weed-free plots on each farm were small, so total yield in each plot was compared by ANOVA, rather than comparing yields in treatment plots relative to their adjacent weed-free plots. Sites were compared in separate analyses after similarly removing treatment effect as a random factor. Treatments without fungicide were compared across all farms, and tests of fungicide treatments were performed using data from the three conventional farms only. Comparisons between individual treatments were performed by assigning orthogonal contrasts, allowing for unbalanced design.

Carrot size heterogeneity was assessed by calculating Gini coefficients of carrot root fresh weight for each plot, with a correction for small sample size (Weiner & Solbrig 1984). These values were then compared between treatments as above. Coefficients of variation were regressed against mean carrot weight for each plot, and a range of functions was fitted using nonlinear least squares (MathSoft 1999).

The biomass distribution within individual plants was investigated for carrots from the first harvest, when competition effects were likely to be strongest.

The equation $W_r = aW_s^b$ (W_r is root fresh weight, W_s is shoot fresh weight, a and b are constants) was fitted separately for each treatment. The length of the longest leaf of each plant was similarly fitted against shoot fresh weight. Coefficients were obtained using weighted least squares (Gamma distribution). Effects of the treatments on these variables were tested for by regressing the natural logarithm of root weight and leaf length against the natural logarithm of shoot weight, using quasi-likelihood generalised linear models in S-Plus 2000. Both these methods allow for mean-variance relationships (MathSoft 1999, Venables & Ripley 1999). Analyses were performed using fresh weights, after first determining if treatment had any effect on water content. The water content of roots and shoots of 73 carrots, randomly selected across all treatments at Rosé, was regressed against fresh weight, testing for treatment: fresh weight interactions.

The proportion of carrots that overtopped their neighbouring *S. vulgaris* plants in each plot was calculated from plant heights. This proportion was arcsine transformed, then fitted as a quadratic function of time in a linear model, with plots nested within sites as random intercept terms, fitted by REML. The percentages of groundcover provided by carrots and *S. vulgaris* were graphically presented as Loess splines over time, with Poisson error distribution (MathSoft 1999).

Results

Site Conditions and Carrot Growth

There were differences in carrot yield between sites at the first harvest ($F_{4,13} = 10.3$; $P = 0.001$), but these became less important by the second harvest ($F_{4,13} = 1.9$; $P = 0.17$) (Table 1). Rosé had noticeably higher carrot yields than other sites at the first harvest, possibly because all plots there were watered shortly after sowing. Treatment effects were consistent across all farms for both harvests. Environmental conditions, as measured by data loggers were similar across all sites (data not shown). Carrot emergence was noticeably staggered and patchy at all sites.

Table 1. Location, production method, and carrot yield (kg m^{-2}) from *S. vulgaris*-free plots at two harvest times, in the five farms used for field trials. See text for statistics and details.

Site	Location	Production	Harvest 1	Harvest 2
Courlevon	46°53.4'N, 7°6.3'E	Conventional	1.3	7.7
Cousiberlé	46°53.9'N, 7°7.5'E	Organic	1.0	6.1
Sedilles	46°46.2'N, 6°56.4'E	Organic	0.6	6.0
Posieux	46°46.1'N, 7°6.8'E	Conventional	0.8	7.2
Rosé	46°47.2'N, 7°3.4'E	Conventional	1.9	7.2

Rust Spread

Infection appeared much earlier in plots with inoculum sources than in those without, and fungicide applications delayed the onset and intensity of rust epidemics. Mean values of estimated time when 50% of plants were infected were 7 June in the *S. vulgaris* plus inoculum treatment, 10 July in *S. vulgaris* alone plots, and on 25 July for fungicide treated plots. We estimated that 50% of *S. vulgaris* plants were infected in the site without any inoculum sources (14 July) was within the range for this treatment at other sites, suggesting that inoculum sources did not unduly affect epidemics in other plots on the same farm.

If some spore did spread from plots with inoculum plants, this did not appear to unduly affect carrot yield in nearby plots without inoculum plants. Percentage yield loss in plots with *S. vulgaris* at the site without inoculum sources was within the range of similar plots at other farms. Fungicide application had no effect on carrot yield in plots with *S. vulgaris* and no inoculum at the second harvest ($F_{1,15} = 0.13$; $P = 0.73$) despite rust epidemics occurring later in these plots, or in *S. vulgaris*-free plots ($F_{1,15} = 3.1$; $P = 0.10$). Glasshouse trials confirmed that Difenoconazol had no direct effect on either carrot biomass ($F_{2,55} = 0.6$; $P = 0.55$) or *S. vulgaris* in the absence of rust ($F_{1,14} = 0.34$; $P = 0.57$), and strongly reduce severity ($F_{1,14} = 22$, $P < 0.001$) and the likelihood ($\chi = 6.9$; $P = 0.009$) of rust infection on *S. vulgaris*.

Carrot Yield

Plots without *S. vulgaris* had higher carrot yields than all other plots, but plots with *S. vulgaris* plus inoculum sources produced higher yields (52% yield loss compared to weed free) than those with *S. vulgaris* and no inoculum plants (82% yield loss, Fig. 1). These effects were consistent across two harvests. Carrot yields from weed-free plots at all farms exceeded typical Swiss carrot yields of 4.6 kg m^{-2} (Wixinger et al. 2000). Differences in yield between treatments were due more to differences in the size of individual carrots (Fig. 2), than to the number of carrots.

Size inequality varied between treatments (Gini coefficients; $F_{2,8} = 11.6$; $P = 0.004$, Fig. 2). Inequality was highest in the *S. vulgaris* treatment, lowest in the *S. vulgaris*-free treatment, and intermediate in the *S. vulgaris* plus inoculum treatment (Fig. 2).

The coefficient of variation of carrot root fresh weights (CV) at the final harvest decreased with mean root weight (μ) ($F_{1,14} = 73$, $P < 0.001$). This relationship was well described by the equation $CV = 222 - 38 \ln \mu$ ($R^2 = 0.87$). The y -intercept of this equation varied with site ($F_{4,14} = 5.0$; $P = 0.01$), but gradient did not

($F_{4,10} = 0.93$; $P = 0.49$). The number of 1st grade carrots in *S. vulgaris* plus inoculum plots was not significantly different from weed-free plots (Table 2).

Allometry and Shading

Root dry weight was linearly correlated with the fresh weight ($R^2 = 0.95$), and shoot dry weight was likewise related to fresh weight ($R^2 = 0.99$). Treatment had no effect on water content of roots ($F_{4,68} = 0.6$; $P = 0.7$) or shoots ($F_{4,63} = 2.0$; $P = 0.1$). Fresh weights were therefore used for analyses of carrot allometry, similarly to Stanhill (1977a) and Currah & Barnes (1979).

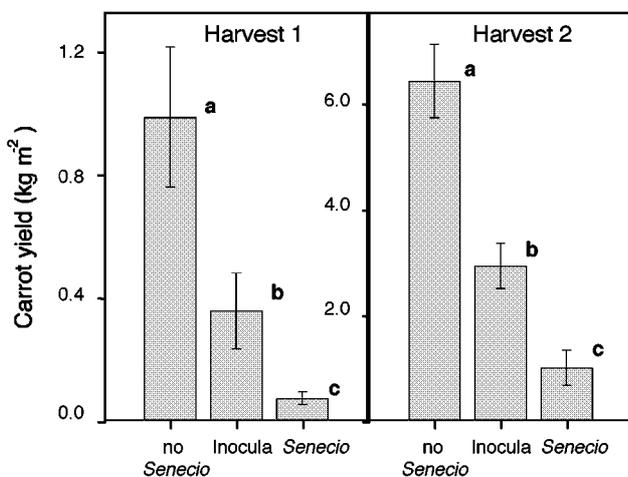


Fig. 1. Total carrot yield (root fresh weight) at two harvests, under 3 treatments; *S. vulgaris*-free (no *Senecio*), *S. vulgaris* plus inoculum plants (Inocula) or from *S. vulgaris* alone (*Senecio*). Error bars show standard errors of mixed effects linear models after site effects were removed as random variables. Different letters denote significantly different means ($P < 0.05$).

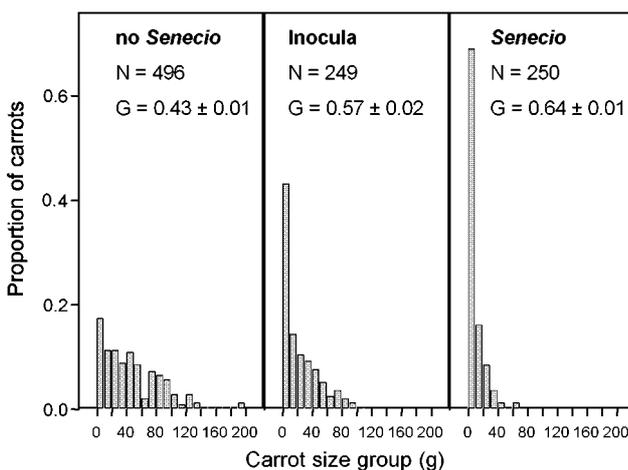


Fig. 2. Size distribution of individual carrot roots from the final harvest in three treatments: *S. vulgaris*-free (left), *S. vulgaris* plus inoculum plants (centre), and carrots with *S. vulgaris* alone (right). Data was pooled across all sites for histograms, and N shows sample size. Values of G are mean \pm s.e.m. of Gini coefficients that were calculated separately for each treatment and site.

By modelling root fresh weight (W_r) as a function of shoot fresh weight (W_s) in the equation $W_r = aW_s^b$ (a and b are constants), we found that the overall root:shoot ratio (a) did not vary between treatments ($F_{2,937} = 0.5$; $P = 0.63$; Fig. 3), but the coefficient b (a descriptor of how the root:shoot ratio varies with plant size) varied between treatments ($F_{2,937} = 24.5$, $P < 0.001$). Larger carrots in plots with *S. vulgaris* plus inoculum invested proportionally more biomass into roots than those in the other two treatments (Fig. 3). The most striking differences in plant morphology between treatments was in the leaf length (L), where both coefficients a and b in the equation $L = aWsb$ varied significantly between treatments ($F_{2,937} = 69$; $P < 0.001$, and $F_{2,983} = 18$, $P < 0.001$ respectively). Carrots had proportionally longer leaves in the plots with *S. vulgaris* and no inoculum plants, and the presence of rust inoculum reduced this effect (Fig. 3).

Table 2. Mean (and 95% confidence intervals) number of first grade carrots at the final harvest over three treatments; weed-free, *S. vulgaris* plus inoculum sources, and *S. vulgaris* without inocula. Means with different letters are significantly different ($P < 0.05$). The number of replicate plots for each treatment is also shown.

Parameter	Treatment			P
	No <i>S. vulgaris</i>	Inoculum	<i>S. vulgaris</i>	
Number of replicate plots	10	5	5	
Number 1st grade carrots (m^{-2})	31.0 ^a (23.4–38.6)	25.2 ^a (18.3–32.1)	9.5 ^b (2.6–16.4)	< 0.001
Number 2nd grade carrots (m^{-2})	10.55 ^a (7.0–14.9)	3.91 ^b (1.5–7.5)	0.02 ^c (0.0–0.8)	< 0.001

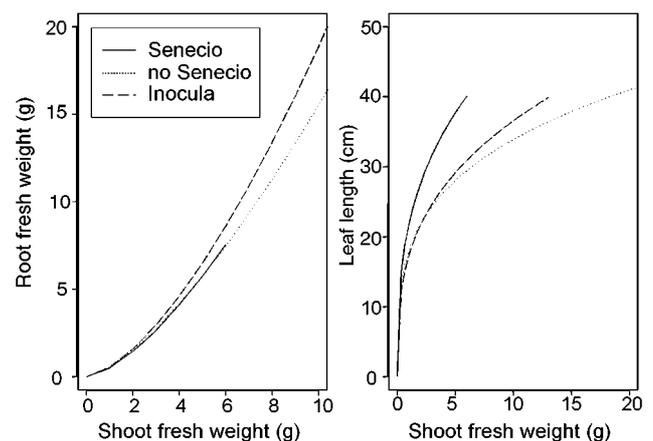


Fig. 3. Root fresh weight versus shoot weight (left), and leaf length versus shoot weight (right) for carrots from the first harvest. Lines show values predicted by equations of the form $y = ax^b$. Equations were fitted separately for each treatment; *S. vulgaris*-free (dotted line), *S. vulgaris* plus inoculum plants (dashed lines), or *S. vulgaris* alone (solid lines). Raw data are not shown for clarity, as there are thousands of points.

The proportion of carrot plants that overtopped neighbouring *S. vulgaris* plants varied overall with the addition of inoculum plants ($F_{1,58} = 5.8$; $P = 0.02$), and trends over time also varied (linear treatment:time interaction; $F_{1,58} = 28.1$; $P < 0.001$). The addition of inoculum plants allowed more carrots to overtop *S. vulgaris*, but differences between treatments were not large until c. one month after the addition of inoculum plants (Fig. 4). Carrot foliage had a higher percentage ground cover in *S. vulgaris*-free plots, and rust inoculum decreased this effect, especially one month after addition of inoculum plants (Fig. 5).

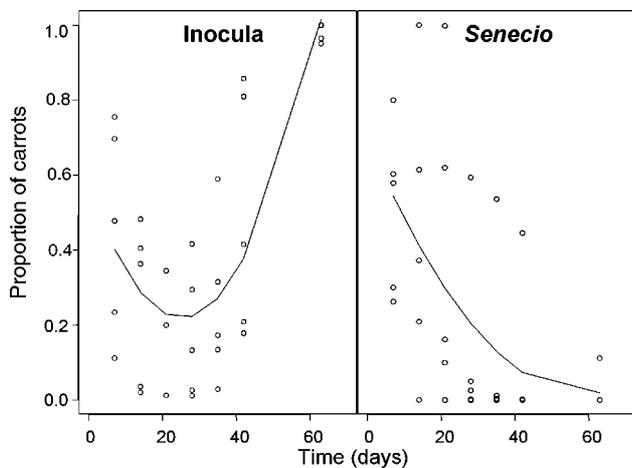


Fig. 4. The proportion of carrots that were taller than neighbouring *S. vulgaris* plants under two treatments: *S. vulgaris* plus inoculum plants (left), and *S. vulgaris* alone (right). Lines show backtransformed predicted values from linear mixed effects model, with proportion as a quadratic function of time. Time is shown in days since 23 May 2001.

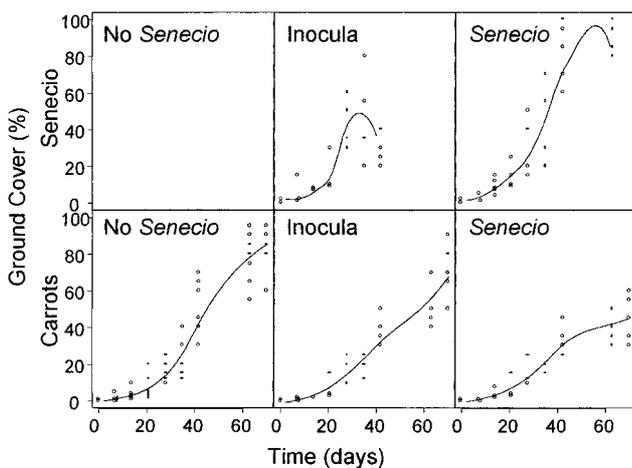


Fig. 5. Percentage ground cover of *S. vulgaris* (top), and carrot (bottom row) foliage over time (in days since 23 May). Three treatments are shown; *S. vulgaris*-free (left), *S. vulgaris* plus inoculum plants (centre) and *S. vulgaris* alone (right). Lines were fitted using Loess splines with Poisson error distribution.

Discussion

Rust Spread

Placing inoculum plants into field plots resulted in earlier rust epidemics within those plots, and effects appeared to be largely confined to each treatment plot. Fungicide applications delayed the onset of rust epidemics in the field, but this had no effect on carrot yields. This may be because crops are generally most susceptible to competition with *S. vulgaris* early in the growing period (Peacock 1991, S. Vogelgsang unpub. data). Difenconazol had no direct effects on either *S. vulgaris* or carrots in the glasshouse or field.

Carrot Yield

The key result from our experiment is that crop losses due to *S. vulgaris* were reduced from 82% to 52% of the weed-free plots when inoculum plants are placed in plots. Although the total yields from plots with rust inoculum were much less than from weed-free plots, the number of first grade carrots was similar. Carrots in this size range produce much of the farmer's income (D. Baumann pers. comm.) and are commonly sold by number rather than weight in Switzerland (Anon 1994). This suggests that the presence of a weed will not necessarily reduce farm profits if its competitiveness can be reduced – this is the SMA to biocontrol (Müller-Schärer & Frantzen 1996). This is the first replicated experiment to investigate the SMA under realistic agricultural conditions. Our results suggest that weed control measures need not rapidly kill the weed to be effective.

The presence of poorly competitive weeds might even be preferable to “clean” crops. Ground cover can impede germination of more competitive late emerging weeds, increase soil moisture, and reduce nitrogen loss from the soil (Horwith 1985, Müller-Schärer 1996). The rust reduced the size of *S. vulgaris* plants, but did not result in noticeably quick weed kill, as also found by Müller-Schärer & Rieger (1998). Most investigations of weed biocontrol agents in crops focus on weed growth and survival, rather than the crop because the mycoherbicide approach is the dominant paradigm in crop weed control (see reviews by Auld & Morin 1995, Charudattan 2000).

Carrots in our experiment were subjected to high levels of competition from *S. vulgaris* (c. 270 seeds m^{-2} , within crop rows). Natural weed infestations resulted in carrot yield losses of c. 40% (Peacock 1991), much less than in our experiments (82%). Previous field trials in *S. vulgaris* – crop systems used much lower weed densities; c. 50 m^{-2} (Müller-Schärer & Rieger 1998, Baumann et al. 2001) evenly spaced throughout plots,

and 22 m² within crop rows (Frantzen 2000). Differences in carrot yield between *S. vulgaris*-free plots and plots with inoculum sources are likely to be smaller at lower *S. vulgaris* densities, eg in presence of rust, lettuce yield was largely unaffected by *S. vulgaris* unless at high density (Paul & Ayres 1987). Therefore yield losses from weed competition may be minimal when the SMA is applied to crops with natural levels of weed infection. The effects of rust infection at a range of *S. vulgaris* densities on crop yields should to be quantified before the SMA can be proposed for practical application. The effects of *S. vulgaris* competition remains to be modelled as a function of time, however, we found treatment effects on carrot yield were very similar at 9 and 13 weeks after sowing.

Size Distribution, Allometry and Shading

We found that competition from *S. vulgaris* increased size inequality within carrot populations, a common phenomenon, especially when competition is asymmetric (Weiner 1986). Li et al. (1996) found similar results for carrots suffering intraspecific competition. In our study, size variability was reduced when rust inocula were added, contrary to the results of Frantzen (2000) for celeriac. This difference between our study and Frantzen's (2000) could be due to how evenly rust spread throughout the plots. We applied inoculum sources evenly throughout the plots, whereas Frantzen (2000) induced epidemics from one end of a 10 m long plot.

Plant size distributions are commercially important in carrot farms, as carrots can be either too large or too small for market. Carrot emergence is often staggered (Villeneuve & Leteinturier 1992), as it was in our experiment. This may result in a range of plant sizes. When plants compete for light, size inequalities may result from some plants overtopping others, and competitive effects are most likely to be seen after canopy closure (Weiner 1986). Shading appears to be important in the carrot – *S. vulgaris* system, as carrots grown with *S. vulgaris* had proportionally longer leaves. Carrots may compete with each other for light (Reid & English 2000), and light interception by celery and leeks reduced both size and reproduction of *S. vulgaris* plants (Baumann et al. 2001). Paul (1989) found that *Euphorbia peplus* plants growing with *S. vulgaris* had much more skewed size distributions than *E. peplus* monocultures. Interestingly, infecting *S. vulgaris* plants with rust had little effect on *E. peplus* size distribution. *E. peplus* was generally overtopped by *S. vulgaris*, even when rusted, and Paul terminated his experiment 39 days after inoculation. In our trials the largest height differences between carrot and rusted *S. vulgaris* occurred later than this, and carrots and *S.*

vulgaris had similar heights at the beginning of the experiment.

The coefficient of variation in carrot root weight decreased with the logarithm of mean plant weight. Li et al. (1996) found a similar relationship for carrots grown under varying levels of intraspecific competition in a glasshouse. We found coefficients of variation varied overall between sites, but the relationship between CV and mean carrot weight across treatments was consistent across sites.

Allocation of biomass to carrot roots and shoots appears to be mainly determined by carrot cultivar (Hole et al. 1983) and not by intraspecific competition (Stanhill 1977b, Hole et al. 1983). Li & Watkinson (2000), however, found carrot root:shoot ratios were affected by both inter and intraspecific density, and their results, like ours, were variable and difficult to interpret. These papers, and our experiments investigated carrot storage root, and biomass allocation to fibrous roots may be more affected by competition. Interspecific interactions had strong effects on the relative leaf lengths of carrots, suggesting that carrots competed with *S. vulgaris* for light.

Addition of rust inoculum strongly changed the shading and groundcover dynamics in our experimental plots, reducing *S. vulgaris* plant height and groundcover. Rust infection resulted in decreased net photosynthesis of *S. vulgaris* plants, due mainly to changes in total leaf area (Paul & Ayres 1987). Plants in our experiments were grown in presumably high nutrient soils, and experienced several hot dry spells after rust had spread, and both these factors are likely to maximise the effect of the rust on *S. vulgaris* plants (Paul & Ayres 1984). Effects of rust pathogens can vary with environmental conditions between years (DiTommaso et al. 1996), however effects of the rust were consistent between sites in our experiment.

Conclusions

Interactions between carrot and *S. vulgaris* appeared to involve competition for light, and adding rust sources into experimental plots allowed more carrots to overtop neighbouring *S. vulgaris* plants. Adding these sources of rust inoculum to *S. vulgaris* infested crops resulted in fewer very small carrots, and more carrots of marketable size than in plots with *S. vulgaris* without inoculum plants. Moreover, adding rust sources resulted in more evenly sized carrots, an important economic yield attribute. There were large differences in total carrot root yield between weed-free plots and plots with *S. vulgaris* plus rust inoculum sources, but these differences are likely to be much less when carrots grow under more realistic, lower levels

of weed competition. Further investigations into this system should ideally use naturally occurring weed infestations.

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