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Population dynamics of the annual plant *Senecio vulgaris* in ruderal and agricultural habitats

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Abstract

The annual plant *Senecio vulgaris* has migrated from ruderal to agricultural habitats resulting in weed populations. The population dynamics of *S. vulgaris* and its naturally associated rust fungus *Puccinia lagenophorae* were investigated as a basis for the biological control of *S. vulgaris* with the rust. A detailed basic study at a single ruderal site and a parallel investigation at each five ruderal and five agricultural sites were conducted from April to November 1997. During the whole period of study the spatial distribution of plants was aggregated and plants showed a relatively large size hierarchy as indicated by mean values of the Gini coefficient higher than 0.5. Seedling establishment appeared to be a major factor influencing the dynamics of *S. vulgaris*. The importance of seedling establishment, together with the observed short generation time of 5 weeks and the broad range of plant sizes at reproduction classifies *S. vulgaris* as a ruderal strategist. The population dynamics of *S. vulgaris* differed between the ruderal and the agricultural habitat. Plants of *S. vulgaris* at the ruderal habitat survived over winter, resulting in greater population sizes (0.1 to 1 of the maximum) and a majority of plants in flower and seed set (81.9%) in spring. At the agricultural habitat, where only a few *S. vulgaris* winter due to weed control measures, population sizes in spring were smaller (0 to 0.16 of the maximum) with mainly vegetative plants (66.7%). The limited number of suitable hosts at the agricultural habitat in spring lead to a delay of rust infection until August, in contrast to the ruderal habitat where the rust was already present in April. In both habitats mature plant stages were more susceptible to rust infection than vegetative stages. Manipulating the dynamics of the host over winter may enhance rust epidemics in spring serving as biological control of *S. vulgaris.*

Die annuelle Pflanze *Senecio vulgaris* ist aus ruderalen Habitaten in die Landwirtschaft abgewandert, wo sie sich als Unkraut etabliert hat. In dieser Studie wurde die Populationsdynamik von *S. vulgaris* und ihres natürlich vorkommenden Rostpilzes *Puccinia lagenophorae* in bezug auf die biologische Kontrolle von *S. vulgaris* mit dem Rost untersucht. Es wurden eine detailierte Basisstudie an einem ruderalen Standort sowie parallel dazu verlaufende Untersuchungen an je fünf ruderalen und landwirtschaftlichen Standorten von April bis November 1997 durchgeführt. Während des gesamten Beobachtungszeitraumes war die räumliche Verteilung der Pflanzen aggregiert, und die Pflanzen wiesen eine relative starke Größenhierarchie, angezeigt durch Durchschnittswerte des Gini Koeffizienten größer als 0.5, auf. Die Etablierung von Keimlingen scheint ein wichtiger Fakor für die Populationsdynamik von *S. vulgaris* zu sein. Die Bedeutung der Etablierung von Keimlingen, sowie die beobachtete kurze Generationszeit von fünf Wochen, und die breite Streuung der

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Pflanzengröße zu Beginn der Reproduktion klassifizieren *S. vulgaris* als einen r-Strategen. Die Populationsdynamik von *S. vulgaris* zwischen dem ruderalen und dem landwirtschaftlichen Habitat war unterschiedlich. Pflanzen von *S. vulgaris* im ruderalen Habitat überwinterten, was eine größere Population (0.1 bis 1 des Maximums) sowie eine Mehrzahl an blühenden und Samen bildenden Pflanzen (81.9%) im Frühjahr zur Folge hatte. Im landwirtschafltichen Habitat konnte *S. vulgaris* aufgrund von Unkrautkontrollmaßnahmen kaum überwintern, so dass die Populationen im Frühjahr kleiner waren (0 bis 0.16 of des Maximums) mit der Mehrzahl der Pflanzen im vegetativen Stadium (66.7%). Im landwirtschaftlichen Habitat führte die geringe Anzahl geeigneter Wirtspflanzen im Frühjahr zu einer Verzögerung des Auftretens von Rostinfektionen bis August, im Gegensatz zum ruderalen Habitat, wo der Rost bereits im April anwesend war. In beiden Habitaten waren reproduktive Pflanzenstadien anfälliger für eine Infektion mit dem Rost als vegetative Stadien. Die Manipulation der Wirtspflanzendynamik über Winter könnte die Entwicklung von Rostepidemien im Frühjahr fördern und als biologische Unkrautkontrollmaßnahme gegen *S. vulgaris* eingesetzt werden.

Key words: biological weed control – demography – pathogen

Introduction

Plants from natural or ruderal habitats invading agriculture face a new environment. The colonising species may nevertheless increase in population size or density and result in weed populations (Putwain et al. 1982). Weed populations are, as any plant population, assemblages of individuals that may vary widely in genotype, age, size and developmental stage. Variability of weed population responses to environmental conditions may have important consequences for weed population dynamics and their evolutionary responses to selective pressures (Navas 1991) and may result in temporal and spatial patchiness of plant susceptibility to control procedures (Mortimer 1984). Van Groenendael (1988) suggested that the success of weed management could be improved by taking into account the variability of weed population responses to specific control procedures. The study of plant population dynamics is therefore a prerequisite to proposal of particular weed control strategies.

The annual species *S. vulgaris* (Asteraceae), common groundsel, is subdivided into two subspecies (Harris & Ingram 1992). The subspecies *vulgaris* is the common weedy form, while the subspecies *denticulatus* (O.F. Muell.) P.D. Sell is less common. Within the subspecies *vulgaris* two varieties are recognised: var. *vulgaris* is the more frequent non-radiate variety containing only hermaphrodite disc florets, while var. *hibernicus* is a less frequent radiate variety bearing capitula, which contain an outer ring of pistillate ray florets. In general it is assumed that only plants of the variety *vulgaris* are weeds (Frantzen & Hatcher 1997) and therefore in the following the term *S. vulgaris* refers to *S. vulgaris* ssp. *vulgaris* var. *vulgaris*. Coastal sand dunes probably comprise the only natural habitat of groundsel. These coastal forms then gave rise to ruderal ones (Kadereit 1984). When *S. vulgaris* occurs in agricultural habitats it is considered an annual weed in horticultural crops, orchards and plant nurseries (Holm et al. 1977). There are no natural habitats for *S. vulgaris* in Switzerland and it is mainly associated with ruderal habitats such as gravel pits, waste grounds and roadsides from where it has likely migrated to agricultural habitats. The population dynamics of *S. vulgaris* has so far only been studied in relation to the build-up of herbicide resistance (Putwain et al. 1982). In the present study the population dynamics of *S. vulgaris* was investigated in relation to the occurrence of the rust fungus *Puccinia lagenophorae*.

The autoecious rust fungus *P. lagenophorae* is naturally associated with *S. vulgaris*. This biotrophic fungus is one of the primary pathogens infecting groundsel (Frantzen & Hatcher 1997). Rust infection influences the fitness of *S. vulgaris* through inhibition of plant growth and reproduction as well as increased plant mortality (Paul & Ayres 1986ab, 1987a). The rust is currently being investigated with respect to the biological control of *S. vulgaris* (Frantzen & Hatcher 1997). Infection by *P. lagenophorae* may influence population dynamics of *S. vulgaris*. Conversely, groundsel population dynamics may influence the dynamics of the rust fungus.

The objective of the present study was to compare the population dynamics of *S. vulgaris* at ruderal and agricultural habitats. A detailed basic study comparing an agricultural and a ruderal site would have been best. However, such a study is troublesome due to the ongoing cultivation practices at an agricultural site. A quantification of the population dynamics of *S. vulgaris* is an important prerequisite for its control, but has not been studied so far. Therefore, the study was divided into a detailed investigation at a single ruderal site to gather basic information about the population dynamics of *S. vulgaris* focusing on spatial distribution and size variation over time and a parallel investigation at five ruderal and five agricultural sites investigating the dynamics of plants and rust fungus. The main questions addressed were i) Does the population dynamics of *S. vulgaris* differ between ruderal and agricultural habitats and if so, what may be the possible factors causing the differences? ii) Does the population dynamics of *P. lagenophorae* differ between ruderal and agricultural habitats and if so, are the differences related to those in the population dynamics of *S. vulgaris*?

Material and methods

Sites

Five ruderal and five agricultural sites were selected in Switzerland in 1996 (Table 1). Only sites with a *S. vulgaris* population larger than 30 individuals were considered. Ruderal sites were only selected if there was no agriculture in the immediate vicinity. The agricultural sites chosen represented various annual and perennial crops and weed control included chemical and nonchemical measures. For geographical correspondence, pairs of ruderal and agricultural sites were selected within the same geographical area with a minimum distance of 2 km between two corresponding sites and a maximum distance of 6 km. The largest distance between any two sites was 150 km. One population at a ruderal site, Arconciel, was selected for the in-depth study. This study is further referred to as the basic study.

Data collection

Basic study

An area of 14.3 by 14.3 m was selected at the ruderal site Arconciel. The number of plants and their position were determined using a counting frame of 1.1 by 1.1 m, which was further divided into 11 x 11 smaller quadrates of 0.1 by 0.1m each. Always starting at the same corner, the frame was moved over the whole area subdividing it into 13 × 13 quadrats of 1.1 by 1.1 m. Each plant in the study area was marked and its position was determined to the 0.1 by 0.1 m scale. From June onwards numbers of *S. vulgaris* were too abundant to use both scales over the entire area. Thus only the first 6 columns of the 13 × 13 quadrat area were sampled on both scales, marking plants on the 0.1 by 0.1 m scale, and the following 7 columns were sampled on the 1.1 by 1.1 m scale without marking plants.

Data were collected monthly in the period from May to October 1997. Plants were classified according to developmental stage as (1) seedling (≤ 1 cm height), (2) vegetative, (3) flower bud, (4) flowering and (5) setting seed. The fraction of plants in one stage in the preceding month having the same or another stage in the following month was calculated. The size of plants was measured as the length from the base to the terminal apical meristem. Plants were also classified as either being infected by *P. lagenophorae* or not.

Dynamics of ruderal and agricultural populations

The ruderal *S. vulgaris* populations were considerably smaller than the agricultural ones (Table 1). Therefore, at the ruderal sites all groundsel plants were assessed, while at the agricultural sites a subsample was taken by establishing a diagonal transect across the whole area and assessing plants every 0.5 m along the diagonal. Green cover strips between crop rows were disregarded. Data were collected monthly in the period from April to November 1997. Numbers of plants were counted and plants were classified according to developmental stage as (1) vegetative, including seedlings, (2) flower bud, (3) flowering and (4) setting seed. Plants were also classified as either being infected by *P. lagenophorae* or not. Crop management at the agricultural sites was recorded.

Table 1. Ruderal and agricultural study populations of *S. vulgaris*.

Ruderal habitat			Agricultural habitat		
Location	Description	Estimated area (m^2)	Location	Description	Estimated area (m^2)
1a Sion[a]	waste land	5	1b Sensine	vineyard	460
2a Müntschemier	road-side	66	2b Praz	vineyard	3830
3a Arconciel	gravel pit	205	3b Chesopelloz	apple orchard	21320
4a Hauterive	gravel pit	150	4b Corjolens	vegetables	100
5a Courtepin	waste land	90	5b Coussiberle[b]	vegetables	270

[a] a and b constitute pairs of corresponding ruderal and agricultural sites within the same geographical area. The minimum distance between two corresponding sites was 2 km and the maximum distance 6 km.

[b] Organic farm

Data analysis

Basic study

Spatial autocorrelation, i.e. the probability that the value of a variable measured in a cell is similar to the values measured in neighbouring cells, was quantified using the Moran statistic. In this study a cell can be considered to represent a quadrat at a specified scale, while the variable is the number of plants. The Moran statistic may thus be used as an indicator of intraspecific competition. It was computed as (Frantzen 1994):

$$\text{eqn 1} \quad I = \frac{\sum_{ij} w_{ij} z_i z_j}{w \sum_{i=1}^{n} z_i^2} \quad \text{and} \quad z_i = x_i - \bar{x} \quad z_j = x_j - \bar{x}$$

in which I is the Moran statistic with a value between -1 and +1, n is the number of cells, w_{ij} a weight that defines two cells i and j as neighbours or not, W is the sum of the weights, x_i the value of a variable in cell i and x_j the value of a variable in cell j. Cells were defined as neighbours by distance, in which the maximum distance $\sqrt{2}$ referred to the eight cells adjacent to a cell. Whether the Moran statistic differed significantly from zero, thus representing a spatially clumped distribution, was tested by a randomisation test (Gilligan 1986). Significant positive values indicate that plants are aggregated and significant negative values that plants avoid each other. Spatial autocorrelation analysis was performed at the 1.1 by 1.1 m scale only, since over the whole observation period there were not enough cells at the 0.1 by 0.1 m scale with at least one plant to warrant statistical analysis.

The variation in plant sizes within a population was expressed using the Gini coefficient (Weiner & Solbrig 1984). The Gini coefficient has a minimum of zero and a theoretical maximum of one. If all plants in a population are of the same size, the coefficient is at the minimum. An increasing coefficient indicates increasing size inequality, which might be used as an indicator of competition effects. The Gini coefficient was computed as (Dixon et al. 1987):

$$\text{eqn 2} \quad G = \frac{1}{2\bar{x}n\,(n-1)} \sum_{i=1}^{n} (2i - n - 1)\, x_i$$

where x_i is the value determined for a unit and n is the number of units.

Dynamics of ruderal and agricultural populations

Observed frequencies of *S. vulgaris* plants were analysed using hierarchical log-linear models based on the G-statistic (Sokal & Rohlf 1995). Modelling started with a saturated model containing all interactions explaining all variance of the data (G = 0, P = 1). To select the most relevant interactions, explaining a substantial part of the variance, the interactions were removed one by one from the model and the resulting increase in the G-value was computed. If the removal of an interaction resulted in a significant increase of G ($P \leq 0.05$), it was left in the model. Tested variables included habitat with 2 categories (ruderal and agricultural), site with 5 categories, month of observation with 8 categories (April-November), plant stage with 4 categories (vegetative, flower bud, flowering and setting seed) and infection with 2 categories (infected or not). Subsequently, likelihood ratio tests based on the G-statistic were used to analyse specific two-way interactions (Sokal & Rohlf 1995).

Results

Basic study

The population of *S. vulgaris* increased in number from May to July and subsequently decreased (Table 2). Concurrent to the decrease in total plant number, a decrease in new seedling numbers and an increase of plant mortality was observed. In June a fraction of 0.47 of the seedlings marked in May was in a reproductive stage, i.e. either flowering or setting seed, whereas in the periods June-July and July-August the fraction of seedlings entering reproduction was less than 0.1 (Table 3). In the periods August-September and September-October, no seedlings developed to the reproductive stage. Mortality was lowest in the period June-July for all plant developmental stages. The mortality of seedlings increased substantially from July onwards, while a relatively high mortality of plants setting seed was observed during the entire period of study, as expected for an annual.

The Moran statistic indicated a non-random, aggregated spatial pattern of *S. vulgaris* plants, except in May (Table 2). If the various developmental stages were considered separately, only plants setting seed were aggregated in May (data not presented). In July, August and September plants of all stages were aggregated, whereas in June and October some stages were no longer spatially aggregated (data not presented). However, analysis of the different plant developmental stages lead to a smaller number of observations for each stage, reducing the power of the randomisation test.

The *S. vulgaris* population at Arconciel had a relatively large size hierarchy of individuals during the whole period of study as indicated by mean values of the Gini coefficient higher than 0.5 (Fig. 1). During the whole period of observation the Gini coefficient

Table 2. Population dynamics and spatial autocorrelation of *S. vulgaris* at Arconciel from May to October1997.

Month	Number of plants[a]	Number of marked plants[b]	Number of new seedlings[bc]	Number of dead plants[bd]	Moran statistic[e]
May	131	131	---[f]	---[f]	0.02 (ns)
June	2395	1151	760	59	0.18 (≤ 0.001)
July	2825	1476	535	253	0.31 (≤ 0.001)
August	1649	811	283	857	0.18 (≤ 0.001)
September	391	230	48	550	0.32 (≤ 0.001)
October	314	235	110	72	0.28 (≤ 0.001)

[a] Number of plants comprise the whole *S. vulgaris* population, including the number of new seedlings.

[b] Number and position of *S. vulgaris* plants were determined at a 1.1 by 1.1 m and a 0.1 by 0.1 m scale. From June onwards numbers of *S. vulgaris* were too abundant to use both scales. Thus half of the area was sampled at both scales, marking plants at the 0.1 by 0.1 m scale, while the other half was sampled at the 1.1 by 1.1 m scale without marking plants.

[c] Seedling is defined as a vegetative plant ≤ 1 cm in height.

[d] Plants without any green tissue were considered dead.

[e] Moran`s spatial autocorrelation statistic based on a 1.1 by 1.1 m scale. The P value of the statistics is given in parentheses, with ns being non significant at $P > 0.05$.

[f] No plants had been marked before May.

Table 3. Transition probabilities of *S. vulgaris* developmental stages at Arconciel from May to October 1997.

	Stage at time t + 1						
	Seedling	Vegetative	Flower bud	Flowering	Setting seed	Dead	n[a]
Stage at time t							
May-June							
Seedling	0.0	0.14	0.12	0.32	0.15	0.28	86
Vegetative[b]	–	–	–	–	–	–	–
Flower bud	–	–	0.0	0.0	0.0	1.0	1
Flowering	–	–	–	0.0	0.0	1.0	15
Setting seed	–	–	–	–	0.13	0.87	29
June-July							
Seedling	0.18	0.44	0.05	0.06	0.002	0.26	645
Vegetative	–	0.37	0.23	0.25	0.02	0.12	310
Flower bud	–	–	0.0	0.03	0.73	0.25	40
Flowering	–	–	–	0.07	0.59	0.35	46
Setting seed	–	–	–	–	0.21	0.79	24
July-August							
Seedling	0.23	0.19	0.03	0.03	0.01	0.51	395
Vegetative	–	0.10	0.04	0.09	0.11	0.66	537
Flower bud	–	–	0.02	0.007	0.10	0.87	136
Flowering	–	–	–	0.02	0.07	0.90	135
Setting seed	–	–	–	–	0.07	0.93	68
August-September							
Seedling	0.16	0.09	0.0	0.0	0.0	0.76	256
Vegetative	–	0.19	0.02	0.05	0.02	0.72	191
Flower bud	–	–	0.06	0.02	0.06	0.86	51
Flowering	–	–	–	0.02	0.02	0.95	83
Setting seed	–	–	–	–	0.0	1.0	95
September-October							
Seedling	0.0	0.0	0.0	0.0	0.0	1.0	10
Vegetative	–	0.11	0.05	0.03	0.0	0.81	36
Flower bud	–	–	0.0	0.0	0.16	0.83	6
Flowering	–	–	–	0.0	0.09	0.91	11
Setting seed	–	–	–	–	0.0	1.0	9

[a] Number of plants marked at the preceding census.

[b] No vegetative plants were present in May.

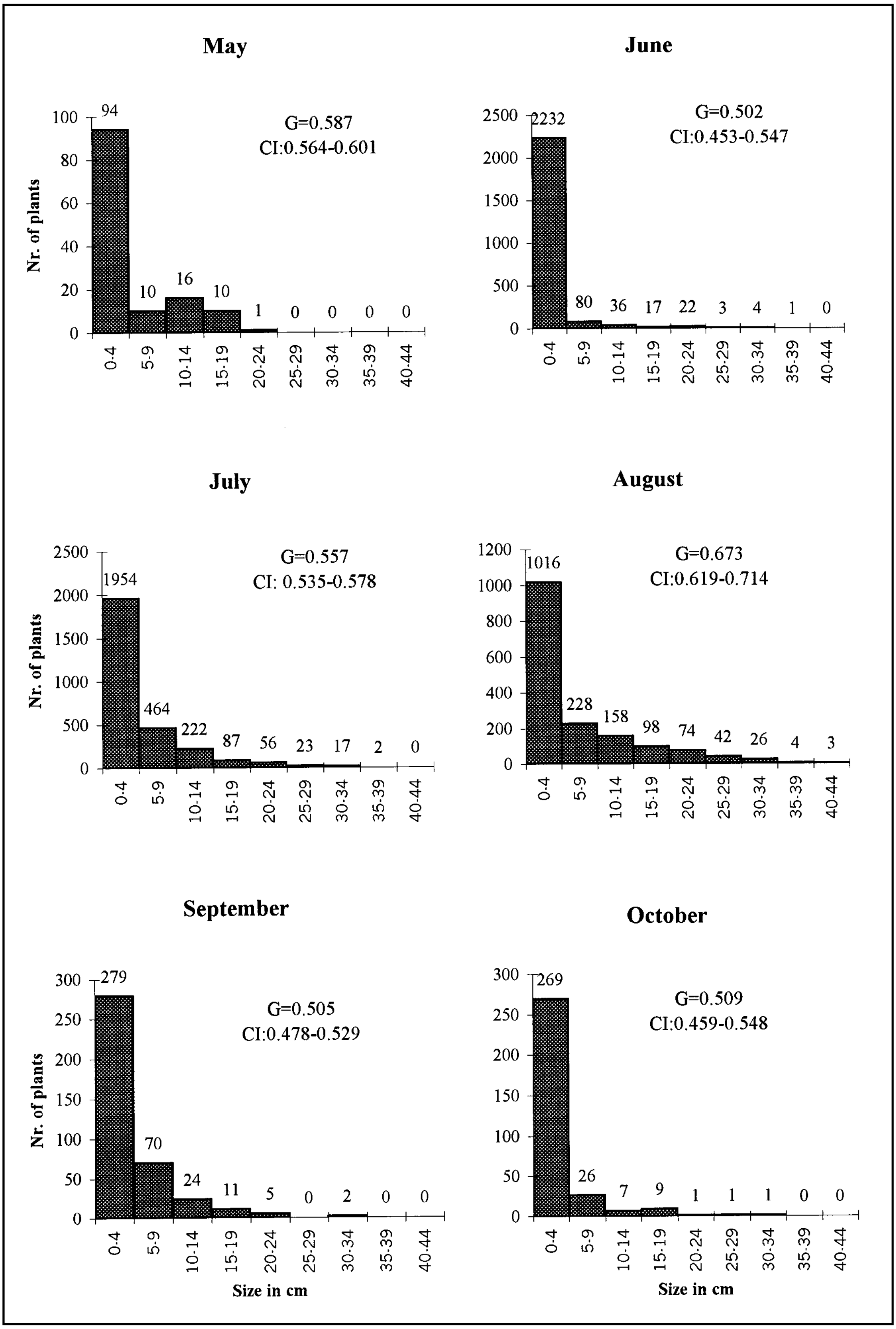


Fig. 1. Size distributions of *S. vulgaris* expressed as the Gini coefficient (G) with a 95% confidence interval (CI) at Arconciel from May to October 1997.

changed only slightly and remained around this value, except in August where it increased to a maximum of 0.6. Plants setting seed showed a broad range of sizes from 4 to 44 cm. The size hierarchy of plants at seed set was lower than that of the whole population with Gini coefficients ≤ 0.3 (data not presented) during the whole period of study indicating that taller plants did not dominate the population of plants at seed set.

Only six infected plants were observed at Arconciel during the whole period of study. This was unexpected regarding the rust incidence in the previous year. Hence the rust data were not analysed.

Dynamics of ruderal and agricultural populations

The analysis using hierarchical log-linear models did not indicate significant five-way interactions between variables and a substantial part of the variance in the population dynamics of *S. vulgaris* and *P. lagenophorae* could be explained by three- and four-way interactions or less (Table 4). Population dynamics of *S. vulgaris*, expressed as the variable month, differed between habitat and site within habitat as well as between plant development stage (Table 4, interaction 1). In April, at the beginning of the study, the population sizes at the agricultural sites were relatively low with 0 to 0.16 of the maximum, whereas the population sizes at the ruderal sites were in the range of 0.1 to 1 of the maximum (Fig. 2). At all sites of both the ruderal and the agricultural habitat the number of *S. vulgaris* plants was relatively low in September. Weed control was part of the management at each

Table 4. Significant interactions indicated by a hierarchical loglinear model[a] explaining the dynamics of *S. vulgaris* and *P. lagenophorae*.

(1) Habitat × Site × Stage × Month
(2) Habitat × Infection × Month
(3) Site × Infection × Month
(4) Habitat × Site × Stage × Infection
G = 105.8 df = 238 P = 1.000

[a] The model was fitted to observed frequencies of *S. vulgaris* plants distributed over the variables habitat (ruderal and agricultural), site (5 sites per habitat), month of observation (8 months, April-November), plant stage (vegetative, flower bud, flowering and setting seed) and infection, (plant infected or not).

Table 5. Effect of time on the frequency of plant developmental stage of *S. vulgaris* at ruderal and agricultural habitats[a].

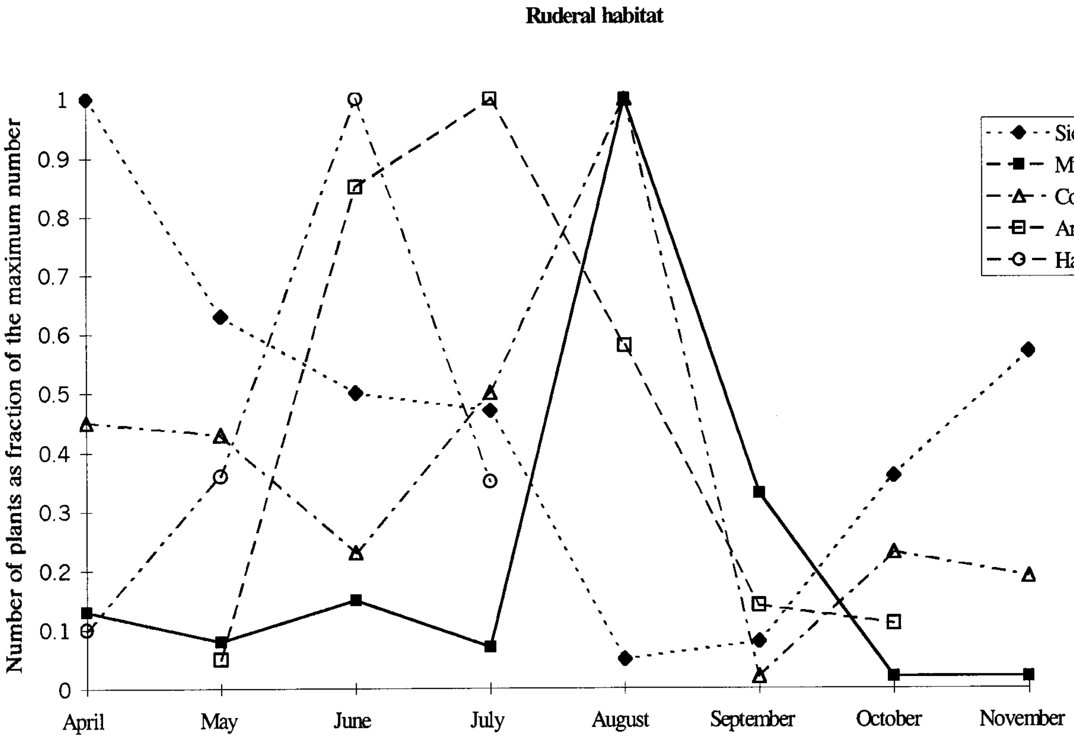
Ruderal habitat[b]					Agricultural habitat[b]				
Month	Vegetative	Flower bud	Flowering	Setting seed	Month	Vegetative	Flower bud	Flowering	Setting seed
4	63	49	289	218	4	8	0	0	4
5	164	16	133	444	5	244	24	0	0
6	2502	117	108	395	6	112	44	6	0
7	2720	268	337	158	7	90	24	20	15
8	2401	212	370	293	8	104	18	58	56
9	401	47	105	102	9	16	4	9	24
10	497	23	29	16	10	112	18	4	4
11	208	10	17	0	11	65	18	50	5
G = 2973.2 P ≤ 0.001[c]					G = 438.8 P ≤ 0.001[c]				

[a] Entries represent plant numbers.
[b] All plants were assessed at the ruderal habitat, including the basic study, whereas plants were assessed along a diagonal transect at the agricultural habitat.
[c] Effects of time on plant developmental stage were tested for significance using a log likelihood test (G-test).

Table 6. Effect of plant developmental stage on the infection of *S. vulgaris* by *P. lagenophorae* at ruderal and agricultural habitats[a].

Ruderal habitat[b]			Agricultural habitat[b]		
Plant stage	Uninfected	Infected	Plant stage	Uninfected	Infected
Vegetative	8797	159	Vegetative	701	50
Flower bud	711	31	Flower bud	132	18
Flowering	1298	90	Flowering	92	55
Setting seed	1453	173	Setting seed	58	50
G = 287.4 P ≤ 0.001[c]			G = 154.8 P ≤ 0.001[c]		

[a] Entries represent plant numbers.
[b] All plants were assessed at the ruderal habitat, including the basic study, whereas plants were assessed along a diagonal transect at the agricultural habitat.
[c] Effects of plant developmental stage on probability of infection were tested for significance using a log likelihood test (G-test).



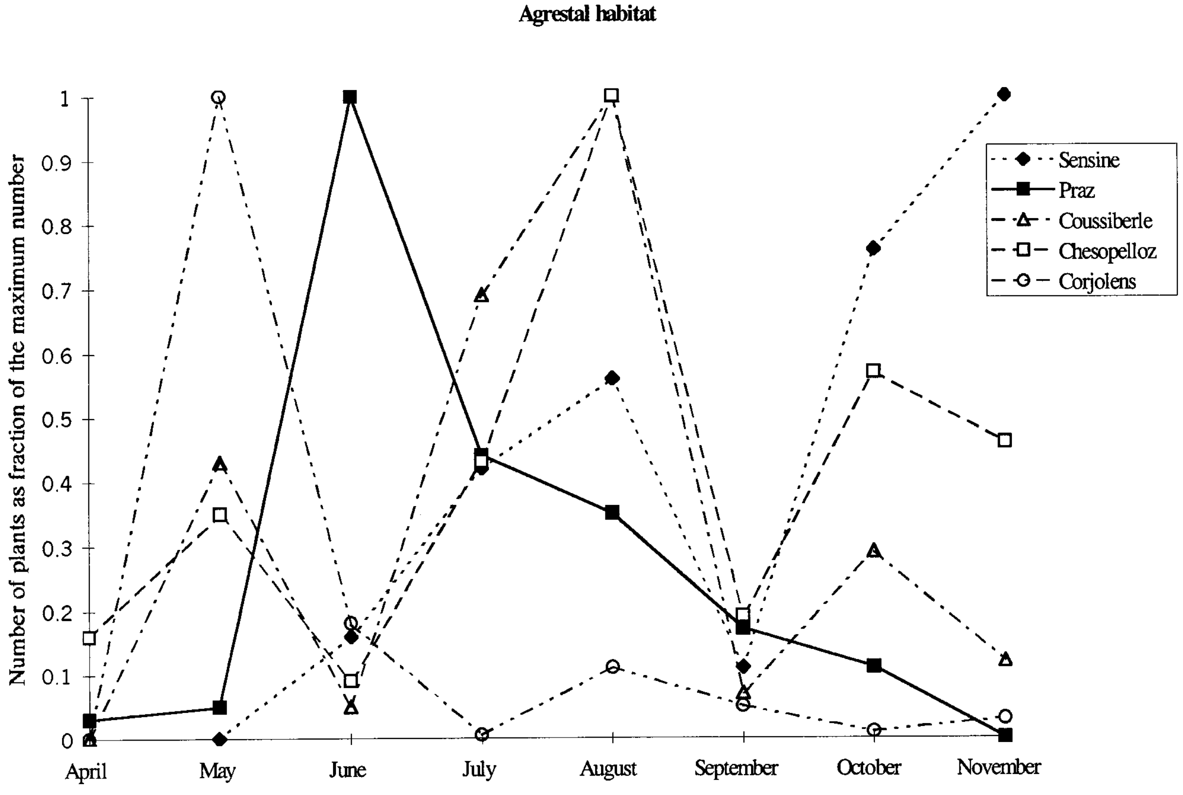


Fig. 2. Population dynamics of *S. vulgaris* at ruderal and agricultural sites from April to November 1997. Plant numbers are expressed as fraction of the maximum number of plants determined at each site for the whole period of study. At the site of Sensine data collection started in May and at the site of Hauterive data collection already finished in July due to destruction of the site by road works. Note that data were collected at the site of Arconciel from May to October 1997. Same symbols indicate pairs of corresponding ruderal and agricultural sites within a distance of 2–6 km.

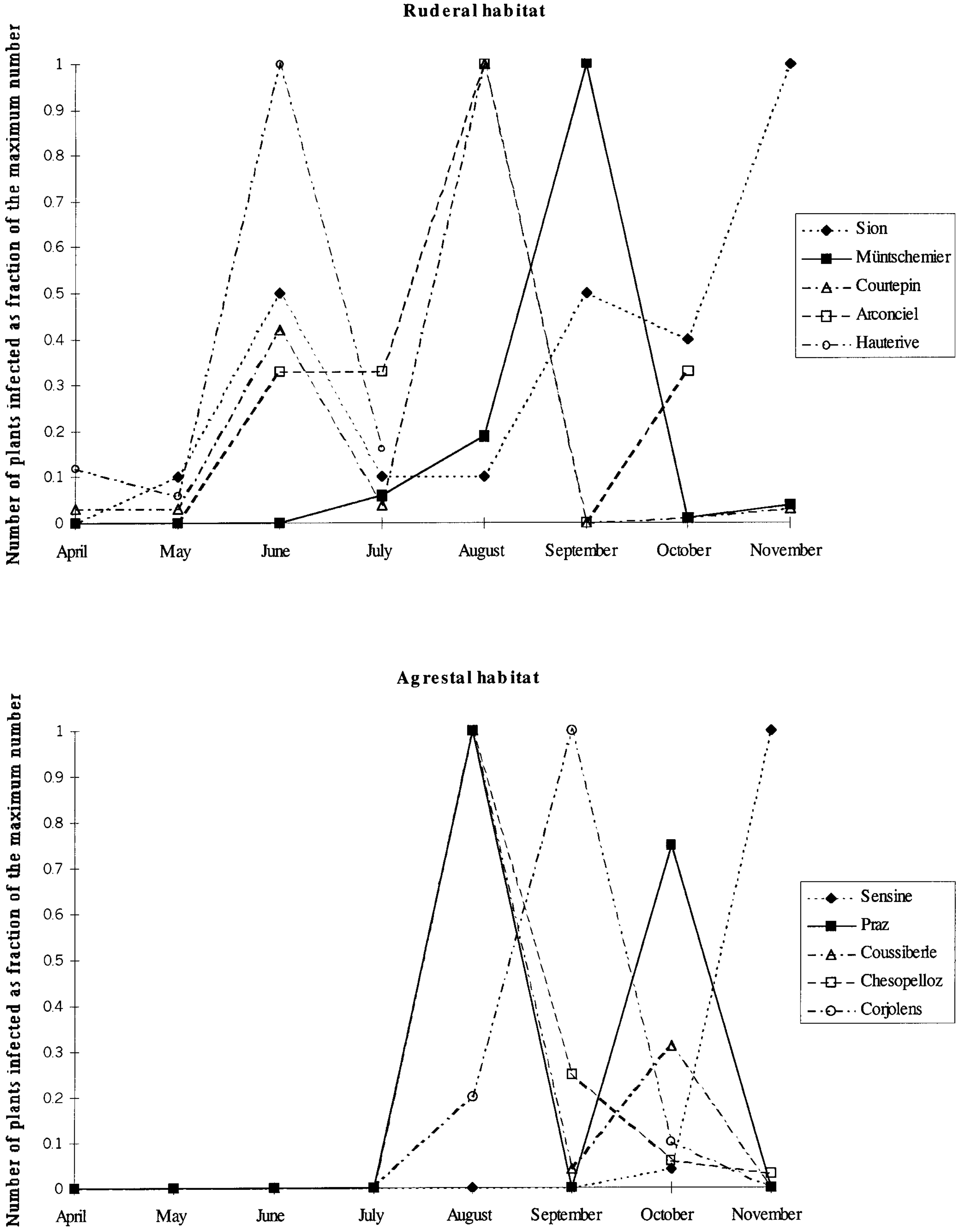


Fig. 3. Dynamics of *P. lagenophorae* at ruderal and agricultural sites from April to November 1997. Infected plant numbers are expressed as fraction of the maximum number of infected plants determined at each site for the whole period of study. At the site of Sensine data collection started in May and at the site of Hauterive data collection already finished in July due to destruction of the site by road works. Note that data were collected at the site of Arconciel from May to October 1997. Same symbols indicate pairs of corresponding ruderal and agricultural sites within a distance of 2-6 km.

agricultural site, however management strategies in general varied considerably and could not be related to the population dynamics of *S. vulgaris*. Dynamics of *S. vulgaris* differed between sites within a habitat (Fig. 2). Disregarding site effects, a significant effect of time on the frequency of plant developmental stage was detected for both habitats (Table 5). Flowering plants and plants setting seed were dominant at the ruderal habitat in April and May while they were prevalent at the agricultural habitat in August and September.

Dynamics of *P. lagenophorae*, expressed as the effect of the interaction of infection by month on plant numbers, differed between habitats (Table 4, interaction 2). The rust was present at the ruderal habitat from April to November, whereas at the agricultural habitat no rust was detected before August (Fig. 3). However, infection rates were generally higher at the agricultural habitat with 7–46% in comparison to 2–11% at the ruderal habitat (Table 6). Independent of habitat, dynamics of *P. lagenophorae* differed between sites (Table 4, interaction 3). The effect of plant developmental stage on rust infection depended on habitat and site (Table 4, interaction 4). Disregarding site effects, a significant effect of plant developmental stage on infection was observed in both habitats (Table 6). Rust infection was predominantly prevalent on plants setting seed at both the ruderal and the agricultural habitat. The interaction of habitat and plant stage resulted from a relatively higher number of plants in the stages flower bud and flowering at the agricultural habitat (G-test based on the row totals presented in table 6, $P \leq 0.001$).

Discussion

The population dynamics of *S. vulgaris* at the ruderal site Arconciel was characterised by a steep increase in numbers of seedlings from May to June together with the death of the older and thus taller reproductive plants, having reached the end of their life span. This resulted in a more equal distribution of plant size. Concurrently, the increase in plant numbers changed the random distribution of plants into an aggregated one. Seedlings developed rapidly reaching seed set already within 5 weeks. Holm et al. (1997) also reported seed production in *S. vulgaris* 5 to 6 weeks after seedling emergence. A decreasing number of new seedlings from July onwards, together with advancing plant development and subsequent gain in size, resulted in an increasing size hierarchy in August. The numbers of new seedlings decreased although reproducing plants were present. Relatively high mortality rates of seedlings and vegetative plants from July to October were observed, suggesting intraspecific competition, possibly resulting in the death of younger plant stages and at the same time inhibiting new seeds to germinate by limiting available light. Light is one of the most important factors for germination of groundsel (Popay & Roberts 1970). In August the site was heavily overgrown with other plant species with an estimated 80% plant coverage (data not presented), which may have caused interspecific competition and a lack of safe germination sites for seeds. In addition, August was very dry, probably causing further plant stress and inhibition of germination. Mortality rates for plants reproducing, i.e. having flower buds, flowers or seeds, from July onwards were also high. Since the development of *S. vulgaris* was very rapid it is most likely that plants with flower buds and flowers reached seed set and died before the following census was carried out. Although a matrix model for plant populations was not used for data analysis due to missing data on seed production and subsequent germination, the results obtained suggest that seedling establishment is a major factor influencing plant population dynamics of *S. vulgaris*. Seedling establishment as a major factor influencing groundsel dynamics as well as a short generation time fit into the classification of Grime (1979) defining *S. vulgaris* as a ruderal strategist. This classification is also supported by the broad range of plant sizes at seed set indicating high plasticity for reproductive size in *S. vulgaris*. Harper & Ogden (1970) reported a similar observation with *S. vulgaris* maintaining its energy budget, allocated to the seeds, at 21% over a sevenfold difference in total plant weight.

The population dynamics of *S. vulgaris* differed between the ruderal and the agricultural habitat. At the ruderal habitat a major number of groundsel plants was already observed in early spring, with the majority of plants either flowering or setting seed, suggesting that *S. vulgaris* plants at the ruderal habitat had overwintered. At the agricultural habitat the number of groundsel plants in early spring was relatively low with the majority of plants in the vegetative stage. Groundsel plants may winter vegetatively as a basal rosette continuing development to seed set in the following spring (Paul & Ayres 1986a). Results indicate that wintering groundsel plants with subsequent seed production and germination in spring are a major source for the build-up of groundsel populations early in the season. Groundsel is a prolific seeder producing 1100 to 1800 seeds per plant (Holm et al. 1997). In contrast, groundsel plants were nearly absent at the agricultural habitat in early spring probably due to weed control measures in the previous autumn or current spring. Subsequently, groundsel populations in the spring had to build-up either from the soil seed bank or from re-colonisation. Popay & Roberts (1970) reported dormancy of groundsel seeds as nearly absent. Having a low degree of seed dormancy, generally most seeds germinate immediately and seeds that do not germinate show a relatively short period of survival in the soil (Roberts & Feast 1972). The only report of dormancy in groundsel is that of Ren & Abbott (1991) who discovered summer dormancy in *S. vulgaris* from the Mediterranean region. If, however, the soil seed bank is of minor importance, *S. vulgaris* populations at the agricultural sites in spring have to build-up by re-colonisation. This would require dispersal of *S. vulgaris* seeds from outside the agricultural sites, which is possible as their morphology is adapted to dispersal by wind (Andersen 1992).

The observed difference in groundsel population dynamics between ruderal and agricultural habitats in spring resulted in a major difference of the dynamics of *P. lagenophorae* between ruderal and agricultural habitats. At the ruderal habitat the rust was already present early in spring, while at the agricultural habitat it did not appear before August. This suggests that the rust survives as mycelium within the host over winter at the ruderal habitat, whereas it could not survive over winter at the agricultural habitat due to the relatively low number of wintering hosts. Survival of *P. lagenophorae* over winter as mycelium within plants has been demonstrated by Frantzen & Müller-Schärer (1999). Thus weed control measures in autumn and early spring do not only remove *S. vulgaris* but also *P. lagenophorae* from the agricultural habitat. The build-up of *P. lagenophorae* epidemics at the agricultural habitat in spring seems not only inhibited by a limited amount of inoculum, i.e. wintering mycelium, but also by the abundance of *S. vulgaris* plants in relatively young stages compared to the ruderal habitat. Results of the present study suggest that younger plant stages are less susceptible to rust infection than older stages, which has been demonstrated in controlled experiments by Wyss & Müller-Schärer (1999).

The population dynamics of *S. vulgaris* was not determined by *P. lagenophorae* on the short-term. An increased disease incidence could not be related to a reduction in plant numbers. However, accumulated effects of infection over generations may substantially inhibit competitiveness in relation to other species (Paul & Ayres 1987b, Paul 1989, Paul & Ayres 1990) and seed production (Paul & Ayres 1986b, 1987a) of *S. vulgaris*. Especially the reduction of competitiveness by the rust is of interest with respect to the system management approach of biological control. Rather than eradicating the weed this approach is based on the management of a weed pathosystem in such a way to stimulate epidemics on the target weed population reducing the competition exerted by the weed on a crop (Müller-Schärer & Frantzen 1996). A theoretical framework was developed to relate epidemics to plant competition (Frantzen & Müller-Schärer 1998), which is presently parameterised. The results of this study show that at the agricultural habitat the rust does not appear before summer but, possibly due to better infection conditions, builds up high infection rates in a relatively short time, which demonstrates the potential of *P. lagenophorae* to generate epidemics in populations of *S. vulgaris*. However, the rust arrives too late in the season to reduce competition of *S. vulgaris* with a crop. Early in the season rust infection seems to be hindered by weed control measures at the agricultural habitat in autumn and spring resulting in a lack of host plants for the wintering of *P. lagenophorae* and preventing the start of new natural epidemics in spring. It therefore seems a feasible strategy to adapt weed control regimes in order to allow *S. vulgaris* plants to winter as suggested by Frantzen & Hatcher (1997). Infected groundsel plants, which survive over winter, may serve as inoculum sources in the spring inducing new rust epidemics and non-infected plants provide mature plant stages being more susceptible to rust infection enhancing rust epidemics. Hence rust epidemics in an agricultural habitat would be stimulated early in the season in order to reduce the competitiveness of *S. vulgaris* before a crop enters the critical period when it is rather sensitive to competition.

The present study demonstrated that the population dynamics of *S. vulgaris* differed between the ruderal and the agricultural habitat. The difference is due to the wintering of *S. vulgaris* in the ruderal habitat leading to greater population sizes and a majority of plants in mature stages in the spring compared to the agricultural habitat. The dynamics of *P. lagenophorae* also differed between habitats, being affected by the dynamics of the host. Manipulating the dynamics of the host over winter may enhance rust epidemics in spring serving as biological control of *S. vulgaris*.

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